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City University of New York, Ph.D., 1976
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COMPARATIVE ECOLOGY AND BEHAVIOR OF RED-BREASTED MEADOWLARKS (AVES, ICTERIDAE) AND THEIR INTERACTIONS IN SYMPATRY

by

MICHAEL GOCHFELD

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1975

This manuscript has been read and accepted for the Executive Committee in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

May 29, 1975
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INTRODUCTORY REMARKS

This study was undertaken to compare the ecology, behavior, and morphology of the South American Red-breasted Meadowlarks (*Pezites* and *Leistes*) in order to understand their relationships and the means by which three species coexist sympatrically. In addition, the information would facilitate comparisons with the North American yellow-breasted meadowlarks. These groups were long suspected of being closely related, and this relationship has recently been emphasized by L. L. Short (1968) who suggested that all these forms be treated in one genus, *Sturnella*, instead of three genera. In a relatively short visit to the pampas, Short had recognized several conspicuous differences in the ecology and behavior of two species, *P. defilippii* and *P. militaris*, and I found that the differences between these species are consistent.

As the study evolved, I focused attention on several topics. The discovery of a differential frequency of nest parasitism by *Molothrus bonariensis* led to a study of the means by which the differential parasitism arises. Observations of non-overlapping territories of *P. defilippii* and *L. m. superciliaris* led me to focus on the interspecific aggression and how inter- vs. intra-specific aggression could be measured.

Although the Red-breasted Meadowlarks are widespread and conspicuous, relatively little life history data have been previously published, and a large part of this report deals with descriptive aspects of ecology and behavior, especially vocal behavior, and nesting. Detailed descriptions of displays were not made and will be conspicuously absent in this paper.

During the course of this study I examined many meadowlark specimens from South America and measured several variables on which the morphometric analysis is based. By focusing attention only on the taxa in question I was able to examine patterns of geographic variation and to consider ecogeographic influences on morphology, but without examining additional characters and additional taxa, it is not possible to make a detailed study of the phylogeny of meadowlarks. In the concluding section, I consider some possible phylogenies, mainly to focus attention on the kinds of information already available and the areas that need further investigation.

There were many instances during the field study when I found interesting tangents. Some, such as the comparative role of male and female in feeding the young, and differential brood parasitism, I was able to pursue. Others, such as contagiousness of vocal displays, I was forced to set aside for future study. Still other lines,

such as comparison of foraging behavior and measurement of territory size, which were part of my initial plan, had to be set aside because of difficulties which were insurmountable in the field.

In retrospect, the study raised many questions; but it clarified the overall relationship among the meadowlarks, confirmed many of Short's suggestions and conclusions, and indicated how their coexistence on the pampas is maintained.

SECTION I. Chapters 1 - 3

1. Background
2. Techniques
3. Study Areas

This section introduces the Red-breasted Meadowlarks of South America and their distribution. Knowledge of meadowlark distribution in Argentina is updated. My methods of observation, nest-finding, trapping, censusing and recording are described. The statistical techniques employed in the study are briefly indicated. The main study areas are also described.

CHAPTER 1 BACKGROUND

GENERAL INTRODUCTION

The Sturnelline or Meadowlark assemblage is a group of either six or seven species of medium-sized oscines belonging to the entirely Western Hemisphere family, Icteridae. The resemblance in shape and posture to old world Starlings (Sturnidae) accounts for the generic name Sturnella as well as for the common English name, Military Starling, applied to some of the South American representatives. Three genera have usually been recognized in the Meadowlark group: Sturnella, Pezites, and Leistes, although Short (1968), impressed by the similarities among the forms, recommended that they be treated as a single genus, Sturnella. My own findings support Short's statements regarding the similarities, but throughout this report I will for convenience continue to refer to the three separate genera.

The ecology, behavior and evolution of these birds are of interest for several reasons. Similarities in habits and plumage indicate the close relationship among all forms within the group, yet there is an apparent transition in the structure of the bill from the conical bills of Leistes to the long slender bills of Pezites and Sturnella, which are quite specialized for the

Icteridae. The ecological factors associated with these differences are of interest, as is the suggested derivation (Short 1968) of the relatively specialized Sturnella, through a Leistes-like form from the relatively unspecialized marsh blackbird group (Agelaius-like birds).

Within the Sturnelline assemblage, sympatry between very similar congeners occurs in both Sturnella (magna and neglecta in central United States) and Pezites (militaris and defilippii on the Argentine pampas). Sympatry also involves L. m. militaris which is sympatric with S. magna in central and northern South America and L. m. superciliaris which is sympatric with P. militaris and P. defilippii. The comparative biology of Sturnella in sympatry has been studied by Lanyon (1957), Szijj (1963), and Wiens (1969) while sympatric forms of Pezites have been studied by Short (1968) and by me (present report). The three genera are biogeographically distinctive in that Sturnella is primarily North Temperate (although it occurs southward to Amazonian Brazil); Pezites is primarily South Temperate (but occurs north to equatorial Ecuador); and Leistes is mainly Tropical (although it reaches 40° S. Lat. in Argentina, and 4000 m altitude in Bolivia).

The group is of further interest because of the well-known but little-studied convergence between Pezites

and Sturnella on the one hand, and the red- and yellow-breasted members of the genus Macronyx (family Motacillidae, African Longclaws) on the other. Between these groups are plumage and ecological similarities, and Sturnella and M. croceus are usually offered as the clearest example of convergent evolution among birds. Field study of the comparative biology of these groups, may shed light on the factors influencing this convergence.

In this study I have conducted field investigations of the comparative biology of Pezites and have made superficial observations on Leistes. I compare this information with data gathered by Lanyon (1956 a, b, 1957 et seq.) on North American meadowlarks. A general aim of this study has been to clarify the 'evolutionary ecology' of the group in the sense proposed by Orians (1962) and Lack (1965). I have been particularly interested in behavioral and ecological features associated with the sympatric coexistence of militaris and defilippii in Argentina. I have focused attention on such problems as habitat selection, food utilization, type of pair bond, role of sexes, general breeding biology, territory structure, and vocal behavior, but none of these topics has been studied exhaustively. From literature review and field work I have attempted to map the distribution of the meadowlarks in South

America. I have made a morphometric study of all forms of Pezites and Leistes to shed light on the magnitude of variation among and within groups as well as on the possible occurrence of clines associated with climate or on character displacement.

Although the study has not been oriented toward taxonomy, and although I have not attempted to make any detailed anatomical studies, I have incidently obtained information which clarifies the status and relationships of the different forms and allows evaluation of Short's study (1968).

Finally, I should point out that Meadowlarks are among the most numerous, regular and conspicuous components of the avifauna of New World grassland communities (Cody 1966; Lanyon 1957; Stewart and Kantrud 1972; Wiens 1969; personal observation). Considering that about 21% of the earth's land surface is grassland or herbaceous vegetation (Rumney 1968:110), clarification of the biology of meadowlarks is a useful contribution to understanding the ecology of such communities.

LIMITATIONS

This study was conceived in broad terms to explore the variety of areas in which significant similarities and differences in ecology, behavior, and morphology, between sympatric species occurred.

It was often necessary to spend only a few days gathering data on a particular aspect of a problem, which might require several seasons to study in detail. I have settled in several cases for a relatively superficial exploration of certain aspects of the biology, hoping to focus attention on those which deserve more detailed study, and to clarify those which are of most general interest --- for example, parallels between North Temperate and South Temperate sympatric meadowlarks.

It will be necessary on many occasions to indicate that data are suggestive but inadequate, or that new sets of data are required to adequately test hypotheses or demonstrate features. Where possible, I tried to use 1970 data to formulate ideas which could be tested in 1971, but this was actually limited to very few aspects.

A severe limitation was my inability to obtain meaningful observations on foraging behavior or food selection in meadowlarks in the wild. Rarely could I observe a foraging individual for more than 30 seconds.

Particularly, I had no observations on superciliaris and only a few on defilippii. It would have been interesting to test Cody's (1968 b) suggestion that sympatric species (regardless of relationahip) show different behavioral strategies in foraging. This proved very difficult even in aviaries.

TAXA OF RED-BREASTED MEADOWLARKS

In this study I have considered seven forms of meadowlarks. Largely for convenience in referring to subgroups within the meadowlarks, I have continued to use the generic names *Pezites* and *Leistes*, and I will retain the species designations usually associated with these names. This choice is strictly for convenience, and does not imply disagreement with Short's (1968) conclusions. In Table 1 I compare the nomenclature used in this paper with that of Short (1968) and Blake (1968). I did not make a detailed study of the northern form of *Leistes* (*L. m. militaris*) and I use the term *superciliaris* in reference to the form I studied. In my brief experience with the northern form of *Leistes* I did not find striking differences and, pending further study, I treat the two forms as conspecific. Like Short (1968), I found that *bellicosa* differs in many behavioral features from the other forms of *Pezites*, and I treat it as a separate species.

Several additional subspecies have been proposed within these genera, (see final section). The most important is *P. b. albipes* described by Philippi and Landbeck (1861) from Arica (now Chile) and included by Blake (1968). It is also worth noting that four subspecies of *Sturnella magna*, at least two of them

sympatric with L. m. militaris occur in northern South America. A detailed account of the nomenclatorial history of these meadowlark genera is given separately (Gochfeld M. S. 1).

TABLE 1. Taxonomic treatment of the Red-breasted Meadowlarks

Taxa treated in this report	Blake (1968)	Short (1968)[a] [all in Sturnella]
Leistes militaris militaris	L. m. militaris	S. [militaris] militaris
Leistes militaris superciliaris	L. m. superciliaris	S. [militaris] superciliaris
Pezites militaris militaris	P. m. militaris	S. [loyca] loyca loyca
Pezites militaris catamarcanus	P. m. catamarcanus	S. [loyca] loyca catamarcanus
Pezites militaris falklandicus	P. m. falklandicus	S. [loyca] loyca falklandicus
Pezites defilippii	P. m. defilippii	S. [loyca] defilippii
Pezites bellicosa	P. m. bellicosus P. m. albipes	S. [loyca] bellicosa

a = in treating the two groups of red-breasted meadowlarks as congeneric with the yellow-breasted Sturnella, Short (1968) used superspecies enclosed in [].

DISTRIBUTION OF RED-BREASTED MEADOWLARKS

Current knowledge of the distribution of South American Red-breasted Meadowlarks is summarized on the map (figure 1). The main imperfection in documented distribution, involves the two forms of *Leistes* in central Brazil. Changes in the range of *Leistes* can be predicted, from its recent extension into Ecuador and the Cauca Valley of Columbia (Stevenson 1972, Carlos Lehmann, personal communication), since forest clearing is proceeding rapidly in many parts of the continent. A detailed account of range and locality data based on the literature and specimens (Gochfeld M. S. 1) will be deposited in the Department of Ornithology Library, American Museum of Natural History.

A brief summary of the range is given below:

P. m. militaris: Eastern Argentina from central Buenos Aires and western Argentina from southern Catamarca, and Chile from southern Atacama, southward to Tierra del Fuego.

P. m. catamarcanus: Northwestern Argentina from central Jujuy to central Catamarca, up to at least 3300 meters, but not reaching the true altiplano.

P. m. falklandicus: Falkland Islands.

P. bellicosa: Western South America from coastal

Ecuador south to the Atacama desert, and in scattered localities in the Peruvian Andes.

P. defilippii: Pampas of southern Brazil, Uruguay, and northeastern Argentina, avoiding wooded areas and marshy areas.

L. m. militaris: Southwestern Costa Rica (L. Kiff personal communication) through northern South America to central Brazil. Recent range extensions documented in Ecuador (Limoncocha; Norton et al 1972, Pearson 1972, Stevenson 1972) may perhaps reflect lack of previous field work. However, extension in Columbia is well documented for recent times (Haffer 1967 a, F. Carlos Lehmann pers. comm.). Recorded once from northeastern Peru at Xeberos (Sclater and Salvin 1873). Southern limit of range in Brazil not exactly known, but recorded from the upper Rio Madeira near Machados (Hellmayr 1910). Chapman (1917) stated that it was known from western Ecuador, but this was obviously an error and was corrected subsequently (Chapman 1926).

L. m. superciliaris: Central Brazil southward to about 40° S. lat. in Argentina. One record from southeastern Peru (near Quince Mil, Puno, Hellmayr 1919). It is widespread in Bolivia, where it occurs up to 4000 m in Cochabamba. One record from Chile, Johnson

(1967).

DISTRIBUTION OF MEADOWLARKS IN ARGENTINA

Before discussing the ecology and behavior of meadowlarks in Argentina, it is necessary to clarify the distribution of the different forms. The most recent distributional checklist of Argentine birds (Olrog 1963) has several inaccuracies. Based on examination of specimens and review of the literature I found the following distributional problems which needed clarification:

1. militaris and defilippii in Buenos Aires Province.
2. m. militaris and m. catamarcanus in western Argentina.
3. militaris in Patagonia.

A detailed summary of available information on distribution is given separately (Gochfeld MS I), but in this section I present information clarifying the above three distributional problems.

1. The Lesser Red-breasted or Pampa Meadowlark (defilippii) was apparently abundant over most of the Pampas. Durnford (1876, 1877) mentions it as very common and widespread in the Buenos Aires region, and said that it formed huge flocks in winter. Hudson (Sclater and Hudson 1888) was familiar with the species, but one infers that it was not a common breeding bird

near La Plata. Wetmore (1926) found that defilippii was most common in southwestern Buenos Aires Province, stressing that this was the same area where militaris was common. He suggested that the range of defilippii was perhaps diminished by cultivation. Marelli (1933) found militaris and defilippii widely distributed over southern Buenos Aires Province. I interviewed many people, and at least three of the people I visited, two in Buenos Aires and one in Bahia Blanca, recalled that in their youth (1920's) or in their grandparents' "day" (1890's), "pecho colorados" were considered very abundant in contrast with their present status. It is not clear whether these recollections would apply to defilippii or to all three species, but the former is likely since it is the most gregarious species.

Olrog (1963) reports defilippii as resident from southern Brazil and Santa Fe, through Buenos Aires and La Pampa, and suggests that it might be migratory. Although I have not measured specimens of defilippii from La Pampa, there are eggs, nests, and sight records from near Trebolares (35°40'S; 63°40W; British Museum Natural History collection). A specimen from La Pampa, identified as defilippii and exhibited in the Natural History Museum in Salta, is actually a female militaris.

To clarify the distribution of defilippii I drove through eastern Buenos Aires Province, from Buenos Aires

to G'ral Lavalle, then to Azul, Tres Arroyos and Bahia Blanca. A second route was from Dolores to Tandil, Juarez, and through the Sierra Ventana range (see figure 2). I searched also in the Buenos Aires "panhandle" south of Bahia Blanca. A fourth route passed west to Rio Colorado and north through eastern La Pampa along route 35. A fifth route passed north through western Buenos Aires, along route 33 to Trenque Lauquen and then east to Buenos Aires. A sixth route was along the Parana River, from Santa Fe to Buenos Aires. I did not cover northwestern Buenos Aires, eastern Cordoba, nor western Santa Fe, all of which should be suitable for defilippii.

The outcome of these transects was rather surprising. Aside from an unmated, silent male observed on the northern pampas near Chascomus, I saw no defilippii until I got into the central part of the province near Tandil and Azul. The species was common throughout the southern part of the province and from Bahia Blanca north to Pigué, but beyond that point I failed to find it. It was most abundant in the area between Bahia Blanca--Saavedra--and Sierra Ventana, within which region I did most of my field work. Its apparent absence from the central and northern part of the province in mid-November, suggests that it cannot now be common there. Orians (personal communication)

recently found a small population breeding on coastal dunes near La Plata. I failed to find it in coastal vegetation at Cabo San Antonio and Monte Hermosa.

While defilippii has been considered the meadowlark of the pampas, militaris was thought to be absent from the pampas as a breeding bird. Olrog (1963) mentioned it as an autumn migrant to Buenos Aires Province and Cordoba. This apparently ignores published records by Gibson (1918) and Wetmore (1926) that the species was common and apparently breeding at Cabo San Antonio, and Wetmore's report (1926) that it was common and probably breeding near Carhué. Moreover, there is a series of both meadowlark species from Sierra de la Ventana, in the Buenos Aires Museum. Short (1968) documented the occurrence of militaris as a breeding bird in southern B. A. Province, where it occurred sympatrically with defilippii.

I found birds on territory at Cabo San Antonio and in coastal vegetation near Bahia Blanca and in Chubut. On the pampas it was very common along the roads throughout southern B. A. and was often seen with defilippii.

2. The second distributional problem concerns Olrog's (1963) statement that in western Argentina the nominate race militaris breeds from Neuquen southward while the

recently described race catamarcanus breeds from Jujuy south to San Juan and perhaps Mendoza as well. Specimens from Mendoza collected by C. S. Reed were examined in the Buenos Aires Museum and proved to be nominate militaris. I drove a south-north transect from Mendoza to Jujuy, attempting to clarify the distribution of these two forms.

Most of my time was spent in inter-Andean valleys at elevations of 1000-2500 meters. The region is arid, and the vegetation includes Creosote Bushes (Larrea spp.) and mesquite-type trees (Prosopsis spp.) with an aspect suggestive of the Arizona-Sonora desert. Along streams grow various tall grasses including Poa spp. and Stipa spp., some of the former exceeding two meters in height. The main crop in much of San Juan and La Rioja appears to be grapes. In both the riverside tussock grass and grape orchards I found militaris. I collected specimens in San Juan and La Rioja, all of which were in breeding condition and seemed to be on territory. These birds were all darker than m. catamarcanus and appeared to belong to the nominate race.

I worked for four days in southwestern Catamarca in the vicinity of Tinogasta where I found meadowlarks common in tall brush and in grape orchards. Specimens collected there appear typical of militaris in their dark coloration, although the locality is less than

100 km. from the type locality of catamarcanus.

I spent only one day at this type locality, Corral Quemado, located 55 km. north of Belem, Catamarca (27°20' S; 66°58' W). I was surprised to find that local residents claimed to be unfamiliar with the species, even when I showed them a mounted specimen. It was certainly not common, for I saw only three individuals on the edge of gardens along the small river. One specimen was collected, an adult female accompanying a full grown young. This bird (A.M.N.H. specimen 821916) appears intermediate in color between militaris and catamarcanus. A male seen nearby appeared quite dark, but could not be collected.

I drove northeastward to Santa Maria, and in the valley of the Rio Santa Maria, meadowlarks were quite common, frequenting gardens and especially the tall tussock grass along the river. Several males were singing, seemed to be on territory, and had enlarged gonads. A series of specimens collected along this river valley included pale birds that were typical of catamarcanus and intermediate birds. Nearby, on a sparsely grassed plateau above the river, I flushed a group of three dark-appearing meadowlarks. A male with small gonads was collected. It was dark, typical of militaris, and may have been a migrant.

I observed meadowlarks for several days in the

vicinity of Santa Maria, Catamarca and Amaicha del Valle, Tucuman, and the birds observed and the few specimens collected were pale individuals. Pale birds were also observed in the Quebrada de Humahuaca, Jujuy, from where I have seen several specimens all typical of catamarcanus.

Olrog's (1963) range must therefore be changed as indicated above. The race catamarcanus ranges from Jujuy to northeastern and central Catamarca, while nominate militaris ranges from southwestern and perhaps central Catamarca southwards. There appears to be a zone of intergradation in central Catamarca, particularly along the Rio Santa Maria.

3. The question of how militaris is distributed in Patagonia was raised by the existence of three independent latitudinal clines in size (wing length) occurring in populations in eastern Argentina, the Andean foothills and in Chile. I did not attempt to see whether there is any chance that birds might move across the Andes in southern Argentina and Chile, but did attempt to determine whether there was an opportunity for gene flow across the arid Patagonian plains between the coast and foothills populations.

A review of literature provided little relevant information, although Durnford's statement (1877) that

it is a sure sign of water, suggested that it might be distributed along river valleys. Most of the relatively few specimens from Patagonia are inadequately labelled. In November 1970 I drove from Bahia Blanca through the valley of the Rio Negro to Neuquen and investigated bird distribution in the vicinity of Zapala. In December, I drove from El Bolson eastward, sometimes passing along the Chubut River, until I reached the coast near Trelew. It is not necessary here to dwell on meadowlark distribution in the Andean foothills, since it proved to be common from San Martin south to El Bolson, and was often found in clearings in Nothofagus forests (mentioned also by Navas, personal communication). I found a few individuals of militaris in irrigated areas in the Rio Negro Valley, and also in tussock grass marshes along the Rio Chubut. The populations were small, but the birds were found all along the rivers, indicating a potential bridge between the coastal and foothills population.

The specimens relevant to the above discussion were examined in several museums, and all specimens taken by me (see appendix 2) are deposited at the American Museum of Natural History.

SUMMARY OF FIELD WORK ASSOCIATED WITH THIS STUDY

ARGENTINA: November 1970 to January 1971 and October-November 1971

Pezites defilippii on the pampas of southern Buenos Aires Province.

P. m. militaris on the pampas of southern Buenos Aires Province.

in Patagonian scrub of eastern Chubut

in Patagonian grassy steppes and wooded "parkland" in western Neuquen and Rio Negro

in vineyards of the arid Andean foothills in San Juan, La Rioja and southern Catamarca.

P. m. catamarcanus in middle and high elevation tussock-grass river bottoms of northern Catamarca, Tucuman, Salta and Jujuy.

Leistes m. superciliaris on pampas of southern Buenos Aires Province and in marshes of Corrientes.

PERU: July to October 1972

P. bellicosa riverine marshes on the arid coast in southern Dept. of Lima.

Cultivated fields in the vicinity of Huanuco City.

VENEZUELA: May 1970 and February 1974

Leistes m. militaris Llanos of Guarico and Barinas,

and grasslands of southern Bolivar.

SURINAM: April 1972

Leistes m. militaris cultivated fields and flooded pastures on the coastal plain.

COLOMBIA: April 1973

L. m. militaris Cauca Valley and cut over mountain pastures.

TABLE 2 SUMMARY OF ITINERARY IN ARGENTINA

FIELD DAYS

PERIOD 1970 - 1971	Bahia Blanca	Saudade	Patagonian Circuit	Northern Buenos Aires	Northwestern Argentina	Northeastern Argentina
Nov. 7-16	2	5	-	2	-	-
Nov. 17-24	2	4	-	2	-	-
Nov. 25-Dec. 5	3	-	11	-	-	-
Dec. 6-24	6	13	-	-	-	-
Dec. 25-Jan. 15	-	-	-	-	22	-
Jan. 16-22	-	-	-	2	6	3
2nd Trip 1971						
Oct. 14-31	3	10	-	4	-	-
Nov. 1-20	4	9	6	2	-	-

CHAPTER 2 TECHNIQUES

FIELD STUDY TECHNIQUES

This section outlines general techniques of field work, measurement and analysis. Additional details are provided in each chapter where necessary.

I made direct observations with binoculars, 25 X telescope, or naked eye to locate birds and observe their behavior. On study areas I usually employed a closed jeep as a blind while observing, trapping or experimenting (fig. 3). I watched males as they outlined and defended their territories, and wherever possible I observed behavior of females as well as courtship and copulation (the latter only rarely). I noted the orientation of females with regard to the male territories, particularly for P. defilippii where unmated females were conspicuous and easy to observe. In Argentina I was able to use the rooftop luggage carrier of a jeep as an observation post about 3 meters above ground. Such elevation was useful for observing birds foraging on the ground unless they were in tall vegetation.

In all study areas I made at least a rough map of the main vegetation types, using artificial posts as markers if necessary. These maps or overlays were used

to outline the approximate territories of different birds. Much information both on position of birds and on other aspects of behavior was recorded on tape.

NEST FINDING

Nest finding was a most important and most difficult aspect of the field studies. Most writers (e.g. Roseberry and Klimstra 1970; Marchant 1960; Pereyra 1923) emphasize that Meadowlark nests are well-concealed and difficult to discover. The birds generally gather nest material close to the nest, so cannot be observed flying with the material. The male does not necessarily perch close to the incubating female, in fact in P. defilippii the male rarely sings near the nest, particularly if he is courting a second female. The female usually sits very close on the nest, not flushing until almost stepped on; hence random search for nests is inefficient. Moreover, females flushed from eggs once or twice are very likely to abandon their nests (Lanyon 1957; Marchant 1960; and present study).

Three techniques were used for finding nests:

1) random search in a territory or field, concentrating on the area of greatest activity of males and females.
2) systematic search, beginning either as a spiral from where a female is observed, or as a series of

parallel transects through a territory (often on horseback).

3) observations of adults returning with food for nestlings.

Roseberry and Klimstra (1970) found 450 Meadowlark nests in 8 seasons, employing systematic searches with 4 to 8 people walking in tandem along a roadshoulder. This method (#2) was generally fruitless in my experience, except on horseback. Considering the amount of time involved, more nests were discovered by random search or by accident, than by systematic search. The third method proved most efficient when it was necessary to discover a specific nest. Due to behavioral differences among the species, it proved much easier to find nests of P. militaris than of P. defilippii or P. bellicosa.

CENSUS

Several census techniques were utilized to evaluate possible differences in habitat preference for meadowlarks in Argentina. On the study areas I attempted to map the location of each territorial bird with respect to various structural features and its territorial neighbors. I also evaluated the distribution of the species while driving transects through different habitats. On several transects, particularly in the

pampas, I stopped every 10 or 20 km, noted whether any meadowlarks were present, and described the habitat. On other transects, amounting to nearly 6000 kilometers, I paused only when a meadowlark was seen from the car. After identifying it I attempted to determine how many birds were present, and made a brief habitat description, usually including vegetation type, heights, and estimated ground cover.

TRAPPING OF ADULT BIRDS

Territorial males were captured most often in a treadle-trap or in remote-operated traps containing a mounted decoy of a male militaris accompanied by a tape loop playback of a song. A variety of traps were used, either on ground or on fence, and each trapping attempt was also viewed as a form of playback test (see figs. 4, 5). Success varied considerably depending on different factors which influence the percent of successful attempts and the trapping time required for males of three Pezites species. Factors involved in strength of response of a territorial male to a decoy and tape loop, either with a trap or without, are considered in chapter 12.

Mist-nets are generally inefficient for capturing open-country birds because of the lack of defined flight pathways and because of net visibility. Odum and Hight

(1957) were able to trap flocking finches by using teams of people to drive birds into long lines of nets, but Martin (1969) indicated that this method is nearly useless for capturing wide-spaced territorial birds. He used a V-arrangement of nets, sometimes closed at the top, deployed around a nest, with great effectiveness. Dykstra (1968) also successfully trapped open area birds using mist-nets with a decoy. I used mist-nets successfully only at night in the wet pastures in Peru. Nets were set up at dusk on the edge of a field where meadowlarks roosted and after dark four people walked abreast, flushing the birds ahead of them. Several birds of both sexes were captured this way, although not all were subsequently found on territory.

Adult female Pezites were mainly captured on their nests during the nestling phase. Although adult female P. militaris frequently accompanied their mates in approaching a decoy in a trap, they never came within two meters of the trap itself, always remaining behind the males.

For nest trapping I placed a dome of mist-net material over the nest site, supported either by the vegetation, or by wire arcs. The perimeter of the dome was fastened to the ground with wire hoops, except for a "door" which consisted of an elevated flap of net. The flap was weighted by a wooden stick, supported by a

vertical stick (see fig. 5), and a long string was attached to this second stick. When the female came to the nest to feed the young, the string was pulled and the flap dropped closing the dome. In some cases the arrival of the female at the nest was monitored by a microphone placed next to the nest, and attached to the tape recorder by a 140 foot cable. This allowed me to monitor the vocalizations of the young at the time the adult arrived, for the adults themselves, particularly the females, are secretive and mostly silent as they approach the nest. This technique was described for me by Dr. W. E. Lanyon, based on his experience with Sturnella.

Females were also taken on the nest by jack-lighting them at night, and capturing them with a hand net on a 4 foot handle. This proved to be much less time-consuming than trapping, and involved less alteration to the vegetation, but was also less certain.

HANDLING OF TRAPPED BIRDS

All birds captured during daylight were weighed with Pesola balances, and their bills, wings, tails and tarsi were measured. The main purpose of trapping was to mark birds for individual recognition, but in certain cases birds were retained in captivity and transported to the United States for breeding (prior to the 1972

U. S. Dept. of Agriculture ban on live bird imports).

COLOR MARKING

For individual recognition, birds were marked with colored plastic leg bands of the wrap-around variety. In one case two bands were missing after only one week, but in most cases where birds banded in 1970 were observed in 1971, the bands were still in place. Lanyon (1957) found no band loss in his study, with some individuals observed as long as four years. Each bird received four plastic bands, two on each leg, so that if one band were missing its loss would be apparent. Although the 4-color combinations offer a great number of possible combinations (see Buckley and Hancock 1968; Duncan 1971), I was more concerned with having the leg bands conspicuous, I opted for using two bands of the same color on each leg in most cases. Thus the distance at which the essentially 2-color combinations could be read was at least doubled (see fig. 5). For each location and each species one leg received a "constant" color and the other an "individual" color. Where possible I gave females the same color combination as their mate, and second females had only one band different from that of the first female (an exception to my 2-color rule). Thus male BB/YY might have two females designated as BB/YY and BB/YR. Since color combinations

TABLE 3. Color-marked Meadowlarks

PEZITES MILITARIS

SAUDADE 1970 ♂♂♂♂	♀♀♀♀		Saudade 1971 ♂♂♂♂	♀♀♀♀	
GG/GG	GG/GG	GG/YG	GG/GG(present)	YG/GG	
GG/YY			YY/YY		
GG/WW	GG/WW		YY/BB	YY/BB	YY/YB
GG/BB			YY/RR		
GG/RR			YY/WW		
			YY/GG	YY/GG(not released)	
7km East of Bahia Blanca 1970			7km East of Bahia Blanca 1971		
RR/RR	RR/RR		RR/GG		
RR/YY	RR/YY		RR/BB		
RR/WW					
32km West of Bahia Blanca 1970			32km West of Bahia Blanca 1971		
BB/BB			BB/BB(present)		
BB/RR	BB/RR		BB/WW		
Bariloche (El Condor) 1970					
BB/YY					
BB/GG					

PEZITES DEFILIPPII

SAUDADE 1970 ♂♂♂♂	♀♀♀♀		Saudade 1971 ♂♂♂♂	♀♀♀♀	
BB/BB			RR/RR		
BB/RR			RR/BB	RR/BB	RR/YB
BB/YY			RR/YY		
BB/GG			RR/GG		
BB/WW	BB/WW		RR/WW		
BB/WBk			BB/WB(present)	BB/BW	
BB/YG			RR/YG		
BB/RW			RR/RW		
7km East of Bahia Blanca 1970			7km East of Bahia Blanca 1971		
WW/WW	WW/WW	WW/WB	GG/YY (mated to) ♀WW/WB		
WW/BB			GG/BB		
WW/RR	WW/RR		WW/RR(present)	WW/RR (present)	
WW/YY			GG/WW	GG/WW	
WW/GG					

PEZITES BELLICOSA

Bujama 1972		
WR/WW[a]	WR/WW[a]	
WR/BB	WR/BB	
WR/RR[a]		
WR/GG		
WR/YY		
WR/BR	WR/BR	
WR/GR		

a = These birds were obtained in mist nets and were not subsequently found on territory. Two other males were trapped and retained in captivity.

were duplicated for species as well as sex, it is necessary for me to refer to an individual bird by species, sex and color bands (e.g., P. mil. ♂ BB/YY). Although more cumbersome for writing, this was more than compensated by convenience in recognizing the birds in the field. This is a major problem with meadowlarks, which spend much of their time in the grass where their legs cannot be easily seen. The duplication of color combinations among mates was less of a problem since all forms of Leistes and Pezites (contrary to Sturnella) have marked sexual dimorphism, and the sexes can always be distinguished at a greater distance than the plastic bands. The duplication of color combinations among species was not a problem, since I avoided duplication at any given locality. Moreover, even when silent, the species of Pezites can usually be distinguished in the field.

Following Lanyon (1957) I also marked the birds with dye, using airplane "dope" (Testor brand). This lacquer with an acetone base is relatively quick drying. I applied a thin film with a wooden applicator, in a broad band over the upper wing converts and across the primaries while they were held in a spread position. Care was taken to minimize matting ot the feathers. The paint remained visible for at least six weeks (the duration of my observations). In most cases I had the

paint combinations match the band combinations, but in so doing, I found that birds marked with yellow, white and orange, could be distinguished at a greater distance than those marked with red, green or blue.

RECORDING TECHNIQUES

Throughout my field studies I used a UHER 4000-L report tape recorder operated by either Nickel-cadmium batteries (if recharging was possible) or by alkaline dry cells. In 1970 I used a UHER M-514 dynamic microphone in a 24" parabolic reflector with a UHER Pre-amplifier. This provided good amplification and wind-screening, but was cumbersome to manipulate when negotiating the innumerable barbed-wire fences on the pampas. In many cases I dispensed with the parabola, and used the "naked" microphone for recording. It was very beneficial in subsequent seasons to have available the AKG CK-9 directional microphone with an AKG company B46E preamplifier, which I used in Argentina, Peru, Venezuela, and Surinam. The convenience of this microphone which could be handled easily while climbing fences or while sitting in a car, made up for its slightly lower pickup and screening properties.

For most recording sessions, some songs were recorded at 7.5 i.p.s., while the majority of songs were recorded at 3.75 i.p.s. to conserve tape. Verner and

Milligan (1971) could not detect differences on sonographic analysis between songs recorded at these two speeds.

Whenever possible, tape speed was verified at the beginning and end of each recording session, by recording a 440 Hz. tone from a pitch pipe. This was essential since I was often forced to use non-rechargable batteries and frequently wore them out during recording sessions. It also served to detect more subtle differences in recording speed due to machine changes as emphasized by Lanyon (1969).

ANALYSIS OF VOCALIZATIONS

The sound analyses were performed on a Kay 6061 B sonograph. In most cases both narrow and wide band filters were employed to emphasize frequency on the one hand and temporal discrimination on the other.

I also investigated two other analytical techniques which rely on computers. In the first, I placed sonograms on an X-Y digitizer tablet (Computek brand), and by marking points of interest on the sonogram, automatically created a digital file with song parameters. In the second technique, the tape recordings (which are equivalent to analog inputs) were played directly into the analog-to-digital converter of a Xerox XDS-7 computer, and the signal was converted directly to

a power vs. time function and stored in a digital file on tape. Frequency spectrum analysis was performed by Fourier Transformation routines, which created a data matrix of time vs. frequency vs. amplitude. This provides exact estimates of amplitudes which are otherwise inferred by the relative darkness of sonograms. Both of the computer techniques are undergoing further development, but for this report only information obtained from visual examination of the sonograms will be utilized.

STATISTICAL ANALYTICAL TECHNIQUES

A wide variety of statistical techniques were employed in preparing this report. Univariate statistics based on the normal curve were obtained on the morphometric analyses of all groups of specimens. Ultimately I used the program UNGROUP (Sokal and Rohlf 1969) which provides in addition to usual statistics, several measures of goodness of fit to a normal distribution. Although morphological data are probably more often log-normal than normal in distribution (Salthe, personal communication), most of the data obtained in this study did not deviate significantly from normal. This does not preclude, however, a better fit of the same data to the normal curve after transformation.

Non-parametric or distribution-free statistical tests and corresponding tables were derived from Siegel (1956) and Bradley (1968). These authors discuss the circumstances in which one or another of related tests may prove superior. In several cases of doubt where related tests provided discrepant results, I have included the results of several different analyses for comparison.

Multivariate statistical analysis was performed using the MULDISC5 program for analysis of variance and multiple group discriminant analysis, based on programs in Cooley and Lohnes (1971) as modified by L. F. Marcus and J. M. Gulledge. In several cases results were verified by running the same data through the U.C.L.A. Biomedical programs.

CHAPTER 3 STUDY AREAS

DESCRIPTION OF STUDY AREAS AND HABITATS

My field work in South America covered a variety of the non-forested habitats of that continent. Rumney (1968) provides a working classification of the World's climatic and vegetation zones, using 17 categories. My meadowlark studies took me into "mid-latitude prairie", "steppe grasslands", "subtropical interior deserts", "coastal deserts", "tropical savanna woodland", and "mid-latitude forest, mixed". The early vegetation classification of Beard (1955) is of little use since it slights grasslands.

PAMPAS

The chief study areas for P. militaris, P. defilippii, and L. m. superciliaris were in the southern part of the Argentine pampas, one of the three great grassland areas of the Southern Hemisphere (Rumney 1968: 374). The pampas stretch northward about 1000 miles (1600 km) from the vicinity of Bahia Blanca (38°S. lat.). Although the maximum east-west extent of the pampas is nearly 500 miles (800 km), they are much narrower near Bahia Blanca, where a narrow band of low woodland ("espinal" or "monte"), bounds it on the west. This woodland, dominated by thorny trees, particularly

Prosopsis spp. and Geoffroyia decorticans runs mainly north-south with trees becoming taller as the moisture increases in the north, where it merges with the true chaco of north-central Argentina. I worked also in the ecotone between the grassland and the monte, where P. militaris occurred in what may be its natural habitat. This monte which reaches the coast just below Bahia Blanca, separates the pampas from the desert scrub vegetation of northern Patagonia. Much of the "monte" is being cleared for grazing, and most of the pampas have been converted from natural grasslands, to pastureland or cultivation (e.g., Murton et al. 1974), with "soft" European grass species, replacing the natural bunchgrasses (Stipa spp.) and the tall Pampas Grass (Cortaderia selloana). That this is not an entirely one-way replacement, is demonstrated by the quickness with which Stipa reappears in areas that have been over grazed or have lain fallow.

Even until the late 19th century, trees were sparse on the pampas (Hudson 1918, Murton et al. 1974). Natural trees on the pampas were mainly Tala (Celtis tala), but with the arrival of Europeans, many species, particularly Eucalyptus spp. have been introduced. Equally important are the numerous weed species, such as Mustards (Brassica spp.) and thistles of various genera. The latter sometimes completely dominate the pasturelands

(Murton et al. 1974), and a good account of their growth and role in the ecology and economy of the pampas is by Hudson (1918).

The pampas are mainly flat, rising very slightly from sealevel to about 400 meters elevation in the west. The soil is an alluvial mixture of sand and clay overlain by a fine yellowish loess (Rumney 1968). Two sierras exist, the Sierra del Tandil (up to 500 m) is near Azul, and the Sierra de la Ventana (up to 1300 m) lies north of Bahia Blanca. The northern pampas tend to be wet with large lagoons or esteros, surrounded by Juncales (marshes of Scirpus sp.). These areas are not favored by meadowlarks. To the north these merge into marshes of Santiago del Estero, Corrientes, and eastern Formosa. The southern pampas tend to be much drier, with fewer freshwater lagoons, and more saline lakes. The north-south temperature gradient is illustrated by the following lists of hours-of-frost and cold days/year (Rumney 1968).

	Hours of Frost	Days with T < 10°C
Buenos Aires	600	30
General Lavalle	1000	90
Bahia Blanca	1400	90

Although still a grassland, the human modification of the pampas has undoubtedly had an effect---never to

be known---on bird populations, and as Lack (1965) has pointed out, the population atructure and ecology of a species in a modified habitat, may not be a close reflection of conditions during the evolutionary history of that species.

The study areas in southern Buenos Aires Province lie in a zone which, both floristically and physiographically, bears a close resemblance to the prairies of North America. Although the dominant Bluestem grasses (Andropogon spp.) of the latter are not found, there are several dominant genera of grasses (e.g., Festuca, Bromus, Poa, Panicum, Stipa) common to both continents. Tables 4A & 4B show average annual rainfall and temperature at several locations relevant to the present study.

PAMPAS STUDY AREA I; Estancia La Saudade

La Saudade is located at 37° 46' S; 62° 25' W, and 370 meters altitude, 8 km. south of Saavedra and 92 km. north of Bahia Blanca. The Sierra de Cura Malal, part of the Sierra de la Ventana, is located 4 km. east of the study area, and rises over 500 meters above the pampas. These hills cast a mini-rainshadow on the plains to the west, for the average precipitation near La Saudade (extrapolating data from Rumney 1968) is less than 16" per year (300-400 mm) compared with more than

20" (500-800 mm) just east of the mountains (F. Nazar, personal communication)

The chief crop is wheat, planted in late August and September in plots varying from 5 or 10 hectares up to 150 hectares, although larger plots are planted at other estancias. In my records, wheat comprised 80-90% of the cropland of the study area, and nearly 50% of the total area. Other crops included barley, oats, alfalfa and sorghum. Pastureland accounted for 30-35% of the area in and around La Saudade, dominated by a variety of soft grasses and weed species, with scattered patches of Stipa spp. In the study area itself, which extended for 2 km. along a dirt road, and 500 meters to either side, pasture accounted for just under 40% of the land in 1970 and not quite 30% in 1971. There is considerable crop rotation, so that a wheatfield may be used as pasture the following year.

In addition to pasture and grain, the study area was bordered by the artificial tree plantations around the estancia buildings, and also contained a narrow "monte" running along the usually dry Arroyo Saudade. The road dividing the study area was 12 meters wide, half of which was abandoned and covered with vegetation. Luxuriant growth of thistles, mustards, Bromus spp., Solanum spp., Chenopodium spp., Amaranthus gracilis, Kochia spp., etc. occurred on the fence rows. Vehicular

travel along the road amounted to two trucks/day in 1970, and two/week in 1971. There was, therefore, very little disturbance during my studies. The road allowed me to use my vehicle as a blind, from which all parts of the study area could be observed (although not at one time). The fence poles and utility poles provided convenient, evenly spaced markers for mapping territories, while I inserted additional stakes as grid markers in the field to provide rectangular coordinates for mapping territories. Typical habitats are shown in figue 6.

PAMPAS STUDY AREA II; 7 km. east of Bahia Blanca

I studied meadowlarks in pastures along the main highway, route 3, at a point 7 km. east of Bahia Blanca (designated BB7E in tables), near the suburb of Adolpho Romea (38°43' S; 62°14' W; altitude about 30 meters). Climatic data for this area is provided in Verettoni (1964) and is summarized in table 5. Rainfall data for 30 years, showed a variation from 316 to 1010 mm/year (mean = 523 mm = 20.6"). The wet seasons are February to April and October-November, although in 1971, the latter season was nearly rainless.

The study area comprised about 40 hectares on both sides of the highway. The dominant grasses are Stipa spp. (mainly S. ambigua), although thistles and

TABLE 4 A Climatic Data for Selected South American Localities
(after Romney 1968 & Lamp 1972)

LOCALITY			MEAN MONTHLY TEMPERATURE °Celsius		MEAN MONTHLY RAINFALL millimeters		TOTAL ANNUAL RAINFALL (mm)
			Sep-Feb	Mar-Aug	Sep-Feb	Mar-Aug	
Piarco, Trinidad	10°37'N,61°21'W	(12 m)	25.23	26.06	133.5	158.7	1750
Lima, Peru	12°4'S,77°2'W	(137 m)	18.76	17.70	1.5	2.1	21
Belem, Brazil	1°27'S,48°29'W	(24 m)	25.98	25.83	208.3	253.3	2770
Santiago, Chile	33°27'S,70°42'W	(520 m)	16.55	11.00	8.2	50.3	361
Punta Arenas, Chile	53°10', 70°54'	(28 m)	8.57	4.47	29.5	38.3	407
Buenos Aires, Argentina	34°35'S,58°29'	(55 m)	19.18	13.43	83.7	76.5	961
Bahia Blanca, Argentina	39°00'S,62°00'	(10 m)	17.11	11.29	55.8	48.3	632
Stanley, Falklands	51°42'S,57°52'	(53 m)	7.38	4.35	53.9	50.3	625

Monthly means calculated by adding the average temperature or precipitation for the months, and dividing by 6.

TABLE 4B. Climatic data for the Bahia Blanca area (from Verettoni 1964).

	ANNUAL	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Mean Temperature(°C)	14.2	20.4	20.3	17.6	15.2	11.2	8.4	7.5	7.7	10.9	14.0	17.1	19.6
Absolute Max. Temp.	40.9	40.9	39.1	34.5	33.4	27.7	24.9	21.9	23.4	30.0	33.0	36.7	40.6
Mean Maximum Temp.	20.7	27.9	27.9	24.2	21.6	16.7	13.6	12.8	13.4	17.0	21.0	24.4	27.4
Absolute Min. Temp.	-5.1	6.5	7.5	5.5	2.0	-4.0	-5.1	-4.0	-3.2	0.0	0.4	1.5	4.4
Mean Minimum Temp.	9.8	15.3	15.6	13.3	10.8	7.4	4.6	3.8	4.1	6.9	9.4	11.4	14.6
Mean Wind Velocity(km/h)	13	14	14	12	12	11	11	12	11	13	13	13	14
Predominant Direction	NW	E	S	N	NW	NW	W	NW	N	NW	N	S	E
Mean Precipitation	633.0	40.6	69.1	83.0	67.1	52.6	25.1	30.0	29.3	70.0	46.9	67.4	43.9
Days with Frost	13.6					.6	3.0	5.4	4.2	.4			
Days with clear sky	64.3	5.1	6.7	6.7	3.9	.0	6.3	5.8	5.6	4.8	5.5	4.1	5.8
Days with overcast	65.3	3.7	2.8	4.8	3.6	8.8	7.9	7.1	6.3	7.6	6.0	2.9	3.8

other vegetation occurred. Ground cover was nearly 100%, and very few plants exceeded one meter in height. The only elevated perches available were provided by fences and posts along the road. The study area was bounded on one side by a residential community, but homogeneous vegetation extended at least 500 meters on the other three sides. The only land usage that I observed was pasturing of horses, (see figure 7A).

MONTE

Monte is used to refer to any woodland, particularly if it is not extensive. The monte chañar (Verettonni 1964) is a woodland characterized by stands of a single species, the Chañar (Geoffroyia decorticans). However, such woodlands often include several species of Prosopsis. The monte belt which corresponds to the "bosque pampeana" of Parodi (1964) and the "provincia espinal" of Cabrera (1968) extends south from Chaco to just south of Bahia Blanca, a distance of about 1000 km. The wetter climate of the northern portion favors taller trees, while in the south, some monte stands are less than 3 meters tall, and most are under 5 meters. Short (1975) has recently described and illustrated examples of typical chaco woodland from the northern portion of the range, (see figure 7).

Just south of Bahia Blanca, the monte bends eastward

and reaches the coast, and it thereby forms the western and southern limit of the pampas. The chañar is relatively tolerant of saline soils, but on the margins of salt pans it is replaced by the introduced tamarisk (Tamarix gallica) and by Glassworts (Salicornia spp., particularly S. ambigua), as well as other halophytes. Undergrowth in the chañar area includes Diplotaxis terminifolia, Tribolium spp., Marrubium spp., Rumex crispus, Juncus spp., and Gardus nutans. On the margins of the monte, the Chenopod (Atriplex undulata) formed large stands up to 1.5 m tall, and provided 30% ground cover.

Two study areas were utilized, one along route 3, 18.5 km west of Bahia Blanca, where Atriplex and Salicornia were dominant. A second study area was located 2 km south of the junction of routes 3 and 22, (30 km. west of Bahia Blanca) and extended about 500 meters along route 3 and about 700 meters to either side of the highway (about 70 hectares). About 40% was wooded (mainly chañar), while the remainder consisted of open areas with grass, forbs, or Salicornia. Fences paralleled the road and there was a utility wire along one side of the road. These and the road shoulder were important parts of the militaris territories. The road shoulder was 25 meters wide, with Stipa spp. clumps about 30" high offering 90% ground cover. Inside the

fence to the east of the road was monte while to the west there were grassy fields with 8-15" grass, heavily grazed, offering less than 25% ground cover.

SOUTH TEMPERATE WET FOREST

The mid-latitude forest and steppe region was studied using San Carlos de Bariloche (41°41'S, 71°18'W) as headquarters. The study sites were about 850 meters elevation, and I found several habitats where militaris was common. The tall forests of Nothofagus spp. and Libocedrus chilensis of the southern Andes, reach their main development in the wet coastal region of southern Chile, before the cool westerly winds begin their ascent on the west slope of the Andes. Some moisture crosses the Andes, but there is a dramatic moisture gradient along the 40 km. long Lake Nahuel, from the west with rainfall often exceeding 5000 mm/year (200"), to the grassy steppes at the east end of the lake where rainfall average 640 mm (25"). About the midpoint of this transect, the Nothofagus trees are of moderate height and there are often clear park-like areas of grasslands within the woodlands. This transitional belt between evergreen forest and summer-green grassy steppe (Young 1972) extends all the way along the forest to extreme southern Argentina. This ecotone and the grassy steppes provides suitable habitat for P. militaris, and J. Navas

(personal communication) mentioned finding Pezites breeding in small open "islands" within extensive stands of forest.

A study area was visited over a 3 day period, along the road to El Condor, about 5 km. west of the Bariloche airport. This woodland along a small stream was surrounded by grasslands, but contained a variety of herbs, bushes, and small trees, with considerable floral and physical diversity.

On transects across Patagonia to the coast of Chubut and northward along the Andean foothills to Jujuy, I visited a variety of other habitats. In these areas my visits rarely exceeded three days in any one location, and I had no color-marked individuals. Where relevant, data on climate and vegetation will be provided in the text.

FALKLANDS STUDY AREA

Although I did not work on the Falkland Islands (=Islas Malvinas of Argentine publications), I provide a brief description of the climatic conditions, since a large, long-billed race P. m. falklandicus occurs there. O. S. Pettingill, I. Strange, and M. Rumboll have provided me information on this form. All visitors have commented on the harsh climate (e.g., Bennett 1926; E. R. Pettingill 1960), and O. S. Pettingill (1960)

suggest that "probably no part of the world permanently settled by man has a more disagreeable climate". It is cool, wet and windy, and although the total rainfall is only about 650 mm (=26")/year, about 240 days/year have precipitation. Average wind velocity is given as 15-18 mph (24-28 kph), and average monthly maximum summer temperature as 6.1 to 9.4°C, with annual mean temperature of 5.8°C (in 1970) (O. S. Pettingill 1960, Strange 1972, Weller 1972).

The islands lie in the path of westerly gales which as Bennett (1926) noted often occur during migration, bringing various vagrant species from South America, although only a few have become established. Strange (1972) discusses the main effects of the relatively recent European settlements on the habitats and landscape of the islands. Bennett (1926) noted that the islanders frequently burned over pasture land to improve the selection of grasses, and he specifically mentioned that Pezites had begun feeding on potatoes. He also mentions the loss of much of the native tussock grass (Poa flabellata) and Woods (1971) discusses the importance of this grass to most of the native breeding birds, but not Pezites. Additional details on climate and avifauna are provided by Cawkell and Hamilton (1961) and Pettingill (1973) has recently given a detailed account of the nesting of the resident passerine species

including P. militaris.

COASTAL PERU; General Features

The coastal plain and Andean slopes of western Peru are mainly desert, conditions being so extreme that weather stations at Trujillo (8° S. lat.) and Pisco (14° S. lat.) record only 3 and 2 mm of percipitaion per year. Weberbauer (1945:221), Walter (1972:375) and Tosi (1960) discuss the climate and vegetation of the coastal area. At the lowest elevation the land is completely barren, except for stands of xerophilic bromeliads (Tillandsia spp.) as the winter moisture-bearing clouds, rise up the western slopes of the mountains they deposit moisture as dense fog or garrua, between about 200 and 1000 meters elevation, promoting the growth of substantial vegetation, including woodlands, known as fog- or lomas- vegetation.

The dramatic change in precipitation is apparent between the above mentioned coastal stations at Trujillo and Pisco, and the stations at Lima (12° S. lat., 137 m alt.) with 34 mm rain/year and Canete (13° S. lat., 36 m alt.) with 40 mm rain/year, (Walter 1972:376).

Elsewhere along the coast vegetation exists only in river valleys and alluvial plains. The former or "monte ribereno" is low woodland with a variety of small trees

and shrubs. Most of this vegetation has been severely disturbed by cultivation (Weberbauer 1945:230). Where the rivers cut through the flat plains between the coastal dunes and the beach, one finds broad expanses of reeds and other vegetation. Xerophytic trees such as the Huarango (Acacia macracantha), algarrobo (Prosopsis juliaflora), and Vachellia spp. formerly grew in extensive stands, but in most places only remnants remain for the land is much in demand for agriculture. Root crops such as potato, onions, radishes, and others such as corn, pumpkins and melons, are the main species, and I have noted Pezites utilizing several for food.

Below the woodlands are grasslands of Distichlis spicata, which grows as high as 10", but usually provides no more than 80% ground cover (personal measurements). Other vegetation includes glasswort, Salicornia fruticosa on saline soil and reeds such as Phragmites communis, Typha domingensis, and Scirpus sp. around brackish water. Finally there are broad expanses of sandy beaches. Tosi (1960) estimates that these alluvial fans account for about 10% of the area of the Peruvian coastal plain.

THE BUJAMA STUDY AREA

The river plain at Bujama, where I spent a total of six weeks from July to October 1972, is typical. The study area is accessable from just south of km post 97 (about 8 km south of Mala and 100 km south of Lima), and is at lat. 12°55' S.; long. 76°40' west. From the main highway to the beach is a distance of about 4 km, and the valley ranges from about 400 to 800 meters wide, and is bordered by coastal dunes and the Cerros del Perrico, rising to about 40 meters. These hills are barren. The Bujama study area is flat and has two parts, the former woodlands, now almost entirely cultivated, and the salt marsh (now about 20% reclaimed). These were conveniently divided by a road (see figure 10).

In the salt marsh, surrounding the cultivated areas a grass (Distichlis) was abundant, giving way to dense stands of Salicornia and Scirpus.

The Salicornia fruticosa formed luxurious stands with redundant stems piled up creating loose spongy hammocks as much as 12" deep. Two nests of Pezites were found in these mats. For the most part the ground underlying these stands was entirely dry during July and August, and was moist or wet in September and early October.

No climatic data is available for Bujama, and the 40 mm/year precipitation recorded at nearby Canete, is

probably substantially higher than the usual values for Bujama. However, measurable precipitation was noted on three nights, during my stay, totaling at least 5 mm. However, 1972 was an unusual year in having a very strong "El Nino" current (warm equatorial waters that swing southward deflecting the cold Humboldt current offshore). Temperatures were substantially higher than typical according to summaries provided me by Mr. Manuel Plenge of Lima.

LOMAS OF PACHACAMAC

The lomas vegetation discussed by Walter (1972) and Weberbauer (1945) provides large stands of habitat for Pezites with much greater foliage diversity than occurs on the alluvial plains. On 1 Oct. 1972, Stuart Keith and I observed several pair of Pezites at Pachacamac, about 30 km south of Lima. At least one full grown young bird was seen, and the adults vocalized rarely and did not give flight displays. We judged that the breeding season was over, and that it was therefore substantially shorter or earlier (at least in 1972) than the season along the coast. This is in keeping with the ephemeral nature of the lomas vegetation.

HUANUCO

A population of Pezites bellicosa occupies cultivated fields (particularly corn) and arid scrub, around the city of Huanuco (9°55' S; 76°15' W; 1912 meters altitude). I spent only part of one day there studying the birds. Above the fields were dry slopes with bushes and columnar cactus (Cephalocereus spp.) indicating the dry conditions of the region. No Pezites were found on these slopes, although they were quite common on the flatlands and along the Rio Huallaga. Farmers told me that Pezites bred in November, nesting in the fields. I found many males singing and flight displaying in mid September. The area is classified as "Bosque espinosa subtropical" by Tosi (1960), and has a mean annual temperature of 18.6°C±0.8° and mean annual precipitation of 400mm±150mm.

OTHER LOCALITIES FOR PEZITES

At Villa, on the southern edge of Lima I found bellicosa in pastures, reedbeds, and palmetto savannah, as well as on a golf course (where it was accompanied by Molothrus bonariensis). Pezites occurred in the "monte ribereno" along the Rio Lurin and Rio Rimac, and in the latter valley I found a few individuals as high as 2000 meters, and was told that it occurred somewhat further up the valley. I saw Pezites also at Puerto

Viejo, 65 km south of Lima, where it frequented Typha beds around small lagoons in the alluvial plain. Only once did I see a bird fly across completely barren sand dunes, and then it did not stray more than 50 meters from vegetation.

SECTION II. LIFE HISTORY Chapters 4 - 8

4. Pairing and Courtship
5. Polygyny
6. Nests and Nesting
7. Incubation and Nestling Period
8. Brood Parasitism

Detailed life history studies were beyond the scope of my field studies, however, I did obtain information on several aspects of the reproductive biology of meadowlarks which provide initial life history information. In many cases only fragments of information were obtained incidentally to other studies. The information is organized more or less chronologically with respect to the breeding cycle. Particular attention has been devoted to the subject of polygyny and to comparisons of nestling-feeding behavior.

CHAPTER 4 PAIRING AND COURTSHIP

PAIR FORMATION

Pair-formation is one of the most difficult parts of the breeding cycle to witness in meadowlarks (cf Lanyon 1957) and in other species as well (e.g., Anderson and Anderson 1973). In the migratory populations of Sturnella studied by Lanyon (1957), he only once observed the arrival and subsequent pairing of a female bird. Saunders (1932) also had little information on this period. In closely related sympatric forms such as P. militaris and P. defilippii, a detailed study of pair-formation, however impractical, would be of interest. However, even in 1971 when I arrived in early October, most of the territorial males of both species had already paired. I did, however, witness several instances of repairing after I trapped or collected one member of a pair, and for P. defilippii I witnessed three instances of arriving unpaired females, one of which I observed in detail. For the most part the results of species-differences in pair formation must be read from the post-facto observation of pairs, there being no instance of stable mixed pairings known to me, based on at least single observations of over 300 pairs of militaris and 160 pairs of defilippii.

On Oct. 31, 1971, 7 km east of Bahia Blanca, I watched two presumably unmated defilippii females circling, landing, and eliciting chases from various males on the study area. At 2:45 p.m. I observed a female circling about 50 meters up over the edge of the study area. She circled three times in a broad path encompassing some 20 hectares (nearly half of the entire study area), and seemed to elicit a resurgence of primary singing and some flight singing by the males below. At that point I decided to quantify songs given before, during, and after the arrival of females, but never had another opportunity to do so. Her activity took her over about 9 to 12 defilippii and 3 militaris territories, but only the defilippii males paid attention to her. The three militaris males were already paired, at least one of them having two females in evidence. Some of the defilippii males also had females. At this stage in the field work, almost none of the birds had been color banded.

After circling the female dropped suddenly into the territory of one male, who flew about 10 meters to join her. They were out of sight in the grass for no more than 15 seconds, before she got up, uttering a sharp, insistent see-see note (not recorded). The male followed. The male quickly broke off, and the female ascended, circled for perhaps three minutes and landed

in the territory of another bird. For 55 minutes, this pattern of circling, landing, and flying off continued, with at least 12 landings in the territories of five or six of the males, she usually spent 1/2 to 3 minutes out of sight before flying again. Each time she was followed by one or more males with apparently silent chases. While she circled males on the ground were perched, often conspicuously on taller grass clumps, and gave primary songs. Flight songs were infrequent during this period, and did not seem to be part of the mate-seeking behavior.

Eventually she landed with a male whom she had visited at least twice before during the hour period, and this time she stayed out of sight for nearly 12 minutes. When she got up, she gave a doubled jt-jt jt-jt jt-jt note (see Plate 48A), and was followed closely by the male who gave warbled rehearsed song. Instead of rising to her usual height of 10+ meters, she led him in a low, rapid twisting circuitous path, and landed back in his territory. The two birds remained out of sight for more than thirty minutes, after which another sex chase limited to these two birds ensued, and they again landed in the same territory, and remained out of sight for over thirty minutes, after which observations were discontinued. For the remainder of the afternoon no further high-circling flights by females were seen, and it is likely that this anecdotal account

involves the arrival and subsequent mate-choice and pairing of a new female. As far as I could determine, the male defilippii already had a female residing in his territory (see section on polygyny).

On the morning of Oct. 18, 1971 I trapped and retained a male P. militaris in territory 1, 7 km east of Bahia Blanca. Two other P. militaris males from adjacent territories, sang at the decoy from distances of 10 and 30 meters, but did not approach closer to the trap. A mated male P. defilippii who had a singing perch, about 12 meters from the trap, did not show any interest in the decoy or tape loop. The unmarked female of this trapped militaris foraged on the fround within 5 meters of the trap, and made frequent flights across it, always remaining close at hand. After the male had been removed from the trap and territory, I watched while the female continued to make brief flights around the trap (which still contained the now-silent decoy). Within five minutes, the nearby male P. defilippii, flew quickly toward her, sang from a nearby grass clump, and flew back to his territory with the female militaris right behind him. She left his territory briefly a half hour later, and he followed her with a sex chase, giving the warbling rehearsed song. Although I was close by, I heard no call note when the female militaris elicited the sex chase. She returned to his territory, and the

two birds spent most of the next two hours out of sight except for short flights of less than five meters, during which the male followed the heterospecific female around the central part of his territory. He gave occasional primary songs and no flight songs or call notes during the period. Although neither bird was color marked, I felt that it would be possible to describe this as a stable pairing if the two birds were found together that afternoon. When I returned after a five hour absence, presumably the same male defilippii was attending a female defilippii, probably his previous mate, and there was no unmated militaris female to be found. I could not determine whether she was hidden, had left the study area, or had paired with one of the other resident militaris. Five days later, when I next visited the study area, the territory of the captured male militaris had been mostly occupied by a new male and an unmarked female militaris. The above account is the only instance of even temporary heterospecific pairings, although on at least three occasions I saw male defilippii attempting to mate with female militaris while their mates were engaged in other activities. In two of the three cases the females clearly resisted this attention, and in two cases, their mates arrived within 15 seconds, although I could not tell what had attracted their attention to the potential stolen matings.

The most remarkable observation of pairing concerns P. militaris ♀YY/BB who with her mate had been studied for a six week period at La Saudade in 1971. At the close of the field season, I trapped ♂YY/BB with a treadle trap placed on the ground about 10 meters from her nest. After the capture I briefly observed ♀YY/BB on the fence near the trap, but I left the ♂ in the trap for about 20 minutes more. After removing him from the trap, I checked the nest and flushed the from her eggs. I carried the ♀ to my jeep less than 50 meters away for processing. While measuring him I heard a militaris primary song. An unmarked male militaris, whose presence in the area was unsuspected, sang three times, and then dropped from the utility pole to the fence, some twenty meters from the nest, where he was within five seconds joined by ♀YY/BB. Thereafter they acted as mates, and for the next hour the new male defended part of the YY/BB territory against the two adjacent males, both of whom were marked. He conducted much more territorial defensive activity than any other male in the vicinity. Unfortunately this was the last day of my study area and further observations were precluded. I collected both the female and her new mate. This incident reveals that pairing can be instantaneous as indicated by Lanyon (1957). Moreover, there may be a reserve of unmated males of militaris

available to occupy vacated territories, a feature reported in many other studies.

Still unanswered is the problem of what cue allowed this new male to invade the territory since no territorial challenge had been observed for several days, and since territorial activity was low throughout the study area. I had occasionally observed overflying meadowlarks, and it is possible that the arrival of this male was merely a fortuitous coincidence.

COURTSHIP

Courtship behavior functions to bring and keep together two birds, facilitating, and perhaps synchronizing, their mating activity. The importance of the synchronizing role was stressed for pairs by Noble (1939), Lehrman (1959), and for colonies by Darling (1938). The complexities of behavioral chains or releasing behavior involved in courtship will not be considered here, except to note than many aspects of courtship are interpreted as a resolution between conflicting behavior patterns such as the tendency of females to flee vs. their tendency to approach their mate.

Unfortunately since much of the courtship activity of the meadowlarks takes place in tall vegetation, I was unable to study most of the behavioral patterns

associated with pair bond maintenance. Several species differences in pair bond behavior were readily noted however. Males and females of militaris spent much of their time together, often foraging on the ground within one meter of each other. The females often joined their mates both physically and vocally when they flew to defend their territory against a neighboring male or a decoy. For the other species, however, the females and males spent most of their time apart, and females did not join their mates when the latter were engaged in territorial defense. This is particularly true for bellicosa and defilippii for which I had many observations, and probably holds also for superciliaris based on a few observations.

For P. defilippii I made detailed observations on pair-bond maintenance of P. defilippii ♂RR/YY and his unmarked female. On 10/25/71 this female made frequent flight displays, closely resembling those of the male. She ascended steeply, and at the peak of her display, she tumbled head down, with wings held outwards and downwards, and uttered a see-see-see note (see Plate 49) often with a scolding intonation. She then landed near her mate, or flew horizontally giving the "jt-jt jt-jt jt-jt" notes which usually elicited chase behavior on the part of her mate, who followed her, uttering a warbled song. Her display, which was given frequently

(and was seen only rarely among other female defilippii), differed from the male display in her failure to throw her wings up over her back just before the peak of the flight, and in the quality of the song. I interpreted this display as indicating strong sexual excitement, and perhaps as a prelude to copulation, but could not observe the activity of the pair on the ground. I had no reason to assume that this female (the only one in his territory) was different from the female who had been found there on previous days, but could not verify this since she was unmarked.

During the afternoon I observed 26 sex chases for this pair, while only twice did the male fail to follow the female. This behavior continued throughout the afternoon, and was much less intense the following morning, while the female also decreased her flight display frequency (only two seen). Once, when the male was engaged in a boundary encounter, the female landed in the territory of a neighbor who gave a flight song as he flew over and landed near her. I could not see how she responded to this male, but within 30 seconds her mate arrived, and landed between the two of them. She then took off, gave "jt-jt jt-jt" notes, and elicited another sex chase which led her mate back into their own territory. Sex chases will be discussed further under vocalizations.

PRECOPULATORY BEHAVIOR

Precopulatory displays of males and females allow an interaction which is contrary to most behavioral activity of the birds---that is they allow a momentary violation of "individual space" (Conder 1949) which is otherwise routinely maintained. It is quite likely that the resemblance of the female's crouched soliciting posture, with fluttered wings and plaintive notes to the behavior of young birds, induces males to approach and reduces their aggressive behavior (e.g. Selander and Giller 1961).

Gross (1958) notes that for Sturnella copulation usually occurs during the early days of nest building. A receptive female crouches to the ground, shortens her neck, elevates her bill, flutters her wings, and lifts and spreads her tail. He mentions no vocalizations. The male approaches, displays near the female and then mounts. Lanyon (1957: 38) gives a detailed description of copulation for a pair of S. neglecta.

My own observations are limited to two instances of attempted copulation in defilippii and several in militaris. At Bahia Blanca, an unmarked defilippii accompanied by two females was observed 18 October 1971. One female was twice observed to give soft, insistent, "tsee tzee" notes (Similar to those described by Lanyon 1957), while crouching and fluttering her wings, with

tail up and head nearly horizontal. In the second instance the male approached with a stiff gait his neck stretched upwards, strutted around her, but for some reason did not mount. At Saudade, I observed an attempted copulation on 27 October, by a pair of unmarked defilippii. After a vigorous sex chase the female landed in a bare area in pasture and solicited with head down and tail up. The male who had landed about three meters from her, made a short flight to her side and immediately mounted, but copulation was probably not successful, and the female flew off after about three or four seconds. At the distance of 50 meters, I could hear no vocalizations.

On 28 October, a female of defilippii RR/WW solicited with high thin "see-see" notes, while another female in the same territory was on the fence only 10 meters away giving soft "chk" notes. The male arrived shortly and after a brief upright display he mounted but the copulation was again interupted. The female seemed to be silent during the actual mount. About 40 seconds later, she solicited again, but the male gave a primary song. The female took off with the "jt-jt-jt" notes (see Plate 48A), and the male chased her. This time the pair landed out of sight. There were no further observations of copulation for this species.

In 1971 militaris male YY/BB and his mate spent

much of their time along the road at La Saudade, where I observed three completed copulations and two failed attempts over a three day period. On the last of these days, Oct. 14, 1971, I found her nest with two meadowlark and one cowbird eggs. On Oct. 15, there was a new meadowlark egg. The solicitation notes of this female militaris (not recorded) were softer and higher pitched than those of defilippii but the posture was similar to that of defilippii and Sturnella. In each case the male either walked or flew to the female, usually landing just behind her, and assumed an exaggerated upright posture with legs and neck extended, and bill usually aimed downward at the back of the female. He often took a few strutting steps, and usually mounted quickly and remained mounted for periods of 3 to about 8 seconds. Copulation was repeated about 30 and 40 minutes after failed attempts, but was not repeated after apparently successful attempts.

No notes attributable to the male were heard, and the female appeared to be quiet when the male mounted. I did not take notes on post-copulatory display, except to notice that the male strutted briefly in one case, and that the pair flew off within 15 seconds in another case.

Lanyon (1957: 40) notes that male Sturnella often gave whistled notes immediately following copulation,

indicating a high level of sexual excitation. Male P. militaris occasionally gave warbled flight songs, which were not part of usual territorial behavior, and which may represent high levels of sexual excitation. In some cases, where the flight song orginated from the spot at which a female was located, I suspected that the pair had been engaged in pre-copulatory activity. However, for the pair YY/BB which yielded most of my observations, I did not note flight songs given by ♂ YY/BB before or after any of the copulation attempts, nor on any of the three days. However, the fact that flight songs were given twice the preceeding week, may indicate sexual excitement of the male, perhaps when the female is not yet receptive. This interesting aspect of behavior in P. militaris warrants further study.

CHAPTER 5 POLYGYNY

MEADOWLARK PAIR BONDS -- POLYGYNY

The nature of the pair bond between the sexes---whether monogamous, polygamous or promiscuous---is a fundamental ecological feature of a species (Crook 1962, Lack 1968). The evolution of non-monogamous mating systems has been subject to much discussion, though to little direct investigation. Martin (1974) has most recently discussed some of the problems. Early suggestions that polygamy might result from unbalanced sex ratios (see Mayr 1939 for discussion of difficulty in dealing with sex ratio) have been replaced by the notion that such systems are directly adaptive (e.g., Verner 1964, Verner and Willson 1966, Orians 1969).

Based largely on his own studies of the Icteridae and on reports by Verner and Willson (1966, 1969) and others, Orians (1969) provides a series of 7 predictions concerning the evolution of polygyny. Several of these are worth examining here: polygyny should be more common among precocial than altricial birds, more common in marsh-dwellers or birds of early successional stages, more common in species with restricted nest sites and widespread feeding areas, and in species whose clutch size is influenced by factors other than food avail-

ability. Several of these features are readily observable---for example, the relative frequency of polygyny among open-country species (e.g.., Verner and Willson 1969, Crook 1962) and among species with truly precocial young.

The evolution of polygyny has been posed as an interesting question on the assumption that male contribution in parental care is important. Conversely in groups where males make little or no contribution to care of young, as in groups where young require little care because of precocity, the evolution of polygyny poses fewer problems. Orians (1969) notes that male gamete production is essentially unlimited, and that males most likely will always benefit by continuing to acquire mates. The limit to this benefit is reached when acquisition of new mates reduces rather than enhances the overall production of offspring. Williams (1952), Holm (1968) and others have provided data comparing productivity of monogamous and polygynous males to support the male-advantage. Female-advantage is believed ro occur, because some benefit associated with the male or his territory compensates her for the decreased survival probability of her offspring in a polygynous mating. McLaren (1972) has pointed out that there should be a strong evolutionary pressure on males to mate with more than one female and he even proposes

this as the basic function of territory.

Martin (1974) has correctly emphasized that interest in polygyny focuses on simultaneous polygyny, in which case all females mated to a single male are synchronized. He contends that the relatively short breeding season available to bobolinks (Dolichonyx oryzivora) imposes synchrony on a population. Probably, however, asynchronous or successive polygyny is much more common. The greater the interval between layings of polygynous females, the less interesting is the case. The extreme case would be non-overlapping polygyny in which case the male would be available to assist secondary females, and no detriment would be imposed on such females.

The crucial test of the fitness of secondary females vs. primary females vs. monogamous females would compare their productivity. Yet productivity changes during a season, and McClaren (1972) suggested that the slightly lower productivity he found in bigamous Ipswich Sparrow (Passerculus sandvicensis princeps), might be due to the later breeding of bigamous females. It seems likely that the most suitable studies of productivity would be those made on a cohort basis, i.e., by week of brood inception.

Verner and Willson (1969) summarized reports of mating systems of North American passerine birds, and despite the shortcomings they pointed out, their report

is useful for studying mating systems within the Icteridae. The family shows a wide range of mating systems from apparently monogamous pairings of orioles (Icterus spp.), Euphagus carolinus, and Quiscalus quiscalus (Verner and Willson 1969; Erskine 1971) to the promiscuous colonial Oropendolas and Caciques (Psarcolius spp., Cacicus spp. and related genera) (Chapman 1928; Smith 1968; Skutch 1954) to the brood parasitic cowbirds (Scaphidura and Molothrus) for which various systems have been proposed. A number of species are regularly or occasionally polygynous including Agelaius phoeniceus (Orians 1961, Holm 1968), Euphagus cyanocephalus (Williams 1952), Dolichonyx oryzivorus (Martin 1974), Xanthocephalus xanthocephalus (Orians and Christman 1968) and others. The mating systems of most Neotropical icterids are inadequately known.

The Meadowlarks fall into the category of polygynous species. Saunders (1932) first reported polygyny in Sturnella magna and Lanyon (1957) found that 60% of magna males and 53% of neglecta males on his Wisconsin study area had more than one mate. He believed these figures were conservative, and that 70-80% polygyny might be more realistic. I devoted considerable attention to determining whether South American meadowlarks were also polygynous, but I did not attempt to determine the

proportion of polygynous matings, nor the relative frequencies of different orders of polygyny.

DOCUMENTATION OF POLYGYNY

Suggestion of polygyny can come from observations of a male associating with two or more adult females. Even if both females were to prove in breeding condition by behavior or gonadal examination, this would be circumstantial. Merely observing a male copulating with more than one female would be insufficient evidence since males will attempt to steal matings with neighboring females when the opportunity arises. However, aince females will often repel strange males, successful copulation may be indicative of a pair bond in some species. Continued maintenance of a pair bond as well as copulation (e.g., Price and Bock 1973) is important evidence, and marked birds are essential for such a study.

In my study I used the criteria of observing a marked male with two females (at least one of them marked) who had nests in the territory defended by that male during the same period (the last phrase takes into account seasonal changes in territory boundaries). Stronger confirmation of polygyny came with observations of a male feeding nestlings at more than one nest. Such observations are time consuming since polygynous males

often provide little parental care, and may not assist at all in care of secondary young (e.g., Martin 1974).

The following cases meet the above criteria:

1. militaris ♂ GG/GG at Saudade in 1970, had nests of ♀♀ GG/GG and GG/GY in his territory. He fed nestlings at the nest of GG/GG and at least twice accompanied ♀ GG/GY while she carried food to her nest. (10 days)
2. militaris ♂YY/BB at Saudade in 1971, had nests of ♀ YY/BB and ♀ YY/YB in his territory and accompanied both females when they were flushed from the nest. Field study ceased before any young hatched. (5 days)
3. defilippii ♂ WW/WW at BB7e in 1970, was mated to ♀ WW/WW and ♀ WW/WB who both had nests in his territory, and he fed young at both nests. (7 days)
4. defilippii ♂WW/RR at BB7e was mated to ♀ WW/RR and to an unmarked , and he fed young at both nests. (12 days)
5. defilippii ♂ RR/BB at Saudade in 1971 was mated to ♀♀RR/BB and RR/YB and fed young at the former nest, while at the time of my departure eggs had not hatched in the second nest. (8 days)

These five cases demonstrate that polygyny occurs in both species, and numbers in parentheses indicate an educated guess of the interval between onset of

nesting (= degree of asynchrony) of the two females. All five cases showed some degree of successive polygyny.

Beyond these five pair, I found that most militaris and defilippii males appeared to have two females in their territories, and in one case of defilippii, three females, at least for part of the season. During travel through other parts of Argentina I frequently observed male militaris accompanied by more than one female-plumaged bird. Since at close quarters the heavily streaked, non-pink underparts of grown fledglings can be distinguished from the pinker, less streaked, pale-throated underparts of adult females, I was able to determine that in many cases two adult females rather than fledglings, were involved.

For bellicosa I found several cases where marked males mated to marked females who were nesting were also seen attending unmarked females, and although these cases do not meet the criteria for documenting polygyny, it seems likely that more extensive field work would demonstrate polygyny in bellicosa as well. The same applies to Leistes where information relevant to pair-bond include an observation of a male L. m. militaris accompanying three females and displaying in their presence near Upata, (Bolivar, Venezuela, 7 May 1971). Haverschmidt (1968) presents an additional piece of

evidence for polygyny in Leistes.

In view of the interest formerly attached to sex ratio and mating systems, I determined the proportions of males and females in several flocks and on the study area. Considering that female Pezites are much less conspicuous than males, and that nesting females are out of sight for long periods, a ratio of 1.31:1 and 1.27:1 females to males for defilippii in October and November 1971 at Saudade, is consistent with polygyny since almost all the birds counted appeared to be resident on territories.

I did not obtain useful data on sex ratios among nestlings or fledglings, and I found only three flocks in which it was possible to determine sex ratios during the breeding season. A flock of 16 defilippii observed near Tres Picos, 50 km north of Bahia Blanca on 13 Nov. 1970 in the middle of the breeding season, contained 11 males and five females, and the males displayed to each other and to nearby territorial males. In December 1970, late in the breeding season, a mixed flock of meadowlarks was found in the hills 15 km southwest of Saudade. This was probably a post-breeding aggregation. It contained about 9 male and 15 female militaris and about 40 male and 55 female defilippii. At Bujama, Peru, a flock of bellicosa was present on the study area during most of the breeding season. Five counts yielded an average

total of 66 birds, approximately 29 males and 37 females.

The above data were tested for the probability that the deviation from equality was significant, using a binomial test for the small samples and chi square goodness of fit test for the larger. None of the deviations were significant. The very scant evidence available does not support an imbalanced sex ratio for Pezites though clearly more data are desirable. Verner (1963) noted that even with apparently equal sex ratios polygyny is possible, and French (1959) found monogamy among Black Rosy Finches (Leucosticte tephrocotis atrata) despite a distorted sex ratio.

DISCUSSION

The general questions concerning the evolution of polygyny in a population were presented in the introduction to this section. I discuss here mainly possible advantages accruing to females from mating with previously-mated males. Verner (1963, 1964) noted that in heterogeneous areas certain males may, through chance or superiority, stake out territories which are of superior quality with respect to food, nest sites, or security. Martin (1971) seems to have been the first to measure these features in detail, and he verified that territories of polygynous males were superior to those of bachelors with respect to the vegetation features

relevant to nest sites. However, Verner and Engelson (1970) could not demonstrate this for Long-billed Marsh Wrens (Telmatodytes palustris). Martin (1974) examined the relevance of food availability, finding that primary females receiving assistance from males were able to exploit food in optimal foraging sites, often at great distances from the nest, while secondary females were forced to feed close to the nest site, often where food was in short supply.

The wheatfield-nesting defilippii population should offer an opportunity to clarify this problem. In such relatively homogeneous vegetation, there should be no discrepancy in the availability of nest sites or food between territories. If food is more abundant in fence-rows of complex vegetation than in the grain fields a comparison of central vs. peripheral territories with respect to foraging behavior, growth of young, and success would be fruitful. This is complicated by the fact that meadowlarks often gathered food far from the nest, although individuals feeding near the nest would be less conspicuous and might be overlooked. It would be useful to compare the prevalence of polygyny in grain fields and in the adjacent, more heterogeneous pastures.

The first benefit to being a secondary female in a good territory vs. being primary in a poor one, results from inter-territory differences. A second benefit may

relate to the genetic prospects of the males who hold such territories. Assuming that individual males differ in fitness, females would benefit by being able to detect such differences. The primary difference in fitness lies in the ability to produce offspring, and it will be manifest in the ability to hold a territory, attract a female, and keep on displaying. Thus an already mated male is in one sense a proven male, and therefore may be a better male for a newly arriving female.

In species where some males are monogamous and others polygynous, a detailed field study measuring productivity, nestling growth, and long-term survival in nests of the two groups, would shed light on the relative contribution of territory quality and of male quality (as separate from territory). In practice, however, the only clue to the latter will be the former.

If males do not spend much time feeding young, decreased parental care will not be a significant factor opposing polygyny. In Table 5, I have compared the contribution of a full-time male dividing his attention among all his nests for varying orders of polygyny. Although the model is not realistic, since males of polygynous species may spend less time feeding and do not divide time equally among nests, it does indicate that the relative disadvantage to each female declines,

TABLE 5 Tabulation of the amount of combined parental care available to nests of different orders of polygyny (zero order = monogamy), assuming that both parents spend equal time feeding and that the male divides attention equally among nests.

Polygyny Order	Number of Nests in Territory	Amount of Time Available to each nest			% Lost *	% Compared with Monogamy
		Female	Male	Total		
0	1	100	100	200	---	100
1	2	100	50	150	25	75
2	3	100	33.3	133.3	11.3	66.5
3	4	100	25	125	6.1	62.5
4	5	100	20	120	4.0	60
5	6	100	16.7	116.7	2.5	58.5
6	7	100	14.3	114.3	2.1	57
7	8	100	12.5	112.5	1.6	56.3

* Compared to next lower order

the more females there are in the territory. As the male's contribution to each nest declines, it may be more advantageous for him to expend energy in other ways. The model leads to the prediction that higher order polygyny should occur quite often, since the main obstacle with respect to male contribution, occurs between monogamy and polygyny.

Von Haartman (1969) stresses that hole-nesting species are more likely to be polygynous than open-nesters, possibly because the hole affords protection from inhospitable weather and from predation. Martin (1974) found that the real disadvantage for secondary females occurs early in the nesting stage when they must divide time between brooding and gathering food with no help from the male. The Bobolink he studied is unusual in that males assist with brooding as well as feeding at the primary nest. Although male icterids lack a brood patch and are therefore inefficient in transferring heat to eggs, they can function very well in insulating young and protecting them from cool ambient temperatures. Moreover, since the sky provides a cold heat-sink to which exposed nestlings rapidly radiate heat (cf Calder 1974), merely covering the young would be important in thermoregulation. In this respect, hole-nesting, or the use of nests with domes (either intrinsic or extrinsic, see below) may free secondary females to an extent not

possible with open nesting. This may be an additional factor, interacting with predation pressure, selecting for covered nests in open-country, ground-nesting species.

There are several reasons. however, why polygyny is likely to be favored, apart from the differences in territory quality, and these are based on the advantages accruing to polygynous males. It is possible that since half of a female's offspring probably are males, a genetic propensity for participating in polygyny could be perpetuated with females deriving benefit through their male offspring. This suggestion assumes however, that male offspring of polygynous matings are more likely to successfully establish territories and obtain multiple mates, than male offspring of monogamous matings. Thus male genetic superiority (or Darwinian sexual selection is invoked).

In species where males are brightly colored and females are cryptically colored, it may be a distinct disadvantage for males to assist in care of nestlings. Thus females may benefit by not having male care, if male visits served to attract predators. In my observations at meadowlark nests (see chapter 7), I found that males were considerably more careless than females in approaching and leaving the nest on a feeding visit. This would compound the risk for the nest. I have not found any

studies comparing predation losses of primary and secondary nests. Martin (1974) compared success at primary and secondary nests, but apparently found a difference in starvation of offspring which was greater at secondary nests where males were not assisting. One could predict that primary nests where the males were assisting would be subject to greater predation.

Most of the discussions with regard to female advantage have focused on the secondary females. But if males make any contribution at all to second nests, then primary females should benefit by preventing the settling of secondary females. Von Haartman (1969) discusses this problem. Female territoriality could preclude simultaneous polygyny in such species. However, as the first female becomes occupied with incubation, her opportunity for aggression diminishes, and another female may land. This promotes a system where successive polygyny can occur.

The above discussions have focused on polygyny in relation to individual fitness. There are several aspects relevant to the concept of population fitness which must be considered. Although it remains questionable whether population fitness is meaningful (e.g., Salthe 1972: 310) or whether it is merely a form of group-selectionism, the following observations are in order. Polygyny allows a certain proportion of the

population, namely excess males to be considered surplus, and if at a time of scarce food supply submissive males were to die off or emigrate, the population would be benefitted by reduced competition for food. Both males and females might also be considered to benefit directly through individual selection; males through reduction in competition for females, and females through reduction in numbers of "inferior" males.

Also polygyny reduces the genetic variability in a population, since only a fraction of the males contribute all of the male-derived alleles. This may enhance fitness of the population since by tautology the most successful males are the most fit ones. However, in time of drastic environmental change, low variability may lead to extinction through inability to form new adaptive complexes. I view extinction as a strong argument for not discarding the concept of population fitness.

SUMMARY ON POLYGYNY

Although polygyny is relatively infrequent among birds (e.g., Lack 1968), it will probably be discovered in many species when suitable field studies are performed, and occasional polygyny probably occurs in many species. Since observation of marked individuals is almost essential for documenting polygyny, data have

been slow in accumulating (e.g., Zimmerman 1966). Among passerines polygyny is likely to be discovered in open-country species, in species with restricted nest-sites, in cases where food is periodically or spatialy patchy but abundant, and among taxa where the contribution of males to care of young is already less than 50% in monogamous pairings. The apparently regular polygyny observed in meadowlarks is no surprise since meadowlarks fit well several of the above criteria.

It is likely that selective factors underlying the development of polygyny differ from species to species or from population to population. Field evidence that male Pezites may actually jeopardize nests during feeding visits (see chapter 7) indicates one class of factors that has been usually ignored.

CHAPTER 6 NESTS AND NESTING

MEADOWLARK NESTS AND EGGS

This chapter covers the following topics:

Nest Placement and Location

Nest Site Selection

Nest Building

Nesting Season

Nest Structure

Nest Orientation

Nest Concealment and Nest Finding

Clutch Size

Descriptions of Eggs

Nest Fate and Productivity

Although a large part of my field effort was devoted to finding meadowlark nests, the collection of data on behavior at the nest, egg characteristics, and productivity was not a primary focus of this study. Consequently much information in this chapter has been assembled from the literature dealing with South American meadowlarks, and I have usually added pertinent data for North American meadowlarks as well. My own data are added to the appropriate sections, often in the form of tables.

NEST LOCATION AND PLACEMENT

All meadowlark species generally build their nests on the ground in vegetation, and many authors have emphasized that their nests are difficult to discover. Exceptions to ground nesting must be very rare indeed. Lane (1897: 27) was told that in Chile, P. militaris nest in bushes, but this probably means "under bushes" since later authors (e.g. Johnson 1967) do not mention this. However, Pettingill (1973) noted that on the Falklands, militaris occasionally places its nests off the ground in clumps of grass.

Both in North and South America meadowlarks utilize a wide variety of "grassland" habitats, including such agricultural associations as corn, alfalfa and clover. Nests of Sturnella have been reported in orchards and even salt marshes (Gross in Bent 1958). P. militaris, the least grass-loving of the species, regularly nests within woodland associations, providing suitable ground cover is available for nest placement. Nest locations reported for militaris have included "grass" (most authors), rushes (Abbott 1861; Sclater and Hudson 1888), swampy vegetation (Philippii et al. 1954). The race falklandicus is reported to nest in tussock grass, rushes, and under conifers or gorse bushes (Cawkill and Hamilton 1961; Pettingill 1973). Nest cards (W.F.V.Z.) from Pemberton, Goodall, Johnson and Philippii for

Argentina and Chile, record 10 nests in grass, 1 at the base of a thistle, 3 at the bases of thorn bushes, and 2 at the bases of other shrubs. It is also reported to nest commonly in corn and wheat (Bullock 1923). The location of my 25 militaris nests is given in Table 6. Photographs of nests appear in El Hornero (vol. 3:94) and in Pettingill (1973: 125).

Few writers have commented on defilippii nests. Hudson (1920) says only that its nest is like that of militaris. Holland (1895) and Serie and Smyth (1923) describe nests in grass. In La Pampa nests have been collected in alfalfa (B.M.N.H.). All nests I found were either in wheat or in clumps of bunch grass in pasture. Details are given in Table 6.

Nests of bellicosa have been reported in bushes and grass tufts (Marchant 1960; W.F.V.Z. nest cards). Philippii et al. (1944, 1954) note that the nests are similar to those of militaris, and are found beneath weeds or in tall grass. I found bellicosa nests in grass, clumps of forbs, and in mats of Salicornia.

Leistes nests are also reported in various types of grassland (Herklots 1961, French 1974, Haverschmidt 1968 (see photograph), 1970; B.M.N.H. collection). Serie and Smyth (1923) mention that it nests in alfalfa and in northern Argentina superciliaris is known locally as alfalfero, but Pereyra (1923) notes that even in alfalfa

fields it selects grass clumps for nesting.

Although observations of militaris and defilippii indicated a preference for fence-row nesting of the former and for open-field nesting of the latter, it was interesting to compare the kinds of vegetation in which nests were constructed. Interpretation is limited since the differential distribution of vegetation types in the two habitats (fence vs. field) were not determined, but if one assumes that the two species really had a choice of the same available vegetation, it becomes possible to make at least an initial comparison.

The comparison was undertaken in two stages. First I compared the known nests of militaris and defilippii with respect to five vegetation types (see Table 7), bunch grass (=Stipa spp.), other grasses (principally Bromus spp.), wheat, thistle, and bushes. No nests were discovered under forbs (annual broadleafed plants), although such plants as Brassica spp. were abundant. For each species the number of nests and cumulative percentage of nests was listed, and the maximum percent deviation between the cumulative percentages was determined. I deliberately arranged the five vegetation classes to maximize the differences. The maximum deviation is the DMAX value of the Kologornov-Smirnoff two-sample test (Siegel 1956). The maximum value of .36 was less than the critical value (.48 at the .05 level)

which indicates that the two samples were not particularly different. This could however, reflect a bias on my part, since I was working in only part of the available habitat, particularly along roads, and may have undersampled birds breeding elsewhere. Based on my maps for the main parts of the areas I studied at Saudade, I hypothesized the nesting locations for 28 additional nests of defilippii and 10 additional nests of militaris.

Some of these hypotheses are probably quite valid, for example, where I repeatedly flushed female defilippii from clumps of Stipa or where a pair were continually active in a territory entirely in a wheat field. Others, are less reliable.

The hypothetical sample is quite important since I deliberately avoided working in wheat fields to avoid damaging the valuable crops of my host. Thus I failed to find nests of most of the wheat-nesting defilippii which accounted for nearly 50% of the local population. This is discussed in more detail in the chapter on habitat preference. However, the new sample comparisons, yield a DMAX value of .40 (since perhaps no militaris nested in wheat) which exceeds the critical value (.32 at .05 level), indicating a significant difference.

TABLE 6. Summary of nests and contents examined during meadowlark studies.

Abbreviations: BB7E= 7km E of Bahia Blanca; S=Saudade; SV= Sierra Ventana
LP = La Pampa Buj=Bujama

Ac= found by accident mv= found after ♂ visit b = ♀ building
H = found on horseback fv= found after ♀ visit sy= systematic search
c = cowbird calls

E = eggs N = nestlings UNK = fate unknown
FL= Fledged AB = abandoned COL = collected
TR= Trampled PL = Plowed PR = Predated

PEZITES DEFILIPPII

PLACE	HOW FOUND	YEAR	DATE FOUND	MALE	FEMALE	CONTENTS Host	CONTENTS Cowbird	HABITAT & EXPOSURE	DISTANCE TO FENCE	VISIBILITY	FATE
BB7E	Ac	1970	23 Nov	WW/WW	WW/WW	4E	0	Stipa NW	160 m.	0	FL
BB7E	mv	1970	6 Dec	WW/WW	WW/WB	2E/2N	0	Stipa N	190	0	FL
BB7E	fv	1970	10 Dec	WW/RR	-----	1E/3N	0	Stipa NE	17	1	FL
BB7E	fv	1970	6 Dec	WW/RR	WW/RR	2E/3N	0	Stipa E	12	2	UNK
S	Ac	1970	14 Nov	BB/WW	BB/WW	5E	0	Stipa NW	150	0	AB
S	mv	1971	12 Nov	-----	-----	N	0	28"wheat N	100	1	FL
S	sy	1971	14 Nov	BB/WB	BB/BW	2E/N	0	Stipa NW	70	0	COL
S	mv	1971	14 Nov	-----	-----	E/3N	0	32"Wheat NW	22	1	COL
S	H	1971	27 Oct	A	-----	5E	0	15"Wheat up	25	1	UNK
BB7E	ac	1971	7 Nov	-----	-----	4E	0	16"Stipa up	80	1	TR
BB7E	ac	1971	7 Nov	GG/WW	GG/WW	4E	0	12"Stipa SE	40	0	AB
BB7E	b	1971	7 Nov	-----	-----	inc		8"grass SE	55	3	AB

PLACE	HOW FOUND	YEAR	DATE FOUND	MALE	FEMALE	CONTENTS Host	CONTENTS Cowbird	HABITAT & EXPOSURE		DISTANCE TO FENCE (meters)	VISIBILITY	FATE
						PEZITES MILITARIS	(con't)					
S	c	1971	11 Nov	GG/GG	WG/GG	1N	2N	Thistle	NE	0.1	0	COL
S	sy	1971	11 Nov	YY/YY	-----	4E	2E	Thistle	NE	0.5	1	COL
Hinojo	sy	1971	12 Nov	-----	-----	6E	0	Stipa	NW	1.5	0	UNK
S	sy	1971	14 Nov	YY/BB	YY/BB	3E	2E	Stipa	SE	0.1	1	COL
BB18w	ac	1970	14 Dec	♂2	-----	1E	2E	bush	N	1	0	UNK
(Buj=Bujama)						PEZITES BELLICOSA						
Bujama	fv	1972				4N	0	grass	W	4	0	FL
Bujama	fv	1972				1E 3N	0	Salicornia	SW	280.	0	UNK
Bujama	ac	1972				3E	0	grass	NW	10	0	AB
Bujama	fv	1972				4E	0	forb	W	6	1	UNK
Bujama	ac	1972				2E 2N	0	grass	W	2.	0	COL

SUMMARY STATISTICS BY SPECIES	CLUTCH SIZE <2	3	4	5	6	7+	Mean ± S.D.	DISTANCE TO FENCE[a]	VISIBILITY mean ± S.D
defilippii	0	1	6	4	0	0	4.27 ± .65	76.75 ± 61.0	.81 ± .98
militaris	10[b]	3	7	2	1	2	2.96 ± 2.16	1.79 ± 3.6	.80 ± .94
bellicosa	0	1	4	0	0	0	3.80 ± .40	60.40 ±109.8	.30 ± .40

a =distance to fence or other elevated object (e.g.,bush)
b =small militaris clutches are probabily result of egg removal by Shiny Cowbird.

PLACE	HOW FOUND	YEAR	DATE FOUND	MALE	FEMALE	CONTENTS Host	CONTENTS Cowbird	HABITAT & EXPOSURE		DISTANCE TO FENCE (meters)	VISIBILITY	FATE
						PEZITES	MILITARIS					
BB50n	Ac	1970	11 Nov	-----	-----	7E	2E	Stipa	NE	4	2	PL
S	sy	1970	14 Nov	GG/GG	GG/GG	4E	2E	Thistle	NE	1	0	AB
S	Ac	1970	14 Nov	GG/GG	GG/YG	2N	1E,1N	Stipa	N	0.5	0	AB
S	mv	1970	21 Nov	GG/WW	GG/WW	2N	1E,1N	Thistle	NW	0.1	0	UNK
BB7E	fv	1970	23 Nov	RR/RR	RR/RR	3N	2N	Stipa	W	2.5	0	TR
BB7E	mv	1970	23 Nov	RR/YY	RR/YY	0	2N	grass	SW	0.6	1	PR
BB30W	b	1970	22 Nov	BB/RR	BB/RR	5E	1E	Stipa	W	2	2	AB
BB7E	b	1970	22 Nov	-----	-----	5E	2E	bush	NW	1	1	COL
BB7E	mv	1970	23 Nov	-----	-----	2N	3N	Stipa	W	1	1	UNK
LaPampa	fv	1970	24 Nov	-----	-----	4N	0	Stipa	NE	3	1	UNK
S	mv	1970	16 Dec	GG/RR	-----	3E,1N	1N	Thistle	NE	0.3	1	PR
S	H	1971	26 Oct	YY/BB	YY/YB	4E	2E	Stipa	NE	0.1	0	UNK
Hinojo	c	1971	26 Oct	-----	-----	1E,1N	2N	bush	N	1.5	2	PR
S	sy	1971	27 Oct	YY/GG	YY/GG	2E	4E	Stipa	SE	0.1	0	FL
S	ac	1971	28 Oct	YY/BB	YY/BB	4E	2E	Stipa	SE	0.2	1	AB
S	H	1971	8 Nov	♂5	-----	3E	2E	grass	SW	0.3	0	AB
BB10n	mv	1971	8 Nov	-----	-----	0	2N	Stipa	NW	2.0	1	PR
BB7E	sy	1971	8 Nov	-----	-----	4E	1E	Stipa	N	0.5	1	TR
BB7E	b	1971	8 Nov	RR/BB	RR/BB	7E	2E	Stipa	SE	18.	4	AB
S	H	1971	10 Nov	YY/YY	-----	2E	1E	Thistle	W	3.0	0	PR

TABLE 7 Habitat comparisons for *defilippii* and *militaris* nest sites

A. K N O W N N E S T S

	STIPA #	STIPA C%	WHEAT #	WHEAT C%	GRASS #	GRASS C%	THISTLE #	THISTLE C%	BUSH #	BUSH C%	TOTAL	Cumulative Percent	K - S DMAX
DEFILIPPII	8	.67	3	.92	1	1.0	-	1.0	-	1.0	12	1.00	
MILITARIS	14	.56	0	.56	2	.64	6	.88	3	1.0	25	1.00	
% Difference		.11		.36		.36		.12		0.0			.36

B. H Y P O T H E T I C A L + K N O W N N E S T S

	STIPA #	STIPA C%	WHEAT #	WHEAT C%	GRASS #	GRASS C%	THISTLE #	THISTLE C%	BUSH #	BUSH C%	TOTAL	Cumulative Percent	K - S DMAX
DEFILIPPII	19	.48	17	.90	4	1.00	-	1.00	-	1.00	40	1.00	
MILITARIS	17	.49	1	.50	4	.62	9	.88	4	1.00	35	1.00	
% Difference		.01		.40		.38		.12		0.0			.40

Computation of Critical Value for Kolmogorov-Smirnoff D-Max test at .05 level.

DMAX Crit (.05) = $1.36\,[(n_1+n_2)/(n_1 n_2)]^{.5}$

Critical value of DMAX =.315 which is exceeded by the observed DMAX (=.40) hence the two distributions are different.

For known nests n_1=12 and n_2=35

DMAX Crit = .48 which is greater than observed DMAX. Hence the two samples are not appreciably different.

For hypothetical + known nests n_1=40 and n_2=35.

NEST SITE SELECTION

Although there is information available on habitat selection and nest placement in Sturnella (Gross in Bent 1958, Lanyon 1957, Roseberry and Klimstra 1970, and others) there is hardly any useful information on nest site selection. Since in almost all cases the selected nest site cannot be seen from a distance it will be most difficult to study this aspect of meadowlark breeding biology in the wild. My field observations shed no light on nest site selection. Since the female is exclusively responsible for nest building, one may presume that she also selects the nest site, but this remains to be demonstrated. I noted that many of the Pezites nests were located in depressions in the ground and pre-existing depressions may influence the ultimate site choice. Experimental modification of the ground surface in a male's territory, might shed light on this problem. Marples and Marples (1934) noted that Common Terns (Sterna Hirundo) frequently chose to nest in pre-existing depressions in the ground and although they provided no quantitative evidence supporting this impression it suggests an approach to the same problem in meadowlarks and other ground nesting species.

NEST BUILDING

Although I made no detailed observations on nest building, I have cursory field notes on the activities of five pairs of militaris who were judged to be building nests because the females were seen carrying nesting material. I never saw nest material carried by either Leistes or bellicosa, and only twice by defilippii. Marchant (1960:587) notes that despite the abundance of bellicosa at Ancon, Guayas, Ecuador, and despite finding 12 nests over a period of four years, he never saw the birds carrying nest material nor food for young.

One of the female defilippii carrying material was flushed from near the known nest site, and would not normally have been seen. The same may apply to the other defilippii in which case it would appear that militaris is more likely to be observed with nest material than the other red-breasted meadowlarks. Schroeder (1974) reported that he had an apparently easy time finding nests of S. neglecta by watching them carrying nest material. The other species presumably gather material close to the nest site and transport it on foot, or at least without making conspicuous flights.

Observation in 1971 on militaris pair 1 (male YY/YY; female unmarked) and pair 2 (male and female YY/BB at Saudade, indicate that females may make long trips (often exceeding 100 meters), carrying nest material, and one

male (YY/YY) was seen with nest material as well. Both of these females probably also gathered material near their nests since they were out of sight near the nest for periods of 2 and 3+ hours.

In the five pairs of militaris observed during nest building, the male often accompanied the female on flights to and from the nest site, and he either remained on the fence near the nest or joined her on the ground while she was (I presume) working at the nest. Observations on defilippii were more difficult since I only once observed nest building activity, but it seems likely that males do not remain close to their females during this period.

On two occasions militaris male YY/YY was seen carrying a piece of straw when he and the female flew toward the nest site. On the first instance he remained with the straw on the fence, while she was out of sight in the grass for about 20 minutes. She then flew away toward the woodlot, and he flew with her still carrying the straw. In the second instance both birds remained on the fence for about 15 minutes, while accompanied by a female Molothrus bonariensis. The male dropped his straw after about 12 minutes and began to give a soft "chup" note, while the female flew to the ground after 20 minutes, as if to resume building.

I conclude that although males may occasionally

carry nest material, this is probably not a contribution to nest building, and I have no evidence to suggest that male meadowlarks ever participate in nest construction. Examination of the literature reveals that Bendire (1895) believed that male meadowlarks assisted females in nest building. Saunders (1932) studied 12 pair of S. magna and found no evidence of males participating in nest building. Lanyon (1957) reviews other reports of males participating in nest construction, but indicates that the evidence is inadequate, and he never observed any such case. Kendeigh (1952:271) notes that in most species of Icteridae only the female actually builds the nest, although the male may accompany her (e.g., Williams 1952).

My observations on Saudade pair 1 (militaris male YY/YY) indicate that nest building lasted at least 5 days, probably no more than 7 days. My data are not adequate for any other nests. Saunders (1932) found 3-6 days typical for nest-building by S. magna and Lanyon (1957) reported 6 - 8 days as usual for first nests of both magna and neglecta, while subsequent nests might be completed in 4 days.

NESTING SEASON

The following summary includes a literature review.

B.M.N.H. = British Museum (Natural History)

W.F.V.Z. = Western Foundation for Vertebrate Zoology

Leistes m. militaris

TRINIDAD: March to mid-November (Herklots 1961, B.M.N.H.).

SURINAM: Eggs in Penard collection are dated January to November, and Haverschmidt found nests in March, October and November (Haverschmidt 1968).

Leistes m. superciliaris

ARGENTINA: Holland collected three clutches in October (B.M.N.H.)

Pezites militaris militaris

ARGENTINA: Clutches taken in Rio Negro in November and December and in Chubut in early January (W.F.V.Z.) Durnford found nest with eggs on 4 November (Durnford 1877). I found a family with full grown fledglings on the coast of Chubut on 4 November.

In 1970 and 1971 on the southern pampas there appeared to be no nesting activity prior

to about 20 October on the study area (1971) and nesting activity had declined markedly by mid-December (1970). Clutches have been collected in Buenos Aires Province from October to 11 January (B.M.N.H.).

CHILE: Nesting starts in September and continues to January (Johnson 1967). Seventeen clutches from Valparaiso, Santiago, Aconcagua and Aysen range from 18 September to 20 December, and one from Tierra del Fuego is dated November (W.F.V.Z.).

Pezites m. catamarcanus

TUCUMAN: Near Amaicha del Valle, Lanyon collected a pair with enlarged gonads 27 November 1970. By early January families with fully fledged young were observed in the area, there was little song, and little response to playback, suggesting that territoriality was at low ebb during my entire two week visit to the north-western provinces.

Pezites m. falklandicus

FALKLANDS: Abbott (1861) reported that it begins to breed the first week in October, and

Reynolds (cited by Humphrey et al 1970) found flying young by 2 November. Cawkill and Hamilton (1961) report some eggs laid as early as late August, and Pettingill (1973) gives August-December as the breeding season, and suggests that there may be more than one brood in some cases.

Pezites defilippii

BUENOS AIRES: Five clutches for October and 1 for December (B.M.N.H.). I found birds on territory and pairing in mid-October 1971 at Saudade and Bahia Blanca, and most breeding activity seemed to have subsided by the second week of December 1970.

LA PAMPA: A clutch taken in November. (B.M.N.H.).

Pezites bellicosa

ECUADOR: Clutches from Guayas, Ecuador from mid-March to mid-May (B.M.N.H.). Marchant (1960) found nests only after onset of rains (March to May) and this was the time when males were displaying.

PERU: Displaying is seen from June through September which corresponds to the cool wet period, and I found nests in August and September. On 2 October, fully feathered young were seen in the Lomas of Pachacamac, (30 km S.E. of Lima) but there was essentially no displaying, indicating that the nesting season is either earlier or briefer there.

Near Huanuco I found birds displaying in early September and was told by local farmers that they nest in November.

Pezites bellicosa

CHILE: Goodall et al (1957) report a nest with three fresh eggs, and families with full grown young on 2 November at Arica, and the clutch is in the W.F.V.Z. Johnson (1967) mentions other nests with large nestlings in early November.

The above mentioned data are not exhaustive (there being, for example no data from Brazil, Venezuela or Colombia), but indicate that in Argentina and Chile, the breeding season is mainly in the Austral spring and summer, while further north it is apparently governed mainly by available moisture, occuring, for example in

the Austral winter, which happens to be the wet season on the coast of Peru. An interesting anomaly is the winter nesting which occurs in the Falklands and apparently also on the coast of southern Argentina. Whether this is related to moisture or some other favorable climatic feature, or serves to guarantee a longer breeding season, remains to be determined. There is, as yet, no evidence of August-September breeding activity for Pezites on the pampas.

NEST STRUCTURE

Many ground nesting birds build domed nests regularly or occasionally. Lanyon (1957) reported on 64 magna and 71 neglecta nests, finding no difference in construction between the two species. For both there was considerable variation from open nests without runways to completely roofed nests or nests with elaborate runways roofed over by surrounding vegetation. Roseberry and Klimstra (1970) observed 459 nests of S. magna, which were virtually always in a bowl-like depression from 1-3" deep (4-4.5" in diameter). The nests were usually covered by a canopy of stems bent over the nest (extrinsic covering), and noted seasonal variability, with early nests having less of a canopy. The nests typically had an outershell of coarse grasses and an inner lining of fine grasses. For 220 nests in

use they found 17.3% without canopy, 44.5% with partial canopy, and 38.2% with full canopy. Schroeder (1974) reported that of 7 nests of neglecta 3 had a complete canopy and 4 a partial canopy. Bryant (1914) reported a neglecta nest with a tunnel 5' long.

For bellicosa, Marchant (1960) reported that in western Ecuador nests were half-domed, but did not indicate whether the dome was intrinsic or extrinsic. He noted that nests were often loosly constructed so that eggs slipped through into the body of the nest. These findings differ from my own experience (see below). Goodall (1951) mentions that in Chile, nests of bellicosa were usually half-domed and Johnson (1967) implies that these domes are extrinsic.

Nests of militaris are described as cups Grant (1911), Abbott (1861), Pettingill (1973). Johnson (1967) indicates that nests of militaris are semi-domed, but the only one of his nest record cards (W.F.V.Z.) which describes the nest mentions a cup nest. Reynolds (cited by Humphrey et al 1970) reported a nest with a long tunnel-like entrance under an overhanging canopy. Pettingill (1973) notes that the nest is usually sheltered by the overhanging tussock grass, and mentions one nest with a runway.

I have found no description of defilippii nests in the literature. Short's (1968) general statement about

the domed or semi-domed nests of meadowlarks has been corrected by Haverschmidt (1970) for L. m. militaris. Nests of this form reported by Herklots (1961) and by Haverschmidt (1968, 1970) were characteristically open-topped, sometimes with an extrinsic tunnel through the vegetation. Pereyra (1933) mentions finding nests of superciliaris but gives no description of them. Dabbene (1918) illustrates a cup-shaped nest.

Observations

I found 25 nests (24 completed) of militaris, 12 nests (11 completed) of defilippii in Argentina and five nests of bellicosa in Peru. For all three species, the nests were usually open cups, although often the cup was tilted with the rear wall higher and thicker than the front, which was sometimes flattened flush with the ground. One nest of militaris had what I would consider a partial dome covering about 1/3 of the nest, and this was intrinsic - an upward extension of the rear wall. Most of the others were covered by the clump of vegetation in which they were placed, but the vegetation was not altered in any way. Two nests in Stipa had modifications which might be considered an extrinsic dome, and three had modifications which would be clearly recognized as a runway, although in only one of these was the runway at all roofed.

All the defilippii nests were cups, although almost all appeared asymmetrical, with the rear wall slightly higher than the front wall. Only one of these had sufficient extension upward to be classified as a dome, and this wall barely extended over the nest (perhaps a 1/5 dome). Four of the nests were in Stipa, and one of these had a slight indication of a runway. None of the nests in wheat had any indication of either dome, canopy, or runway.

One of the bellicosa nests had a 1/3 intrinsic dome, and another had the rear wall substantially higher and thicker than the front. The remaining three were cups, although all were well-covered by the vegetation. One nest in grass and the one nest in Salicornia had well-defined runways.

There is clearly substantial intraspecific variation in nest structure for the three species of Pezites, even at one locality.

I collected four nests of militaris, four of defilippii, and one of bellicosa. All were made of grass, and differed only in that defilippii nests, even the bulky one, had little or no coarse grass or outer shell. The weights, dimensions, locations, and species are given for the nests in Table 8. The mean weight of material 19.65±10.62 grams for 4 defilippii nests was not significantly less than 4 militaris nests, (26.5±15.4;

p=.171). The one bellicosa nest was typical of the five found, but the sample is too small for any generalization. Aside from the variation in the amount of material and compactness of the militaris and defilippii nests, the only pattern that emerges is that for both species, nests at Saudade were somewhat better woven and larger than those from Bahia Blanca. The latter nests were all found in a field of dry and rather sparse bunch grass so the choice of material was more limited, but the reality and significance of any such inter-habitat difference remains to be determined.

NEST ORIENTATION

The orientation of the nest opening has been examined for Sturnella by Saunders (1932), Lanyon (1957), and Roseberry and Klimstra (1970). Saunder's results do not differ significantly from random placement, while in the other studies there was a preponderance of nests facing north, northeast and east. Lanyon (1957) indicated that from April to July, prevailing winds in Wisconsin were south, southwest and west, and consequently vegetation was depressed toward the northeast quadrant, the direction in which most nests faced. He suggested that the nest would face the depressed vegetation with its back against upright vegetation. Roseberry and Klimstra (1970) found also a relation

TABLE 8 Nest structure for *Pezites* species

SPECIES	LOCATION	WEIGHT (grams)	INTERNAL DIMENSIONS (cm.)	EXTERNAL DIMENSIONS (cm.)	QUALITY OF WEAVE
BELLICOSA	Bujama	26.6	9x8x3	18x17x7	3+
DEFILIPPII	Saudade	26.4	8x11x3	13x16x5	3+
DEFILIPPII	Saudade	31.0	7x10x3	17x13x5	3+
DEFILIPPII	Bahia Blanca	10.4	-------	10x14x?	1+
DEFILIPPII	Bahia Blanca	10.8	-------	10x13x5	2+
MILITARIS	Saudade	31.5	10x11x3	16x21x7	3+
MILITARIS	Saudade	11.5	-------	14x13x5	2+
MILITARIS	Bahia Blanca	13.5	-------	14x15x4	1+
MILITARIS	Saudade	49.5	9x6x3	16x13x6	3+

(bits of mud in outer shell may be adventitious)

Weight	Mean	S.D.
DEFILIPPII	19.65	± 10.62
MILITARIS	26.50	± 15.39

(Mann-Whitney U = 4; p=.171)

between nest orientation and slope, with nests tending to face downslope, but even nests on slopes showed a tendency to face the northeast quadrant.

My results, albeit based on a small sample, are shown in Table 9, and the direction of prevailing winds for the southern pampas is given in Table 10. Nests of militaris faced mainly northeast while prevailing winds on the pampas were mainly northwest and north, particularly in October. In view of the fact that on the pampas calm prevails only 1% of the time (Verettoni 1964) one might have predicted a greater response of the birds to winds, with nests oriented south or southeastward, (see fig. 11). By December, however, these directions become the windy quarter, and also the occasional storms that strike in the spring months often come from that quarter as well. Thus the northeastward orientation of militaris nests may be seen as a compromise, should the trend be borne out by more extensive data.

Detailed climatic data are provided by Verettoni (1964) for the Bahia Blanca area. She provides a monthly breakdown of the wind direction in the form of percent-time for each direction. The 1.0% average by month for "calm" can be disregarded. I reproduce here a condensed version (see Table 10) for the months October, November, and December, during which nesting

TABLE 9 Nest orientation for meadowlarks on the pampas of Buenos Aires and La Pampa. (* $p<.05$ ** $p<.01$)[a]

DIRECTION	DEFILIPPII		MILITARIS		TOTAL	
# of NESTS	10		25			
	EX	OBS	EX	OBS	EX	OBS
North	1.25	2	3.12	4	4.37	6
Northeast	1.25	1	3.12	7	4.37	8
East	1.25	1	3.12	0	4.37	1
Southeast	1.25	2	3.12	4	4.37	6
South	1.25	0	3.12	0	4.37	0
Southwest	1.25	0	3.12	3	4.37	3
West	1.25	0	3.12	3	4.37	3
Northwest	1.25	4	3.12	4	4.37	8
G STATISTIC	12.20		16.81*		19.49**	
W-NW-N-NE	5.0	7	12.5	18	17.5	25
E-SE-S-SW	5.0	3	12.5	7	17.5	10
G STATISTIC	1.65		5.01*		6.65**	
NE-N-NE-E	5.0	8	12.5	15	17.5	23
SE-S-SW-W	5.0	2	12.5	10	17.5	12
G STATISTIC	3.85*		1.01		3.52	

a= Probability that orientation is evenly distributed for all compass directions (goodness of fit test).

TABLE 10 Wind direction for the Bahia Blanca Area, Buenos Aires Province, Argentina. October, November, December data extracted from Verettoni (1964). Figures are % of time.

MONTH	NORTHWEST & NORTH	NORTHEAST & EAST	SOUTHEAST & SOUTH	SOUTHWEST & WEST	PREDOMINANT DIRECTION
OCT	37.7	14.9	24.2	22.5	north
NOV	31.0	19.4	27.3	21.7	south
DEC	27.4	26.4	29.1	17.2	northwest
Average % of time	32.23	20.25	26.86	20.50	

occurs. The commonest wind directions for these months are north in October, south in November, and east in December. For the three months, I combined NW-N vs. NE-E vs. SE-S vs. SE-W and found a strong predominance of northwesterly and north winds during the breeding season.

NEST CONCEALMENT AND NEST FINDING

Many authors have commented that nests of the meadowlarks are well concealed. For Sturnella magna Roseberry and Klimstra (1970) classified nests as excellently concealed (vegetation had to be parted) = 19.1%; moderately concealed (contents visible from overhead) = 47.8%, and poorly concealed (nests visible from several yards away) = 32%. Tyler (1913) reported an unusual nest in which the incubating meadowlark was visible at a distance of over 100 feet. Although it seems likely that concealment should be related to nest success, Roseberry and Klimstra (1970) found no association between degree of concealment and success. Nice (1964) did, however, report that well-concealed Song Sparrow (Melospiza melodia) nests were more successful than poorly concealed ones. However, as discussed elsewhere (Chapter 8), this may be a sampling artifact since nests found by an observer may be those most likely to be found by a predator.

In my nest-finding experience I was impressed with the difficulty in locating nests, even when the site had been approximately determined. This held for all three species of Pezites. Literature reports on militaris nests usually do not emphasize concealment (for example no mention in papers on falklandicus, e.g., Cawkill and Hamilton 1961; Pettingill 1973). However, Johnson (1967) stressed that militaris nests are well-hidden, and it seems likely that the difference involves interpretation, rather than real differences in the birds or habitat. Marchant (1960) did mention that nests of bellicosa were very well-concealed. Serie and Smyth (1923) comment on the concealment of defilippii nests.

Superlative comments on concealment are reserved for Leistes (e.g., Dabbene 1918). Pereyra (1923) emphasizes that nests of superciliaris are well hidden, but does not say the same for nests of pipits (Anthus spp.). Hudson (1920) states, "the nest is...so cunningly concealed that it is difficult to find", a statement he rarely makes. Venturi (Hartert and Venturi 1909) states that the nest is one of the most difficult to find of all nests, which he attributes in part to the surreptitious behavior of the female.

For each meadowlark nest I found, I categorized its concealment, hoping to relate it ultimately to nest success. Although I did not obtain follow-up information

on some of the nests, I made a tentative evaluation based on nests of known fate.

The subjective concealment of nests of militaris and defilippii is compared in Table 11. Nests were rated on a scale of 0 - 4 as follows:

0. From directly above nest or at 1 meter, nest is invisible.
1. From directly above nest or at 1 meter, nest is slightly visible.
2. From directly above nest or at 1 meter, nest is half visible.
3. From directly above or at 1 meter, nest is fully visible.
4. Nest is at least partly visible from 5 or more meters.

For each value on the scale, the number of nests in each vegetation type for each species is listed. A mean concealment value is given for each habitat but the samples are too small to warrant comparison. I used Mann-Whitney U tests to compare concealment in Stipa and wheat for each species, overall concealment for both species, and concealment for militaris in two years. The latter was attempted to determine whether there might be a between year change in my scoring of nests. The last two comparisons were also made with a parametric t-test, and the between-species comparison with a Median

test. The probabilities given in the table are the two-tailed probabilities that the samples compared are basically the same. In most cases, the probabilities are high enough to indicate that the samples are probably significantly similar rather than different.

The role of concealment as an anti-parasite or anti-predator strategy was considered. However, the nearly universal Cowbird parasitism on militaris indicates that concealment of nest site itself is not enough to prevent parasitism. Data on predation is confined to 5 militaris nests (see Table 12). If nests collected, abandoned, trampled and plowed, are removed from the sample, and nests listed as "unknown" are considered successful, one is left with 7 successful nests (5 in the 0-visibility category) and 5 predated nests (only 1 in the 0-visibility category). Although suggestive, the sample is so small, that there is no significant difference (Fisher Exact probability, 2-tailed = .242).

To estimate the possible significance of the observed difference, I tested a hypothetical example, where the same proportions held but the sample sizes were simply doubled to 14 and 10. In such a case the observed proportions were significantly different at the .05 level. Thus it is possible that nests well-concealed from humans are also well-concealed from predators as

TABLE 11. Nest concealment for 25 militaris and 12 defilippii nests in different vegetation types (see text for details of 0-4 visibility scale).

SCALE	DEFILIPPII			Species Totals		MILITARIS				Yearly Comparison	
	Stipa	Wheat Grass		Total defilippii	Total militaris	Stipa	Thistle	Grass	Bush	1970	1971
0	5	0	0	5	11	5	4	1	1	4	7
1	2	3	0	5	10	6	2	1	1	5	5
2	1	0	0	1	3	2	0	0	1	2	1
3	0	0	1	1	0	0	0	0	0	0	0
4	0	0	0	0	1	1	0	0	0	0	1
TOTALS	8	3	1	12	25	14	6	2	3	11	14
Ave. Score	.5	1.0	3.0	.83±.94	.80±.96	1.	.33	.5	1.0	.818	.785
MWUp=	.22			.87		.19				.58	

t-test (t=.1,p>.90)

Median Test (p > .90)

MWUp is two-tailed probability in Mann Whitney test

TABLE 12 Fate of nests of *militaris* related to concealment. FEP2 = Fisher Exact Probability (2-tailed)

FATE CATEGORY	CONCEALMENT VALUE				TOTAL	MEAN VALUE
	0	1	2	4		
Fledged	1	-	-	-	1	0
Unknown (?fledged)	4	2	-	-	6	.67
Collected	1	3	-	-	4	.75
Abandoned	3	1	1	1	6	1.17
Plowed or trampled	1	1	1	-	3	1.0
Predation	1	3	1	-	5	1.0

COMBINED CATEGORIES	CONCEALMENT	
	0	>0
Fledged or unknown	5	2
Collected/Abandoned Plowed/Trampled	5	8
Predation	1	4

CONTINGENCY TABLE COMPARISONS			COMPARISONS WITH DOUBLED SAMPLE SIZES	
	0	>0	0	>0
Fledged or unknown	5	2	10	4
Predation	1	4	2	8
FEP2=.242			FEP2 <.05	
Fledged or unknown	5	2		
All other	6	12		
FEP2 <.01				

Nice (1964) suggested. However, the crucial test would be to determine predation rates on those nests that are so well hidden that humans do not find them. This is not simply a conundrum, since it may be the human's presence at the nest which exposes it to predation.

I did not keep time records of my own nest finding activities, and without such a time-energy accounting, the data on how nests were found is of limited value. However, from the data in Table 6 several important points can be seen. Most nests were found by accident---that is incubating birds were flushed as I walked close to their nests. Systematic search proved quite useful for militaris, but although I spent much time in systematic attempts to find defilippii nests, only one was discovered in this way. The difference is even greater, because 3 of the 4 militaris nests discovered by horseback were found in systematic searches, while the remaining nest and the defilippii nest discovered by horse, were found accidentally. If these data are compared in a 2 x 2 contingency test the interspecies difference is not quite significant (FEP2=.1190), but is suggestive.

Although data on feeding visits by males and females at various nests of militaris and defilippii indicate that females make 2-5 times as many visits to a nest as their mates, I found 8 nests immediately after a male

visit compared with 4 after female visits. Based on my record of approximately 100 female visits and about 30 male visits to these nests, these data would indicate an inter-sex difference ($X^2=9.5$; $p < .005$). This difference is examined in more detail in a subsequent section.

CLUTCH SIZE

Data from the literature and from my own observations are summarized in Table 13. The data on clutch size are difficult to interpret. From museum specimens it is often impossible to tell whether the clutch was complete when obtained (oologists strongly prefer unincubated eggs and might collect prior to completion) or whether the complete clutch was taken. Literature references frequently give only one value, presumably the mode. It is noteworthy that the lowest clutch sizes reported in Table 12 are based on B.M.N.H. collections, and one should not believe that either militaris or defilippii have local populations with mean clutch sizes of less than 3.

In my own field experience with militaris I found that nests parasitized by cowbirds had small complements of meadowlark eggs, presumably because the parasite destroys or removes host eggs (a feature described by most writers, e.g., Hudson 1920; Hoy and Ottow 1964).

TABLE 13. Clutch size data for meadowlarks (n = number of clutches)

LOCATION	n	RANGE	MEAN ± S.D.	MODE	CITATION
North America	--	3 - 7			
			STURNELLA MAGNA		
North America	--	3 - 7		5	Gross (1958)
New York	23		4.57 ± .15		Saunders (1932)
Wisconsin	101	2 - 6	4.81 ± .16		Lanyon (1957)
			STURNELLA NEGLECTA		
North America	--	3 - 7		5	Gross (1958)
Wisconsin	41	3 - 6	4.83 ± .13		Lanyon (1957)
			LEISTES MILITARIS MILITARIS		
Trinidad		2 - 4[p]			Herklots (1961),ffrench (1974)
Guyana	1	5			A.M.N.H.
Surinam		2 - 4		3	Haverschmidt (1968)

Table 13 (con't) Meadowlark Clutch Sizes

LOCATION	n	RANGE	MEAN ± S.D.	MODE	CITATION
		PEZITES	MILITARIS		
Chile	24	2 - 4	3.09 ± .70		W.F.V.Z.
Tierra d Fuego	2	3	3.0		Humphrey et al (1970)
Chile	9	2 - 4	2.44 ± .53		B.M.N.H.
Argentina	5	4 - 6	5.00 ± .70		B.M.N.H.
Argentina	55	1 - 4	2.60 ±1.14		B.M.N.H. (Holland collection)
Argentina	1	5	5.00		Serie & Smyth (1923)
Falklands	11	1 - 5	2.8; ±1.32		B.M.N.H.
Falklands				3	Abbott (1861)
Falklands				4	Cawkill & Hamilton (1961)
Falklands	5	3 - 4	3.20 ± .44		Pettingill (1973)
Argentina	11	3 - 7[p]	4.72 ±1.42		Gochfeld[cc]
Argentina[c]	25	2 - 9	5.08 ±1.78		Gochfeld[c]

p includes parasitized clutches

c includes meadowlark eggs and young PLUS cowbird eggs and young.

cc This sample included in next sample as well.

Table 13 (con't) Meadowlark Clutch Sizes

LOCATION	n	RANGE	MEAN ± S.D.	MODE	CITATION
		LEISTES MILITARIS SUPERCILIARIS			
Argentina	5	1 - 4	2.40 ±1.14		B.M.N.H.
Buenos Aires		2^{p}			Dabbene (1918)
La Pampa		2^{p}			Pereyra (1933)
		PEZITES BELLICOSA			
Ecuador	9	3 - 5	4.11 ± .60		Marchant (1960)
Chile	--	3 - 4		3	Goodall et al (1957)
Peru	5	3 - 4	3.80 ± .45		Gochfeld
		PEZITES DEFILIPPII			
Argentina	5	1 - 4^{p}	2.60 ±1.14		B.M.N.H.
Argentina	2	4	4.0		Smyth (1928)
Argentina	1	5	5.0		Serie & Smyth (1923)
Buenos Aires	11	3 - 5	4.27 ± .65		Gochfeld

However, there is no evidence that there is a 1:1 relation between host eggs removed and parasite eggs laid, and the mean value for (host + cowbird) clutch in my sample is 5.08, higher than any other reported values.

If one asks whether there is a north-south cline in egg clutch size, as has been reported in Europe for several species the meadowlarks would be suitable test species. For example, militaris nests from northern Argentina (22°S) to Tierra del Fuego (48°S). Unfortunately the data presently available are too meagre to even begin exploring this.

DESCRIPTIONS OF EGGS

In general meadowlark eggs are whitish, speckled with some shade of brownish or purplish, with the markings usually heavier at the large end. Bendire (1895) notes that eggs of magna vary considerably both in shape and size, and notes that the ground color is usually pure white, occasionally with pinkish or green tinge. He continues with description of the variation in color and distribution of the markings. Bent (1958) notes that eggs of neglecta are "practically indistinguishable" from those of magna.

The literature descriptions of egg colorations for Pezites and Leistes are essentially the same. Eggs of L. m. militaris are said to have a deep cream ground

color (Herklots 1961) or pale bluish ground color (Haverschmidt 1968), and both authors discuss similar markings. Smyth (1928) describes defilippii eggs in the same terms, mentioning a rosy white ground color, while Serie and Smyth (1923) call the eggs white.

Eggs of militaris are considered buff to mouse grey (Goodall et al 1957) or dirty white (Cawkill and Hamilton 1961) or off-white (Pettingill 1973).

My own findings based on eggs I examined either in the field or in the British Museum collection, emphasize the overall similarity in the eggs of all meadowlarks. Ground color variation turns out to be subtle indeed, while the considerable variability in the markings from egg to egg, exists with no apparent cinsistent pattern between species.

I also examined several eggs of the Shiny Cowbird (identified by slightly smaller size and eventual production of cowbirds) which were found in nests of militaris. Cowbird eggs varied from nearly pure white with very faint speckling, to almost perfect "mimics" of the meadowlark eggs.

I noted also that eggs of Zonotrichia capensis and Sicalis luteola were also similar in pattern and general coloration to those of Pezites and the spotted cowbird eggs, would probably have appeared mimetic in the nest of these species.

TABLE 14. Summary of egg measurement data for meadowlarks. (n = eggs in sample)

SPECIES	LOCATION	n	AVERAGE	MINIMUM	MAXIMUM	CITATION
magna	N.America	201	27.8 x 20.3	21.6 x 18.3	30.8 x 22.6	Bendire (1895)
magna	New York	95	(weight 5.4-7.7 gm ave = 6.6 gm)			Saunders (1932)
neglecta	N.America	206	28.3 x 20.6	25.7 x 20.1	30.8 x 21.8	Bendire (1895)
militaris	Chile	15	29.5 x 20.6			Goodall et al (1957)
militaris	Falkland	2	29.0 x 21.0	(both identical)		Cawkill & Hamilton (1961)
militaris	pampas	11 S.D.	27.2 x 19.6 .45 .31			Gochfeld
defilippii	Argentina	8	27.0 x 19.0	23. x 17.5	28.5 x 20.0	Smyth (1928) Serie & Smyth (1923)
defilippii	pampas	7 S.D.	25.8 x 18.3 .42 .64			Gochfeld
bellicosa	Chile	3	25.7 x 19.0			Goodall et al (1957)
bellicosa	Peru	9 S.D.	25.1 x 18.4 .66 .41			Gochfeld
L.militaris	Trinidad	10	23.6 x 17.4			Herklots (1961) ffrench (1974)
L.militaris	Surinam		23.2 x 17.4	(weight ave. 4gm)		Haverschmidt (1968)
L.m.superciliaris	Argentina			22 16.5	25 18	Hartert & Venturi (1909)

NEST FATE AND PRODUCTIVITY

I interfered significantly with most of the nests I observed, either by examining the contents frequently, by attempting to trap the females, or by collecting the contents. Consequently I make no attempt to estimate productivity. Nonetheless the fate of the nests I did find is of some interest. Causes of nest loss are indicated in Table 6, and several points can be stressed. Ten nests (23.8% were abandoned, all in the egg phase. Even severe interference by trapping during nestling phase did not cause any definite desertion, although in at least one case, it did expose a nest to predation. Only 1 of the militaris nests was known to fledge young, which may turn out to be significantly lower than the rate for defilippii. Possibly this is related to the presence of cowbirds. Although 13 of 22 militaris nests with cowbirds were found during the egg phase, 4 of 5 lost to predation were lost in the nestling phase. Cowbird nestlings beg noisily and vigorously and may expose nests to predators (Hudson 1920, Gochfeld M.S.3). Moreover, the flight of adults to and from the nest on feeding trips can also attract predators (as it does ornithologists), and the frequency of such flights may be increased in response to the begging of noisy cowbird nestlings.

NEST AND NESTLING: SUMMARY

Although incomplete in many respects, my data on nest placement, nest construction and other aspects of nesting are compared with published information for the meadowlarks. There is a clear overall similarity in most aspects of nesting between *Pezites* and *Sturnella*. Data on *Leistes* are scant, but show similarities to the other forms. Although the findings are consistent with an interpretation of close relationships among all of these forms, many of the features are common to ground nesting species in general.

The following points are made:

1. *militaris* and *defilippii* differ in nest site selection, the latter nesting more often in wheat or grass away from elevated perches. These differences are amplified in the chapter on brood parasitism.

2. As with *Sturnella* male *Pezites* do not build the nest, although *militaris* males frequently accompany females and may even carry nest material. Such nest material probably does not contribute to nest construction, just as in some cases (see Chapter 7) a male may carry food to the vicinity of the nest without actually feeding the young.

3. Female militaris are occasionally seen transporting nest material, while this is rarely true for the other species. The relation between such conspicuous behavior and the frequency of cowbird parasitism is considered in Chapter 8.

4. Nesting seasons in temperate zones are primarily related to the warm season, while on the arid Peruvian coast, the moist winter season is favored for nesting by bellicosa. An anomaly is the occurrence of late winter nesting by militaris on the Patagonian coast and in the Falklands, which may relate to available moisture.

5. Nests of bellicosa tend to be partly domes, but there is considerable variability. Nests of defilippii and militaris rarely have any semblance of an intrinsic dome, although they may be covered by overhanging vegetation.

6. No clear relationship between prevailing wind and nest-orientation is apparent, since prevailing winds shift during the nesting season. The sample was not large enough to reveal intra-season changes in nest orientation. The prevailing orientation can be seen as a compromise between the preponderance of winds from the northwest and the occasional storms from the south.

7. Meadowlark nests are generally very well-concealed. No difference could be detected in the subjective evaluation of concealment of militaris and defilippii nests.

8. During the incubation phase, female meadowlarks are likely to abandon the nest if disturbed, while this is seldom true during the nestling phase. Human disturbance by collecting or trapping was important in my sample. Trampling by livestock and destruction by mowing machines, as well as predation figured in my sample as in studies of North American meadowlarks.

9. Data on clutch size proved inadequate for testing geographical variation, although among South Temperate species militaris would be appropriate for such a study.

10. In general appearance the eggs of all meadowlarks are similar, the pattern being that common to many ground nesting birds. Some eggs of Molothrus appeared very similar to these meadowlark eggs and are considered mimetic as opposed to the nearly pure white cowbird eggs which may occur in the same nests.

11. Data on productivity were not adequate for interpretation, except that for militaris more nests were lost in the nestling than in the egg phase.

CHAPTER 7 INCUBATION AND NESTLING PERIOD

THE INCUBATION PERIOD

Incubation behavior and to a lesser extent physiology have been widely studied, and several reviews and syntheses have been published (e.g. Kendeigh 1952; Baerends and Drent 1970). I devoted scant attention to studying incubation behavior of the meadowlarks, although I did attempt to find nests. In many cases I interfered signigicantly with the progress of nesting, although in a few cases -- mainly during the nestling period -- I did spend time watching nests.

Kendeigh (1952:271) stated that in the Icteridae incubation exclusively by the female is the rule, and that lacking brood patches, males could not truly incubate (Kendeigh 1952:160). For all three species of Pezites, all birds flushed from the nest were females, nor did I ever observe a situation where the female was visible but the male was out of sight, which would be consistent with incubation by the male. The opposite was the rule. Lanyon (1957) mentioned several reports which he doubted, where male Sturnella were reputed to incubate. He noted only females incubating. Although I obtained no information on Leistes, and have found no discussion of it in the literature, there is no reason to suppose that males of that species incubate.

Although courtship feeding by the male at the nest occurs in some Icterids (Kendeigh 1952:271), I did not observe it at 16 nests where I made some observations (approximately 15 hrs.).

Incubation Constancy: I obtained only general information on nest attentiveness. Twice I flushed female P. militaris from nests where the clutch was later proven to be incomplete. Both times were in the early morning. I subsequently checked the nests twice daily, and did not find the females on the nests again until the clutch had been completed. In both cases, fortunately the nests were not abandoned. These limited findings suggest that incubation in that species, probably does not begin until the clutch is complete. The presence of the female on the nest during the laying-period, may be due to her actually laying an egg about the time of my visit.

Nest Abandonment: Lanyon (pers. comm.) informed me that meadowlarks are very likely to abandon their nests if they are discovered during the incubation period, and that the likelihood of abandonment declines as hatching period approaches. Marchant (1960) made similar observations for P. bellicosa, and I also found several nests abandoned early during incubation. One nest abandoned late in incubation and another early in

hatching, may have been due to my placing traps over these nests, and in one case almost catching the female when she came to brood. Baerrends (1970) and Beer (1962) have noted an increase in the incubation tendency or drive of Herring and Black-headed Gulls (L. argentatus and L. ridibundus), as the hatching time approaches, and I have found the same true in Common Terns. It is probably a general rule for birds.

There is good reason for such a rule to exist. Once a nest has been discovered by a potential predator, the adult bird benefits by abandoning the site and trying again elsewhere. However, as the amount of time and energy resources invested in laying and incubating increase, the cost of abandonment may exceed the benefits, so that it becomes advantageous for the bird to "gamble" to see whether the disturbance is followed by predation. Although it would involve little conditioning for a vertebrate predator to associate a flushed bird with a nest full of food, the bird itself may find it more difficult to "determine" whether the source of the disturbance is actually a potential predator.

The "decision" to continue attending a nest is apparently determined by underlying processes rather than by "decision-making", since birds show an increasing tendency to continue attending nests that are manipulated late in incubation or during the nestling phase despite

manipulation that would have caused them to abandon earlier in the season (Gochfeld unpublished, Beer 1962, 1963). Passerine birds have received relatively less attention in this respect, except with regard to abandoning nests that contain parasitic eggs.

Activities of the Male: I noted a decrease in song output for several individuals during the incubation and nesting period. This again is a general rule among songbirds. The slight resurgence of singing after the young fledge is also consistent with other reports (Lanyon 1957).

Length of Incubation: My data on the length of incubation is actually restricted to four eggs of P. militaris in three nests, and is accurate only to within 24 hours. The lengths are 13.5, 13.5, 14 and 14.5, the first and last eggs being in the same nest, one which I disturbed frequently late in the incubation period. This period is defined here as the time from the laying of the last egg to the hatching of the last egg that hatches, which was simplified in the present cases since either I or perhaps a cowbird removed most of the meadowlark eggs. Saunders (1932) and Lanyon (1957) found 13-14 days to be typical for incubation in Sturnella, with prolongation occuring in exceptional cases.

THE NESTLING PERIOD

Brooding Behavior: As during the incubation period, I made few direct observations of brooding behavior. The females of all three species spent much time brooding the young during the first two or three days of life (as noted by Saunders 1932) particularly on cool mornings or evenings. Older broods received less brooding, a fact noted also by others, for example by Willson (1966) for Xanthocephalus where the total time spent brooding the young during the first two days of life approached 45%. By the time the young were fully feathered (>7 or 8 days) the female often did not brood at all. During the first week of life, when daytime brooding declined, the females were usually on the nest at night (and I was able to trap them with a searchlight and handnet). Three defilippii nests and one militaris nest were checked during the second week after hatching on four and three nights respectively. For each species a female was present on only one night check.

The above generalizations, and my observations that male Pezites were not found brooding the young, were based on sixteen nests where my disturbance was small. Incidental to observing the differential feeding behavior of males and females at nests with young, I collected data on the average stay of parents at the nest during

feeding sessions. A "nest stay" was recorded from the time the parent disappeared in the vegetation until it reappeared. Except for the time taken walking to and from the nest, which was probably greater for females than for males as discussed below, the long wait times of females may be related to brooding on these visits. Other observations on the frequency, intervals, and "wait times" of feeding visits are also discussed below. Table 15 shows the average "nest stays" for males and females at several nests.

Comparisons of the species totals for the three females by t-test and Mann-Whitney U revealed no species differences (all $p>.10$).

However, comparisons of nests by different nestling-ages revealed differences as shown in Table 16.

Although it cannot presently be determined what proportion of the "nest stay" involves surreptitious approach, feeding of young, and brooding, the results are consistent with relatively frequent brooding visits by the female, and a decline in frequency as the young mature.

TABLE 15. "Nest stay" times and possible relevance to brooding behavior at nine meadowlark nests.

SPECIES	NEST #	AGE OF YOUNG (days)	FEMALE VISITS #	Mean stay	MALE VISITS #	Ave. Stay	MANN-WHITNEY U	z	p<	
miiitaris	M1	0-3	9	7.33±4.63	1	1.0	20	1.5	.07	
militaris	M2	0-3	12	7.75±9.27	2	1	7	.88	.19	
militaris	M4	5-7	12	2.16±1.02	5	1.40± .54	34	.44	.33	t=1.77
species total			33	5.42±6.59	8	1.25± .46	188	1.89	.03	df= 39
bellicosa	B2	0-3	9	9.66±6.81	none					
bellicosa	B1	3-5	11	2.90±1.37	2	1.5	17	1.91	.03	
bellicosa	B6*	> 7	6	1.83± .75	none					
species total			26	5.00±5.28	2	1.5	17	1.91	.03	t not done
defilippii	D3	0-3d	15	4.13±3.42	2	1	26	1.64	.051	
defilippii	D7	0-3d	6	4.17±3.82	none					
defilippii	D6	3-5	9	2.22± .97	5	1.60± .55	23	.07	.48	t not
species total			30	3.57±3.04	7	1.43± .53	116	1.56	.06	done
Three species total			89	4.67±5.24	17	1.35± .49	817	2.82	.0025	t=2.6 df=104

*Nest not found at this site despite several attempts over 1 week period

TABLE 16 Comparison of "stay-time" by nestling age for all species.

AGE PERIOD	No. of Nests	No. of Visits	Mean	St. Dev.
0-3 days	5	51	6.41	6.33
3-5 days	2	20	2.60	1.23
5-7 days	2	18	2.06	0.94

Mann-Whitney U Test Results

Periods	U	T	Z	p =
0-3 vs 3-5 days	590	688	1.04	.1492
3-5 vs 5-7 days	178	338	.0018	.50
0-3 vs 5-7 days	601	701	1.99	.0233*

*Significant if $p < .05$

ROLE OF SEXES IN PARENTAL CARE

Although male meadowlarks play no part in nest-building, incubation or brooding, they may feed their young to a varying degree. Saunders (1932) and Lanyon (1957) noted that both sexes of Sturnella feed the young, the female more often than the male. Williams (1952) found that male Brewer's Blackbirds (Euphagus cyanocephalus) feed the young regularly, and may do most of the feeding in the first few days while the female is brooding. Maxwell and Putnam (1972) found that Common Grackle males fed more than females at some nests and less at others.

Both sexes of Pezites feed the nestlings, although there are individual and species differences in the participation of the male, perhaps because males may be attending other nests. The number and age of young as well as activity of neighboring males, may influence the male's contribution. Martin (1974) found that male Bobolinks which normally pay no attention to secondary nestlings, may contribute to their care if food is unusually short or the brood is unusually large. The mechanism underlying this unusual behavior change remains to be clarified.

In most cases I found that male meadowlarks contributed little food during the first few days of the nestling period, and in most cases the number of male

visits per day apparently increased gradually during the nestling period. For those nests where I made some observations, I found that defilippii males participated the most and bellicosa the least.

METHODS OF OBSERVATION

In some cases my observations were part of my nest-finding behavior, and were therefore secondary in importance. The following observations include data obtained both before and after I actually located the nests or fledglings. Usually I made observations from a vehicle parked from 100-300 meters away, using binoculars or telescope. I noted the distance and direction from which the adults arrived, the "wait time" (time between landing on a perch near the nest and disappearing into vegetation), the "nest stay time" (see above), while they were out of sight, and the "interval" or time between leaving and returning to the nest. The precision of the times varied depending on other simultaneous observations, but they were usually measured with a stop watch, and should be accurate to within a few seconds.

The adults frequently foraged at long distances from the nest, in most cases feeding outside the defended territory. For example, at Bujama, most nesting bellicosa on the study area obtained corn borers from

two patches of corn, even though many had to fly over 1000 meters back to their nests. The maximum distance measured for a bellicosa flying with a corn borer was 2.4 km. Birds returning to their territory with food were usually conspicuous. For bellicosa I noted that adults carrying food consistently flew about 5-10 meters off the ground, while adults leaving their nest to forage flew much higher, often above 25 meters. I did not notice the same difference for other species.

I noted the following similarities in the feeding behavior of the three species. Adults arriving at the nest usually landed on an exposed perch 2-10 meters from the nest site. If I or another source of disturbance were nearby, they would delay going to the nest, whereas when I was at a distance exceeding 150 meters or in a blind, they would go to the nest with less delay. Females were notably more wary than males (see Tables 17, 18) as can be seen from the wait times.

"PATIENCE"

In several cases, when I was attempting to find nests and was triangulating on the spots where females seemed to be feeding young, I remained within 75 meters of the nest. In these cases, the females would usually remain on their observation posts for many minutes, would change position 2 or 3 times, and would almost invariably

show more patience than I and refrain from going to the nest until I retreated. In 7 instances where I kept detailed notes on bellicosa I found that in one case the female ate the food item after waiting for 43 minutes. In another case she flew back to the feeding grounds, still carrying the food, after 31 minutes, and in one case she went to the nest after 17 minutes, while I remained sitting in view at about 60 meters from the nest. In four other cases, I waited 20-25 minutes, and then withdrew to more than 150 meters.

During these wait times, the females exhibited signs suggestive of "nervousness", flicking wings and tail, jerking the head, and giving soft "alarm" or annoyance calls. The apparent conflict between an urge to feed the young and to flee results in the prolonged and seemingly "patient" waiting. This would afford a patient observer the opportunity to measure the intensity of the tendency to feed young, and perhaps the factors which inhibit the adult from consuming the prey they are transporting.

Male militaris also showed longer "wait times" when an intruder was near at hand than without an intruder, but they were significantly less patient than females. Although for militaris and defilippii, males made about 1/4 of the feeding visits to nests, I discovered twice as many nests (8 : 4) after visits by males than after

TABLE 17. Number of feeding visits, mean "wait time" and comparisons for male and female *militaris*.

Nest Number	Nestling Age	Observation time(hours)	NUMBER OF VISITS Female	Male	% ♂	FEMALE WAIT TIME mean ± S.D.	MALE WAIT TIME Mean ± S.D.	MWU*	Intersex Difference (p, 2-tail)
70-3	0-3d	5.33	35	1	2.8	3.93 ± 1.58	----	4	.193
70-4	0-3	3.58	16	2	11.1	3.44 ± 1.12	----	1	.034
70-5	3-5	7.17	61	9	12.9	4.93 ± 3.13	1.83 ± .87	47	.00006
70-9	5-7	3.17	24	5	17.2	2.83 ± .70	----	15	.009
71-2	5-7	2.75	17	3	15.0	5.68 ± 4.02	----	20	.55
All Nestlings		22.00	153	20	11.6	4.32[t] ± 2.71			
F**-1		1.17	9	11	55.0	2.61 ± 0.93	2.32 ±1.40	4	.0004
F -2		1.92	11	7	38.9	2.32 ± 1.40	----	18	.060
F -3		2.17	16	7	30.4	3.13 ± 1.41	----		.32
F -4		1.25	0	13	100.0	----	1.73 ± .60	--	----
F -5		1.67	9	15	62.5	1.61 ± .60	1.43 ± .80	25	.0146
F -6***	8-9	1.58	13	6	31.5	3.04 ± 2.07		16	.0404
F -7	9±	1.25	8	3	27.3	2.88 ± 1.30		7	.298
All Fledglings		10.62	66	62	48.4	2.67[t] ± 1.46			
Combined Total		32.62	219	82	27.24	3.82[tt] ± 2.52	1.96[tt] ±1.21	2352	<.000001

* Mann-Whitney U statistic and associated two-tailed probability

** Fledglings *** Fledging caused by my disturbance prior to beginning observations

t= T-test comparison of 5 nestling and 7 fledgling broods, t=3.92, df=217, p < .001, for ♀♀

tt=T=test comparison of all males with all females, t=6.38, df= 299, p<.00001.

TABLE 18. Comparison of frequency of feeding visits for male and female militaris.

NEST NUMBER	NESTLING AGE	OBSERVATION TIME(hours)	FEEDING VISITS PER HOUR FEMALES	MALES	NEST CONTENTS militaris eggs	militaris young	cowbirds eggs	cowbirds young	MALE	FEMALE
70-3	0 --3	5.33	6.56	0.19	2	0	1	1	GG/GG	GG/YG
70-4	0 - 3	3.58	4.47	0.56	0	2	1	1	GG/WW	GG/WW
70-5	3 - 5	7.17	8.51	1.25	0	3	0	2	RR/RR	RR/RR
70-9	5 --7	3.17	7.56	1.57	0	2	0	3	unmarked	
71-2	5 - 7	2.75	6.18	1.09	0	1	0	2	GG/GG	WG/GG
All	Nestlings	22.00	6.66±1.52	0.93± .55 (t=7.9)*	(r=.587)**		(Tau=0.40)***			
F - 1		1.17	7.69	9.40					UNmarked	
F - 2		1.92	5.73	3.64					unmarked	
F - 3		2.17	7.37	3.22					unmarked	
F - 4		1.25	----	10.40					unmarked	
F - 5		1.67	5.38	8.98					unmarked	
F - 6	8 - 9	1.58	8.72	3.80					YY/GG	YY/GG
F - 7	9±	1.25	6.40	2.40					unmarked	
All	Fledglings		6.88±1.27	5.24±3.10 (t=1.2)****	(r=-.136)**		(Tau=0.067)***			
All	Broods Combined		6.80±1.33	3.87±3.64 (t=2.5)****	(r= .047)**		(Tau=0.09)***			

*T test for inter-sex difference shows significant difference ($p<.01$)

**Pearson Product-moment correlation coefficient results

***Kendall Tau for correlation, all probability values have $p>.15$ indicating no correlation between sexes.

****T test reveals significant difference ($p=.02$)

TABLE 19. Number of feeding visits, mean 'wait times" and comparisons for male and female bellicosa.

Nest Number	Age of Young (days)	NUMBER OF VISITS Female	Male	% by♂♂	FEMALE WAIT TIME mean ± S.D.	MWU*	Intersex Difference (p,1-tail)
1	3-5	8	3	27.3	7.85 ± 5.06	1	.012
2	0-1	10	1	9.1	14.56 ± 6.31	0	----
3	4-6	7	4	36.4	11.55 ± 5.10	0	.003
8	>6	11	5	31.3	5.64 ± 2.11	0	< .002
10	>9	6	2	25.0	7.26 ± 1.65	0	.036
Results for 5 pair		42	15	26.3	9.40 ± 5.53		
Results for others		13	0		4.68 ± 2.68		
Total for all pair		55	15	21.4 ♀♀♀	8.29 ± 5.37		
				**♂♂♂	1.90 ± 1.16		

* MWU=Mann-Whitney U Test; probability used is one-tailed probability that female wait-time is longer than male wait-time

** Mean and standard deviation for all male visits compared with female visits

female visits. This is a confirmation both of the difference between sexes, and of the adaptive value of caution when approaching the nest.

Not only do females wait longer than males, they tend to disappear into the vegetation far from the nest and to walk towards it. This has been noted also by Johnson (1967), by Venturi (Hartert and Venturi 1909), and Belcher and Smooker (1937). When leaving, they often walk 2 to 5 meters from the nest before they take off. Males, by contrast, usually take off from close to or at the nest, and at least one male made three consecutive arrivals, dropping down directly at the nest site. Tables 17-21 provide data on the role of sexes for miltaris, bellicosa and defilippii giving the observation time, estimated age of young, number of visits and the mean "wait times" for males and females.

MILTARIS

The most adequate data were obtained on feeding visits at nest or broods of miltaris. Table 17 summarizes data on 5 nests and 7 families of fledglings (some of which were disturbed from the nest by me on the day of the observations). A total of about 30 hours was spent observing these 12 pairs. In one case F-4, only the male fed during 1 hour 15 minutes. The obser-

vations were conducted from a vehicle 100-125 meters from the nest, and at this distance my presence did not seem to influence the birds. The mean wait time for 219 visits by 11 females was 3.82 ± 2.52 min. and for 92 male visits (27.2% of total) by 12 males it was 1.96 ± 1.21. The differences are significant by t-test and by non-parametric Mann-Whitney and Kolmogorov-Smirnoff Tests ($p<.001$).

More important, the non-parametric tests revealed that in 11 cases where both parents fed, the inter-sex difference in "wait" times was significant ($p<.05$) in 6 cases. At the 5 nests with 0-7 day old nestlings female wait times averaged 4.32±2.71 whereas for the older nestlings and fledglings it averaged 2.67±1.46. The difference was significant by t-test and Mann-Whitney ($p<.001$).

With essentially no disturbance, the parents made frequent feeding visits, and Table 18 summarizes the average number of visits per hour at each nest. Females made more than twice as many trips per hour (6.80) as males (3.28) at the 11 nests where both fed. At family F-4, the male made 10.4 visits/hour, the highest frequency of any bird. This was accomplished by obtaining food quite close to where the fledglings were hiding. Martin (1974) found that secondary female Bobolinks, deprived of male parental assistance, compensated by

increasing their frequency of nest visits. To test whether this might apply in the present study I used Kendall Tau coefficient of correlation. One would predict that the frequency of female visits would be higher at those nests where males contributed little. The one case of F-4 shows that compensation can occur, and for the other nests a negative correlation is predicted. The Kendall Tau values for all 11 nests and for the nestling and fledgling broods separately did not differ significantly from zero.

Males made at least one feeding visit at all 12 broods under study. Males GG/GG and GG/WW made very little contribution to nests 70-3 and 70-4 during the observation period. Both males seemed to be courting other females. At nest 71-2, GG/GG also made relatively little contribution, but he did not seem to have another female, and was observed on at least four occasions to accompany his female to the nest site, three times with food, and to sit nearby without feeding the young.

Male militaris did not play a major role in feeding during the first days of life. The gradual increase in male assistance was measured by regressing the % of visits by male (male visits/total) on the estimated age of the young. Since fledglings were not found, they were arbitrarily assigned an age of 11 days for purpose of regression. The values fit the equation:

$$\text{Male \%} = 5.78 \times \text{age} - 11.10$$

These same values have a Correlation (Tau = .37) which is barely significant (p=.047).

BELLICOSA

I obtained data on feeding visits and wait times for 10 pairs of bellicosa at Bujama. Four were feeding at known nests, while the nestlings or fledglings of the remaining pairs were not discovered. The data were obtained mainly during nest-feeding activities, and in several cases only a few observations were made at a given nest. Pair 10 was known to be feeding fledglings.

Table 19 compares the behavior of males and females. Females accounted for 78% of the feeding visits, and there was little overlap in the wait times. A Median Test was used to compare the times, and all 15 of the values for male visits fell below the median ($X^2 = 19.01$; $p < .001$). Moreover, if I was in view within 100 meters of the nests, females left the vicinity of the nest after waiting for 30 minutes or more, whereas in at least two cases, males waited for less than five minutes before going to the nest.

For the five broods where age was known (4 nestling, 1 fledgling) I compared the age of young with percentage contribution of male using a Kendall Tau (Tau = .13, $p < .05$) and found no significant association.

DEFILIPPII

Near Bahia Blanca in early December, 1970, I observed adult defilippii feeding at several nests and focused attention at nests in the territories of WW/WW and WW/RR. I took the opportunity to confirm the trivial notion that adults would take longer (longer wait times) to approach the nest if an observer were close (<70 m) than if one were far (>100 m) from the nest. Table 20 shows that for any distance, females had significantly longer wait times than males ($p < .01$) and that they significantly prolonged their wait time in the presence of an observer ($p < .02$ for two females WW/WW and WW/WB. On the other hand the male, WW/WW, did not take longer, at least in the few timed observations on 8 December.

On 10 December when female WW/WW had nestlings approximately 8-9 days old (which fledged when I disturbed them) I timed 8 of her visits and 5 of her mate. The male also made two visits to the nest of female WW/WB who had nestlings about five days old. The data are shown in Table 21.

Although the data are inadequate, it seemed that male WW/WW made more visits to the nest of his secondary female, WW/WB on 8 December than on 10 December. On the former day his absences from nest WW/WW (intervals between visits) were from 19-24 minutes compared with

5-7 minutes for female WW/WW. He visited nest WW/WB at 40-75 minute intervals. On 10 December the intervals between visits to the WW/WW nest were 7-23 minutes while 90+ to 120+ minutes elapsed between visits to the secondary nest. The secondary female, WW/WB, made only slightly more frequent visits than did female WW/WW (not significant).

On the same date male WW/RR fed young at the nest of female WW/RR which conatined 5 nestlings 5-7 days of age. He also seemed to be feeding at the nest of an unmarked female about 75 meters away, and this was confirmed the following day. Female WW/RR was particularly "patient" while I made observations from the jeep about 70 meters from the nest (see Table 21).

During the period of observation on these two mornings I noted 17 visits by two males and 41 visits by three females (male visits = 29.3% of total). Thus these two males contributed substantially to the feeding of young during the observation period and it is interesting that both males fed at both of the nests in their territories, although polygynous males sometimes restrict attention only to primary nests (see Chapter 5).

HELPERS AT THE NEST

Considerable attention has been focused recently on the role of birds other than parents in caring for young. Woofenden (1975) has elaborated the role of "helpers" in the social system of the Scrub Jay (Aphelocoma coerulescens) and Orians (personal communication) has found "helpers" at nests of several Argentine icterids that he studied. At nests where one or both parents were color-marked I did not see any evidence of non-parents feeding young, even when observations spanned more than 12 hours and several days. It would be premature to conclude that there are no "helpers" in meadowlark societies, but at present there is no evidence for their existence.

SIGNIFICANCE OF PARENTAL CARE FOR POLYGYNY

In considering the evolution of polygyny, a chief obstacle is that a female choosing a male "ought" to chose one who will assist her in caring for the young, whereas if he is already mated he may make little or no contribution to care of young (see Chapter 5). This leads to the prediction that polygyny is more likely to arise in species or populations where males make no contribution to care of offspring or at least where their contribution is not critical. The more usual interpretation (e.g., Verner and Willson 1966, 1969,

Orians 1969) is that in habitats where suitable territories are restricted, certain males will defend favorable territories and females mating with such males benefit, even though such males give little or no assistance.

Observations at nests of Pezites indicate that bellicosa males make little or no contribution to care of young, while male defilippii provide up to 1/3 of the care. One would anticipate less of an obstacle to evolution of polygyny in populations of bellicosa than in defilippii. Although I have no suitable evidence at present, there are two extreme possibilities to be investigated a) polygyny evolved in the group before the differences in male participation evolved or b) the potential for polygyny is present, and it appears in those populations or circumstances where male contribution is least necessary.

The observation that males are less cautious and patient than females raises two questions. If males jeopardize nests by their carelessness, it may - at a certain point - become advantageous to dispense with their participation even further, and this would allow a higher order of polygyny. Secondly, it seems likely that male carelessness may reflect relaxed selection for carefulness which one would anticipate in a population where male contribution is already

unessential. Pezites offers an opportunity to examine these issues since there is between-species variability in the contribution of the males. At present the data do not allow one to examine the relative "carefulness" of males among the three species. One would anticipate that since defilippii males participate the most they would also be more careful, but data available now (see Table 20) do not support this.

Male contribution may be most important shortly after hatching, particularly in a temperate climate, when the female must brood the young. After the nestlings are a few days old, female Pezites do almost no brooding during the day (all days in 1971 were warm and dry), and after they are about a week old females are sometimes absent at night as well. My observations indicate that militaris males make negligible contribution during the first days at most nests, but that defilippii males may begin feeding as soon as the young hatch. This is consistent with their greater role in parental care. For militaris there seems to be an increased tendency to feed young as time passes, and males often care for fledglings - perhaps while the female initiates a new nesting cycle (although this was not documented).

Another feature consistent with the greater contribution of defilippii males is the fact that they

respond vigorously to distress calls uttered by their nestlings when handled. This was not noted for the other two species.

Finally, it is necessary to emphasize that the observations were made at only a few localities and that differences in habitat, temperature, food availability and other variables may influence the behavior patterns under discussion.

* * *

TABLE 20. Comparison of female and male wait times for defilippii when observer was more than 100 m or less than 70 m from the nest.

INDIVIDUAL	OBSERVER DISTANCE FROM NEST >100 m	<70 m	Significance[a] of difference for 2 distances	
♂WW/WW	53 44 37 72	84 51 48	U=4	p=.314
♀WW/WW	91 112 80 54 123	345 370 265	U=0	p=.018
♀WW/WB 1st[b]	215 88	(interrupted)		
2nd	145 220 75 85	410 450 600+ 480+	U=0	p=.005
Significance of difference between sexes	U=1 p .01	U=0 p = .008		

a=Mann-Whitney U test and 1-tailed probability

b=First observation period was interrupted by disturbance

TABLE 21. Comparison of male and female wait-times for two male and three female defilippii on 10 December 1970, at 7 km E of Bahia Blanca (BB7E)

PAIR Female	Male	Observation time (hours)	Number of Visits Female	Male	%by♂	Female Wait Time mean ± S.D. (minutes)	Male Wait Time mean ± S.D. (minutes)	MWU[c]	Comparison ♀ vs ♂ p[a]
WW/WW	WW/WW	1.38	8	5	38.5	2.64 ± 1.71	1.07 ± .51	5	p=.030
WW/WB	WW/WW	1.58	9.	2	18.2[b]	2.55 ± 1.38	1.13 ± .29	1	p=.070
WW/RR	WW/RR	2.0	6	3	33.3	9.10 ± 4.19	.98 ± .42	0	p=.024
Total		4.96	23	10	30.3	4.28 ± 3.76	1.05 ± .41	13	p<.002

a = 2-tailed probability by Mann Whitney Test c = Mann Whitney U

b = contribution of ♂WW/WW at 2nd nest (WW/WB) was actually lower than shown here since there was usually a long interval between his visits, often exceeding one hour and this observation period just managed to encompass two visits.

APPROXIMATE INTERVALS IN MINUTES BETWEEN FEEDING VISITS

	Actual observed times in minutes	N	Mean ± S.D.
♂WW/WW to nest WW/WW	17 23 11 7 9	5	13.4 ± 6.54
♂WW/WW to nest WW/WB	90+ 120+	2	---- ±
♂WW/RR to nest WW/RR	14 52	2	---- ±
♀WW/WW	4.5 9 8 6.5 4 17 3 14	8	8.3 ± 4.97
♀WW/WB	8.5 12 6 4.5 7 7.5 9 5.5 11	9	7.9 ± 2.50
♀WW/RR	11 21 12 11 9	5	13.8 ± 4.8
All male visits	Range = 7 to 120+ minutes	9	38.1 ±40.92
All female visits	Range 4.5 to 21 minutes	22	9.1 ± 4.36

Comparison ♀ vs ♂ MWU^c=34 p^a<.02

SUMMARY OF INCUBATION AND CARE OF NESTLINGS

1. At present there is no evidence that male meadowlarks of any species incubate, and evidence on nest-wait times suggests that females may brood young nestlings on feeding visits while males do not.

2. Pezites, like Sturnella, have a tendency to abandon a nest, particularly if it is discovered early in the incubation period. Conversely, even when trapping is conducted during the nestling period, abandonment is unlikely. Since the potential loss of invested time and energy increases during the incubation and nestling periods, one could formulate a general principle that the tendency to abandon should decrease during the nesting cycle.

3. Scant data on incubation time for militaris nests range from 13.5 to 14.5 days. This is close to the 13-14 day estimated for Sturnella. I did not obtain satisfactory data for the other species.

4. Both sexes play a role in feeding the nestlings and fledglings, and there is considerable variation between males of the same species, and perhaps between species as well. Male defilippii contributed about 30% of the feeding visits, while the contribution of

bellicosa was negligible and that of militaris was intermediate.

5. As a rule females approach nests cautiously, landing at and departing from a distance. The actual approach to the nest and departure are thus invisible as the female walks through the vegetation. Some males may do this, but for the most part males land near the nest and usually fly up directly from it.

6. Females substantially increase their caution if an intruder is evident within 70 m (or in some cases more) of the nest. Some males increase their caution, while others do not. Females are not only more "patient" than males, but may be more "patient" than a human observer. Such behavior has a straight forward anti-predator function as evidenced by the fact that I found nests more easily after male visits than after female visits.

7. If males are careless and jeopardize the safety of nests, there may be a selective advantage (or at least no disadvantage) in diminishing male contribution. Thus in species or situations where male cantribution to feeding is important one would anticipate selection for increased caution and "patience" by males. Relaxation of such pressure (as seems to have been the case in the birds studied) suggests that male contribution may often

be unimportant in these species. Thus a chief obatacle in the theory of the evolution of polygyny may not be operating in these birds.

8. Adults of all three species secured some or all of the food for nestlings beyond the boundaries of their defended areas. Thus the territories cannot be considered type A, although certain individuals may maintain type A territories.

CHAPTER 8 BROOD PARASITISM:

INTERACTION OF MEADOWLARKS AND SHINY COWBIRDS

The coevolution of avian brood parasites and their hosts has attracted much attention and offers abundant opportunity for examination of parasite adaptations and host counter-adaptations in the field. The literature on brood parasitism and brood parasites is extensive, and major reviews include Friedmann (1963) and Hamilton and Orians (1965). Most of our knowledge of parasite-host interactions is still anecdotal as, for example, much of the information reviewed by Friedmann (1955, 1960, 1963) and such reports as those of Hudson (1920). Some are based mainly on oological collections (e.g. Hoy and Ottow 1964, Jourdain 1925, Stuart Baker 1942). A few parasitic species or groups have received extensive field attention (e.g. Chance 1940, Friedmann 1929, King 1973, Mayfield 1960, Payne 1965, 1972, 1973). Valuable information has come from observations of parasites in captivity as well (e.g. Nicolai cited Payne 1973, Selander and Yang 1966).

Relatively few of the interesting questions raised by host-parasite coadaptations have received adequate study, and I focused attention on one aspect of this interaction -- the nest finding behavior of the Shiny Cowbird (Molothrus bonariensis) and some counter-

strategies of the hosts. Two basic questions were formulated:

1. What special behavorial strategies can a parasite utilize to maximize gain from nest finding activities.
2. What aspects of host behavior serve to thwart nest-finding.

On the southern pampas, Pezites militaris, P. defilippii, and Leistes (m.) superciliaris occur in local sympatry with the Shiny Cowbird (Molothrus bonariensis), a widespread and common obligate brood parasite. Particularly in 1971 I devoted much attention to the interactions between Pezites and Molothrus.

COEVOLUTION OF BROOD PARASITES AND THEIR HOSTS

Bird species that are obligate brood parasites must be proficient at finding suitable nests belonging to suitable foster species, i.e. those which will accept the parasitic eggs and feed the parasitic young appropriately. The chosen nest must be at the proper stage of the breeding cycle, for if the parasite lays too early (before the host) the host may abandon the nest, whereas if it lays too late the host young will hatch first and outcompete the parasite (Berger 1951). Friedmann (1928, 1929, 1963), Hamilton and Orians (1965) and Payne (1967), among others have reviewed many of

these aspects of the biology of brood parasites.

As with any host-parasite relation coevolution is involved since the host species "must" develop adaptations for minimizing frequency and impact of parasitism. Some of the possible defensive strategies are: hiding the nest well, behaving surreptitiously during nest building or behaving aggressively toward the parasite (e.g., Smith 1968; Prescott 1947; Nice 1937). Once a parasite's egg has been deposited, the host may eject the egg instead of incubating it (Rothstein 1974, Hoy and Ottow 1964), or it may cover it over with nest material, or it may abandon the nest entirely. The latter two strategies involve considerable loss of effort and time, and perhaps loss of some already-laid eggs as well. However, failure to deal effectively with the parasitic egg may lead ultimately to zero productivity for the season, not to mention the increased exposure involved in feeding the noisy and conspicuous cowbird fledgling (Hudson 1920, Ficken 1967).

Gray Catbirds (Dumetella carolinensis) and North American Robins (Turdus migratorius) have long been known to reject the eggs of the Brown-headed Cowbird (Molothrus ater) (Friedmann 1929), although both occasionally fail to accomplish this and end up raising young cowbirds (e.g., McGeen and McGeen 1962, Friedmann 1929). Rothstein (1971) mentions four other North

American species which can be considered consistent egg-rejecters, but notes that most species readily accept cowbird eggs.

Some Shiny Cowbirds lay whitish eggs (non-mimetic) and others speckled eggs (mimetic). Hudson (Sclater and Hudson 1888:103) provides an anecdotal account of a nest of the Brown and Yellow Marshbird (Pseudoleistes virescens) where five non-mimetic cowbird eggs were ejected while three mimetic ones were not. Berger (1948) reported unusually early nests of the American Goldfinch (Spinus tristis), and implied that these were more likely to be parasitized by M. ater than were late nests, although the data are not clear on this point. In any case, delayed nesting might be another strategy for a species to avoid the peak of the Cowbird's breeding period, and a prolonged breeding season would be advantageous. However, the advantage of nesting late to avoid parasitism is presumably often countered by the disadvantage faced by late-fledging young.

Species such as the Yellow Warbler (Dendroica petechia) and the Yellow-browed Tyrant (Satrapa icterophrys) among others, frequently add new nesting material over cowbird's eggs (Friedmann 1929; Hudson 1920). Others, for example the Fork-tailed Flycatcher (Muscivora tyrannus) may abandon their nest after a parasite's egg appears (Hudson 1920).

Abandonment of a parasitized nest is difficult to study because it requires that one find such abandoned nests, while it is usually the activity of a bird around the nest that attracts the attention of an observer, and therefore abandoned nests are much less likely to be discovered than active ones. Moreover, certain species are likely to abandon their nests as soon as they are discovered by humans, whether or not parasitism has occurred. Lanyon (personal communication), Marchant (1960), and I (present study) have found that meadowlarks of several species readily abandon clutches of eggs when disturbed once or twice early in the incubation period. However, the frequency with which cowbird eggs and chicks were found in meadowlark nests suggests that these species, at least, do not usually abandon parasitized clutches.

COWBIRD STUDIES IN ARGENTINA

While studying meadowlarks at La Saudade and elsewhere I recorded my observations of brood parasitism and of parasite-host interactions. In the course of studying the response of meadowlarks to decoys and playback vocalizations, I noted the responses of Molothrus bonariensis (hereinafter referred to as the cowbird) as well. Since I was not studying the cowbirds primarily, I did not use cowbird decoys and vocalizations and the

data presented below must be interpreted with caution in the absence of comparable autospecific response information. Moreover, I color marked only a few cowbirds, and I could not recognize the majority of the individuals that visited my study area. One of the most intriguing problems -- the question of whether individual cowbirds show any host species preferences of "specificity" -- could not be dealt with without marked birds.

HOST SPECIES FOR THE SHINY COWBIRD

Friedmann (1963) summarizes the reported hosts for the Shiny Cowbird. Overall, the Rufous-collared Sparrow (Zonotrichia capensis) is probably the most frequent host, (Gibson 1880, Serie and Smith 1922) with some reports of more than 60% of nests parasitized (e.g., Friedmann 1929; Sick and Ottow 1958), while King (1974) found that at the height of the breeding season 100% of nests were parasitized. Hudson (Sclater and Hudson 1888:103) mentions Pseudoleites virescens as the most common host on the northern pampas.

Table 22 lists the numbers of nests I found for various species where nest contents could be examined, and also the frequency of parasitism. The overall parasitism rate was 28%. In addition I found nests of such common species as Furnarius rufus, Anumbius annumbi, and Pitangus sulfuratus which are known to be hosts

(Gibson 1880, Miller 1917, Friedmann 1963), but I could not examine their contents. In the Saudade-Bahia Blanca region, P. militaris was the most prominent host species, with 22 of 23 completed nests parasitized. By contrast only 2 of the 13 Zonotrichia nests were parasitized which is significantly less than than the militaris rate ($p=.000001$; Fisher Exact Test, 2-tailed). Not counting militaris, only 4 of 59 nests of other species were parasitized, so that the frequency for these species was again significantly less than militaris frequency (Chi Square $=68.6$, $p < .00001$).

MEADOWLARKS AS COWBIRD HOSTS

Gibson (1918), Stone (1927), and Friedmann (1929: 121) mention P. militaris as a cowbird host and Withington (1888) mentions two parasitized nests of P. defilippii. Only 1 of 25 clutches of Pezites militaris in the Western Foundation of Vertebrate Zoology collection included cowbird eggs. Marchant (1960) found several parasitized nests of P. bellicosa. None of the nests of P. bellicosa that I found at Bujama, (90 km S. of Lima) Peru were parasitized but I saw no cowbirds there at any time, while at Villa (10 km south of Lima) Pezites were frequently accompanied by cowbirds, and parasitism no doubt occurred. In view of the many host species summarized by Friedmann (1963) and the scarcity

TABLE 22 Prevalence of Cowbird Parasitism on Passerines in southern Buenos Aires Province

SPECIES	Number of Nests found	parasitized	Number of Host Eggs or Young	Cowbird Eggs or Young	References to other reports of parasitism
Serpophaga cristata	1	0	3	0	1
Anthus correndera	3	0	10	0	2,3
Anthus sp.	6	0	16	0	
Mimus saturninus	4	0	12	0	1,4
Mimus triuris	1	0	3	0	3,5,6
Passer Domesticus	3	0	9	0	1,8
Pseudoleistes virescens	3	1	13	1	2,7
Pezites militaris	23	22	91	41	1,3
Pezites defilippii	11	0	42	0	9
Emberanagra platensis	3	0	14	0	10,7,12
Diuca diuca	1	0	4	0	1,3,6
Sicalis luteola	9	0	41	0	1,7,9
Sicalis f. pelzelni	1	0	4	0	1,9
Zonotrichia capensis	13	2	43	2	1,2,7,9
	82	25	305	44	

REFERENCES: 1. Friedmann 1963; 2. Hudson 1920; 3. Reed 1913; 4. Miller 1917; 5. Pereyra 1937; 6. Wetmore 1926; 7. Gibson 1880; 8. Sick 1957; 9. Friedmann 1929; 10. Hoy 1961; 11. Grant 1911; 12. Holland 1892.

of host records involving Pezites, one might infer that as a rule meadowlarks are infrequently parasitized.

Leistes has been reported as a host by Wilson (1926), Belcher and Smooker (1937), Pereyra (1933), Herklots (1961), Friedmann (1963 and pers. comm.) and Herklots considered it a common host. A clutch from Trinidad had 10 cowbird eggs (B.M.N.H. #1925-7-3010) while Pereyra (1933) mentioned finding 12 and 19 cowbird eggs in two Leistes nests in Argentina.

North American Meadowlarks are also parasitized. Lanyon (1957) reported 9 of 41 (22%) of S. neglecta clutches and 6 of 38 (16%) of S. magna clutches, parasitized by M. ater. The interspecies difference tested by Chi square on a 2 x 2 contingency table is not significant ($p > .50$). Hergenrader (1962) reported 5 of 31 (16%) nests of Sturnella were parasitized, while Friedmann (1929, 1963) considered them uncommon hosts.

In my sample where no defilippii nests were parasitized the difference in the frequency of parasitism for nests of the two meadowlarks (see Table 22) proved highly significant ($p=.000002$; Fisher Exact Test, 2-tail). The proportion of militaris nests parasitized (95%) was high, but not the highest reported (e.g., King 1974).

Three sources of bias might enter into the differential frequencies of brood parasitism observed:

1. I might have found those nests of militaris which were most likely to be parasitized, and those of defilippii which were least likely to be parasitized, for reasons not understood.
2. If defilippii were ejectors, there might be a high rate of parasitism with no cowbird eggs to show for it. However, I saw no cowbird eggs in any defilippii nest nor nearby, and to my knowledge no meadowlarks are known to be ejectors. Moreover, if cowbirds laid in defilippii nests one would expect to find reduced clutches or broods of only 1 or 2 -- the rest having been removed by the cowbirds.
3. If defilippii abandoned nests after parasitism, such nests would be difficult to discover for a human observer, and indeed their presence might go undisturbed. Rothstein (1971) noted this hazard.

At present there is no support for these possibilities, and I assume the observed differential parasitism frequency is real and needs explanation.

NEST PLACEMENT AND DIFFERENTIAL PARASITISM

Initially it appeared likely that differential parasitism was related to nest site differences. Previously I have discussed the differential nest locations of the two species of meadowlarks (see Chapter 6). Of 12 nests of P. defilippii only one was within 3 meters of a bush > 1 m. tall, and none were within 5 meters of fences. Most of the nests were in wheat 14-26" tall or mixed grassland. Two nests in sparse clumps of Stipa were unusual in being entirely visible from above. Nests in wheat were difficult to discover, even when their location was known to within two meters.

P. militaris nests were usually placed within dense vegetation and were usually not visible until the overlying foilage was parted. The nests were often found in fence rows, generally in clumps of thistle. Only one P. militaris nest was found away from tall vegetation. This nest, #22 at BB7 E, was visible from 3 meters away, and was only partially covered by a small thistle. It was abandoned shortly after incubation began, at which time it contained 6 meadowlark and 2 cowbird eggs.

In addition, I searched unsuccessfully for nests in 9 territories of P. militaris, and by watching the activities of the birds, I believed that at least 7 of the 9 nests were a fencerow. I had no reason to believe that any P. militaris at Saudade, nested in wheat. A

source of bias, results from the somewhat greater ease of locating nests along fence rows, since one can search in a single dimension, with greater likelihood of finding a nest. One might argue that the apparent differential habitat distribution of Pezites nests was biased by this search method. However, the 24 located and the 9 unlocated nests account for almost all of the nests likely to be present in the 18 territories I was studying. Even if the 9 unfound nests were all away from fences or tall vegetation, then 23 of 33 nests would have been near elevated pershes, in contrast to P. defilippii (FEP 2= .00012) (see Table 23A).

Using 2 x 2 contingency table and Fisher Exact Probability, 2-tailed test, the actual and hypothesized nests were compared for placement next to fence or any elevated perch and parasitism rate (see Table 23A). The preference of P. militaris for nesting near tall vegetataion in fencerows, is consistent with their observed preference for using elevated song perches (Abbott 1861, Short 1968, Pettingill 1973 and present study).

I used this line of reasoning to evaluate whether my own bias in nest-finding could account for the discrepancy in placement and parasitism. If I was biased against finding militaris nests away from elevated perches or nests that were not parasitized, how many nests would I need to overlook, if there were really no

difference between the species. Similarly, if I were biased against finding defilippii nests near elevated perches or parasitized nests, how many nests would have to be overlooked? These were tested using the same 2 x 2 contingency tables and Fisher Exact test, but manipulating the one cell in question, by increasing its value until the probability of the table rose above .05. Finally, in the unlikely event that my bias operated on both species, I tested (Table 23D) the same data by manipulating two cells.

Although there were certainly at least nine militaris nests and perhaps twice that number of defilippii nests which I looked for at least briefly without success, the data in Table 23B and 23C reveal the magnitude of bias necessary if the two species did not differ in nest site selection. I would have had to overlook either 58 militaris nests away from elevated perches or 36 defilippii nests near elevated perches, or 9 nests in each category. Similarly, if the two species were equally parasitized, my bias would have had to be strong enough to overlook 50 unparasitized militaris nests, 31 parasitized defilippii nests, or 8 in each category. A bias of such magnitude would be extremely unlikely, particularly since for militaris there were only about 15 pair available for study. Therefore, at least for the seasons and years I examined them, there

TABLE 23. Contingency tables tests of bias in nest-finding.

	OBSERVED DATA		LAST SIGNIFICANT TABLE		FIRST NON-SIGNIFICANT TABLE	
Nest placement NEAR or NOT NEAR elevated perches -- *loyca* iteration						
	(a) NEAR	NOT NEAR	(b) NEAR	NOT NEAR	(c) NEAR	NOT NEAR
loyca	23	1	23	57	23	58
defilippii	0	12	0	12	0	12
FEP2	<.00000002		=.0486		=.0511	
Parasitism YES or NO -- *loyca* iteration						
	(d) YES	NO	(e) YES	NO	(f) YES	NO
loyca	22	1	22	49	22	50
defilippii	0	11	0	11	0	11
FEP2	<.00000001		=.0490		=.0518	
Nest-placement NEAR or NOT NEAR elevated perches -- *defilippii* iteration						
	(g) NEAR	NOT NEAR	(h) NEAR	NOT NEAR	(i) NEAR	NOT NEAR
loyca	23	1	23	1	23	1
defilippii	0	12	35	12	36	12
FEP2	=.00000002		=.0480		=.0526	
Parasitism YES or NO -- *defilippii* iteration						
	(j) YES	NO	(k) YES	NO	(l) YES	NO
loyca	22	1	22	1	22	1
defilippii	0	11	30	11	31	11
FEP2	=.00000008		=.0491		=.05	

was a clear difference between the two species in nest site selection and in parasitism rates, which warrants further discussion.

The differential parasitism rate has significance not only for the meadowlarks, but because it affords the opportunity to study the parasite as well. The observations are consistent with the hypothesis that the different nest site preferences of the two species are related to the differential parasitism, and the propensity of militaris for nesting in fencerows favors cowbird parasitism, by affording the cowbird the opportunity to watch nest building activities of their host. This may be an oversimplification, since the one militaris nest away from elevated perches was also parasitized, however, Berger (1951) also noted that field nesting species parasitized by M. ater suffered greater parasitism in nests near woodlots than in nests away from trees. Obviously cowbirds cannot lay eggs in nests they have not found, and information on how cowbirds find nests is not readily available. Although Hann (1941) and Mayfield (1961) deal with this to some extent, there are no studies on cowbirds comparable to those of Chance (1922, 1940) on the European Cuckoo, and I consider this in detail in the next section.

COWBIRD NEST-FINDING BEHAVIOR

Brood parasites must succeed in finding the right nest at the right time. Nests of inappropriate hosts, or nests where incubation has begun are not suitable. Mengel and Jenkinsen (1970), Hann (1937) and Berger (1951) noted that cowbirds appear to watch the nest building activities of potential host species, while Mayfield (1960) noted that Brown-headed Cowbirds seem to observe Kirtland Warblers that are carrying nesting material. Berger (1951) noted the probable importance of elevated perches from which cowbirds could observe such behavior, and noted differential parasitism rates, with more parasitism in edge nests than in field nests.

In addition to watching the hosts' nest-building activity, some authors (e.g. Nice 1937:163) suggest that cowbirds may find nests by direct search as well. Preston (1948) and Mayfield (1960) note that data on distribution of Molothrus ater eggs in host nests is consistent with the hypothesis that these birds lay their first eggs in a "chosen" nest and subsequent eggs at random. But the methods by which such nests are found are not indicated.

Direct search could account in part for the unusual cases of cowbirds laying in abandoned nests of species with conspicuous nests (e.g., the Hornero, Furnarius rufus) (Hudson 1920) etc. but probably does not apply

at all to host species whose nests are as well hidden as those of the meadowlarks. It is unlikely that direct search would be fruitful with such hosts, and it is almost inconceivable that a cowbird could find an inactive meadowlark nest in which to lay, much less that an observer would find the same nest.

My observations suggest that Shiny Cowbirds spend much time watching meadowlarks, particularly P. militaris, from elevated perches near the nest, and I suspect they find nests mainly in this manner. Perhaps the watching also results in synchronization of egg-laying activity as suggested by Hann (1937) and Chance (1940). Gibson (an Argentine oologist) reported (1880) that M. bonariensis discovered nests by watching him on his nest-finding forays. The European Cuckoo (Cuculus canorus) apparently observes nest-building by potential hosts (Chance 1940) but is also said to induce mobbing by the hosts and to move to the area where mobbing is greatest, thereby locating nests (Seppa 1969).

Nice (1937) believed that Brown-headed Cowbirds are less likely to find well-concealed nests, but, as mentioned above, Berger (1951) questioned whether nests that are well-concealed from a human point of view are also well-concealed from cowbirds. In Murray's study (1969) of Le Conte's Sparrow (Ammospiza leconteii) all five of the well-concealed nests were parasitized by

Molothrus ater. Perhaps the actual concealment of the nest is irrelevant if the cowbird can watch nest-building activity. Moreover, since predation acts on brood parasites partly by acting on parasitized nests, there would be a premium on looking for and finding well-concealed nests that might escape predation. At present it is uncertain whether humans, cowbirds or predators are similar in their sampling bias, and the question is academic until the mode of nest-finding itself is clarified.

MEADOWLARK ADAPTATIONS DURING NEST-BUILDING

Perhaps the most conspicuous behavior pattern of birds during the nest-building phase, is the flight to the nest-site with building material. This characteristic picture could serve to condition predators to associate such behavior with a food resource -- although the resource might not be available for several days. In the case of the brood parasite, interested not in future food, but in a present site suitable for egg-laying, the connection between material-carrying and nest-site is an immediately rewarding one.

Thus apart from actual concealment of the nest site, host behavior patterns that keep the hosts, the nest site, or both inconspicuous are important adaptations against brood parasitism. Birds nesting in trees

or in sparsely vegetated sites have little alternative but to fly with nest material, but birds nesting in grassland or dense vegetation, could gather material close to the nest site and walk to the nest without exposing themselves to the eyes of a potential brood parasite. In a species subject to parasitism, such behavior is likely to be selected for. Naive species, as for example Kirtland's Warbler (Dendrocia kirtlandi) may be subject to heavy parasitism because their behavior reveals nest sites (Mayfield 1960).

For meadowlarks, Hudson (1920) and Marchant (1960) state that they never saw adult P. defilippii or P. bellicosa carrying nest material. I never saw either of these species nor Leistes flying with nest material, except on two occasions when I flushed female defilippii from the vicinity of their nests. I conclude that these species regularly gather material near the nest and carry it to the nest on foot. P. militaris seldom flys with nesting material but I have five anecdotal accounts of such behavior in that species, (see below).

PARASITE'S INVESTMENT IN NEST FINDING

When a parasite sits watching a potential host, it makes an expensive time investment. Failure to find a nest in a given session is penalty for choosing an unsuitable host, perch or behavior pattern. In this sense an unsuitable host is not only one which ejects eggs or cannot rear the parasite, but one whose nest is "too difficult" to find in a reasonable time period. If the time invested per nest found is long it means that the individual parasite will find fewer nests per season, which potentially decreases its productivity. A parasite may compensate partly by laying multiple eggs in the same nest, but alternatively it may revise its strategy to minimize its investment.

It may sample quickly by watching a bird for a few minutes and assessing whether it is an appropriate species in an appropriate breeding phase. It should then move on if the situation seems unpromising. This is analagous to foraging behavior in a patchy environment, where the resource is a nest rather than food.

This leads to predictions that parasites should spend more time watching suitable hosts than unsuitable hosts, and I gathered data to test this with reference to P. militaris (judged suitable on the basis of many parasitized nests) and P. defilippii (judged unsuitable). The underlying assumption is that nests of P. defilippii

are so well hidden or are so far from observation perches, that the cowbirds' investment is not adequately repayed, and that therefore they should spend their time watching P. militaris rather than P. defilippii.

PHYSICAL ASSOCIATION BETWEEN COWBIRDS AND MEADOWLARKS

Early in the course of my playback experiments with Pezites I found that cowbirds frequently responded to decoys and vocalizations, and I began to notice that displaying P. militaris seemed to attract cowbirds as well. Since at any given moment there were usually no cowbirds in view along a 500 meter stretch of road, and since cowbirds observed with meadowlarks were usually quite close to them (within 2-3 meters), it was an easy matter to score a positive association (defined as a cowbird sitting within 5 meters of a meadowlark). In practice there was only one case where I noted a 5 meter distance, and few cases of cowbird-meadowlark distances between 5 and 25 meters.

BASELINE OBSERVATIONS

Cowbirds were common in the woodlots and gardens of the Estancia less than 1 km. from the study area, and they were seen on the study area about a dozen times a day, usually for short periods. On three days (11, 13, 15 November, 1971) I noted all cowbirds visiting the study area, and for each I determined the distance to the nearest visible meadowlark. I based my distance estimate on the utility poles (spaced regularly at 75 meter intervals), and on fence posts, and I surveyed for a distance of 225 meters to either side of each cowbird. In only two cases did I find a cowbird with no meadowlark within 225 meters, and I have eliminated these cases. Table 24 gives the percent linear distance for 0 - 225 meters, equivalent to the probability that a meadowlark would be found at a given distance from a cowbird. Table 25 summarizes the data for 55 cowbird observations over a 12 hr. 55 min. period. The observation periods are not unbiased, since although I tried to record observations every 10 minutes, I sometimes missed observations due to other activities, and I was probably less likely to miss an observation period if cowbirds were present near meadowlarks than if they were at a distance. In addition, since only a few cowbirds were marked, I could not determine whether certain cowbirds might be appearing many times, thereby rendering the

TABLE 24

Linear distance along study plot on which Cowbird-Meadowlark Association was determined. Plot lies along the road.

Total distance = 450 m.

Distance d	Cumulative Two-way probability
0 m	0
5	.0222
10	.0444
25	.1111
50	.2222
75	.3333
100	.4444
125	.5555
150	.6666
175	.7777
200	.8888
225	.9999

* Gives the probability that if a cowbird and meadowlark are present, the distance between them will equal any value from 0-225 meters.

The probability of a meadowlark occurring within 5 meters of a cowbird =.022.

TABLE 25. Association of cowbirds with meadowlarks at Saudade during seven observation periods. Based on nearest visible meadowlark. All distances > 25 m. were rounded to nearest 25 m.

Nearest Neighbor Distance (meters)	Cowbirds Represented	P.MILITARIS male	P.MILITARIS female	P.MILITARIS pair	P. DEFILIPPII male	P. DEFILIPPII female	P. DEFILIPPII pair
0-2		1	4	5	0	1	1
3-5		0	5	2	2	1	0
5 - 100		3	1	2	2	5	4
125- 225		3	2	2	4	2	3
0-5	Total Associated	1	9	7	2	2	1
> 5	Total Unassociated	6	3	4	6	7	7
	Total for each meadowlark species	7	12	11	8	9	8

data non-independent. The one color marked female cowbird (netted in a farmyard nearby) that appeared during the sampling period, was recorded twice. The following analyses are made bearing in mind the possible violation of underlying assumptions of the statistical tests. However, unless the probability levels are close to the rejection area (usually .05 level), the tests are tolerant of some violation of assumptions (see for example Bradley 1968). I have analyzed data in 2 x 2 contingency tests using the Fisher Exact Probability test (hereafter referred to as FEP2) (FORTRAN program from Sokal and Rohlf 1969), and the "p" value shown in the accompanying tables is the probability that the null hypothesis is true given the observed results. No statements of significance or designation of significance levels will be made, rather, the probabilities speak for themselves.

I treated cowbird-meadowlark distribution as linear, since only the fences and utility poles were used by the cowbirds. Since the fenceposts were at regular intervals, I could estimate distances quite acurately, and possible errors in estimation are compensated by grouping all distances $>$ 25 meters, into 25 meter classes.

An association was defined as a cowbird within 5 meters of a meadowlark or vice versa. During the survey period when I searched for nearest meadowlarks, along

225 meters of fence to either side of a cowbird, the probability that the nearest meadowlark would be associated was 10/450=.022 (see Table 24).

RESULTS AND INTERPRETATION

The first series of null hypotheses is based on three days of observations on cowbirds that visited the study area. Three factors were examined: 1) the species of meadowlark nearest the cowbird; 2) the distance to the nearest meadowlark, (including association vs. non-association); 3) possible differences between females, males or pairs of cowbirds. I did not note the distance between cowbirds and other species on the study area, or between cowbird and next-closest meadowlark, and it is possible that other less obvious reslationships exist as well. The null hypotheses tested follows (letters and numbers refer to the sub-table in Table 26.

a. For cowbirds, the distance to the nearest meadowlark neighbor is that expected by chance (binomial test P=.022; probability for males (a2) p = .015, for females (a3) and pairs (a4) p<.000001.

b. Cowbirds are equally likely to have associated with them a P. militaris or P. defilippii. For all (b1) p=.012; for females (b2) p=.048; for males (b3) p= > .50; for pairs (b4) p=.074.

c. Male and female cowbirds are equally likely to be found associated with meadowlarks. For militaris (c1) p=.063; for defilippii (c2) p=.423; for any Pezites (c3) p=.067.

d. For non-associated cowbirds there is still a tendency to be found closer to meadowlarks than would be predicted from the available area. For P. militaris p>.50; for P. defilippii p .50. (Not in table).

e. For unassociated cowbirds, the proportion of militaris and defilippii nearest neighbors is similar to the proportion of the two species available along the fence (goodness of fit X^2=8.2; p<.005). (Not in table).

f. For associated cowbirds the proportions of militaris and defilippii nearest neighbors is similar to the proportion of the species available along the fence (goodness of fit X^2=48.2; p<.00001). (Not in table).

g. For non-associated cowbirds; comparing those with militaris vs. defilippii as nearest neighbors, the cowbird-meadowlark distance was equally likely to be less than or greater than 100 meters (p=.888). (Not in table).

h. For pairs of cowbirds, courtship was equally likely to occur in associated and in unassociated pairs ($p=.0131$). (Not in table).

Physical association between two individuals (conspecific or heterospecific) may reflect a positive social attraction between the two, attraction to a particular feature of the environment such as food or shelter, or random dispersal. The first two cannot be distinguished by statistical tests on the above data. The data do demonstrate, however, that cowbirds present on the study area have a strong (non-random) probability of being found close to a meadowlark, particularly P. militaris. The available perches for these species were essentially confined to the fences along the road, were uniformly spaced and were available on both sides of the road. Rarely did I see a cowbird perched on a fence across the road from a meadowlark rather than on the same fence (no such observation during the above sampling periods). In addition, cowbirds were almost never observed feeding on the study area. Therefore I am confident that the physical proximity of cowbirds and meadowlarks was not due to similar responses to available perches or feeding areas.

Having demonstrated that cowbirds associate with meadowlarks it is necessary to determine which species was attracting and which was attracted, Pezites were

TABLE 26. Binomial and contingency table tests for association vs. non-association between Molothrus bonariensis and meadowlarks. Except for (a1) all data are in contingency tables analyzed with the Fisher Exact Probability and the p values represent the cumulative 2-tailed probability that the two groups being compared are not different. Tables a1-a4 are tested with a binomial test for the probability that observed associations (cowbird < 5 m from meadowlark) could have occurred at random (P=.022, Q=.978). See explanations in text.

Binomial Tests (P=.022)

a1 All Cowbirds

Associated	22
not associated	33
n	55

p_{cum} <.00000001

a2 Female Cowbirds

Associated	11
not associated	10
n	21

p_{cum} <.00000001

a3 Male Cowbirds

Associated	3
not associated	12
n	15

p_{cum} = .015

a4 Pairs of Cowbirds

Associated	8
not associated	11
n	19

p_{cum} =.00000001

Fisher Exact Tests on Contingency Tables

b1 All Cowbirds

	<5m	>5m
near militaris	17	13
near defilippii		

p=.0117

b2 Female Cowbirds

near militaris	9	3
near defilippii	2	7

p=.048

b3 Male Cowbirds

near militaris	1	5
near defilippii	2	6

p> .50

b4 Pairs of Cowbirds

near militaris	7	4
near defilippii	1	7

p = .074

c1 Near militaris

	<5m	>5m
male cowbirds	1	5
female cowbirds	9	3

p=.063

c2 Near defilippii

male cowbirds	2	6
female cowbirds	2	7

p > .40

c3 Near any Pezites

male cowbirds	3	12
female cowbirds	11	10

p=.067

g Nearest neighbors of Unassociated cowbirds

	25-100m	>100m
militaris	0	7
defilippii	11	9

p = .888

h courtship in cowbird pairs

	<5m	>5m
Courtship	0	7
No courtship	8	4

p = .0131

breeding and defending territories on the study area, and at least one bird was almost always visible. Cowbirds, on the other hand, covered a much wider area, and although they deposited eggs on the study area, they came and went as transients, and could often be seen making long flights to distant parts of the Estancia. Many times I saw cowbirds arriving on the study area fly directly to a perched meadowlark. The meadowlark occasionally flew away, but I never saw one fly towards a cowbird, except for situations where a cowbird was sitting near a meadowlark and the mate of the meadowlark flew in to join them. There was no reason to doubt that cowbirds were attracted to the meadowlarks, and not vice versa.

I examined in more detail the difference in attractiveness between the two species of Pezites. As mentioned above female cowbirds were much more strongly associated with militaris than with defilippii, and the same applied for all cowbirds, but not for male cowbirds alone, in the survey period. Of the 22 close associations (<5 meters) for all cowbirds 17 were with P. militaris (77%). For non-associated cowbirds, the nearest neighbors were 13 militaris and 20 defilippii. The difference is significant (2x2, FEP2, p=.0000001). On November 14, 1971, during the survey period, I censused meadowlarks and found 5 pair of militaris and

21 pair of *defilippii* with territories abutting on the road (=1.5 km of road). If cowbirds were to pick meadowlarks at random, one would expect a ratio of 5:21 for nearest neighbors. Based on this expected ratio, I tested goodness of fit with a Chi Square test and found that associated cowbirds seemed to strongly favor *militaris* (X^2 goodness of fit =48.2; $p<.00001$). Unassociated cowbirds also had significantly more than the expected number of *militaris* for nearest neighbors (goodness of fit $X^2=8.76$; $p<.005$). It seems unlikely, but not impossible that cowbirds were attracted to *militaris* but did not always approach them closely. If this were true, then I would expect that unassociated cowbirds with *militaris* as nearest neighbors might have a lower "distance" than those with *defilippii* as nearest neighbor. Data in Table 25 show that for 13 cowbirds with *militaris* neighbors the mean distance was 115.4 $\pm$60.8 m. while for 20 with *defilippii* neighbors the mean distance was 110.0 $\pm$50.26 meters (t=0.27, not significant). A more likely explanation lies in the fact that male *militaris* regularly perch on fences and utility poles and are more likely than *defilippii* to be visible at a distance (both to cowbird and human); this could introduce a strong bias if both birds were at a distance.

RESPONSES OF COWBIRDS TO MEADOWLARKS --- REAL AND ARTIFICIAL

The above data collected on a three day survey near the end of my field work in Argentina, involved cowbirds as Index species. They serve for comparison with observations made when meadowlarks were Index species and I observed cowbirds responding to them. While observing meadowlarks I noted where each bird was singing (ground, grass, fence, or utility pole), and whether cowbirds were attracted to them. I recorded similar data for my playback tapes with a Pezites decoy, determining whether placement of the decoy and the type of song played had any significance. More attention should be paid to positive cowbird responses than negative ones, since in some cases there may have been no cowbirds around to respond. Data are presented in Tables 27 and 28 and are analyzed with 2x2 contingency tables and the Fisher Exact test (2-tailed).

RESULTS AND INTERPRETATION

This series of null hypotheses is based on the response of cowbirds to live meadowlarks and to meadowlark decoys and song playback tests. No a priori significance levels are designated. The "p" value listed is the exact probability that the stated null hypothesis is true for each data set. Lower case letters

and numerals refer to subtable of Table 27.

a. For both militaris and defilippii, silent decoys and decoys accompanied by primary song playback, were equally attractive to cowbirds (p=.0034).

b. Live male meadowlarks on fence or ground were equally attractive to cowbirds. For both species (b1) p=.000043; for defilippii (b2) p=.0047.

c. Live male meadowlarks on utility poles or ground were equally attractive to cowbirds. For both species (c1) p=.81; for militaris (c2) p=.152.

d. Decoys with primary song were equally attractive on ground or on fence. For both species (d1) p=.0024; for militaris (d2) p=.0084; for defilippii (d3) p=.274.

e. Live singing males and decoys with primary song were equally attractive to cowbirds. For both species (e1) p=.258; for militaris (e2) p>.50; for defilippii (e3) p>.50.

f. For live male meadowlarks militaris and defilippii were equally attractive to cowbirds. For males on fence (f1) p=.020; for all males (f2) p=.00045.

g. For decoys with primary song, songs of militaris and defilippii were equally attractive to cowbirds (p=.00058).

h. For decoys with songs of *defilippii*, primary and flight songs were equally attractive ($p=.173$).

i. Decoys with *defilippii* songs and silent decoys were equally attractive to cowbirds. For primary song (i1) $p=.173$; for flight song (i2) $p=.33$; for any song (i3) $p=.387$.

j. Decoys with *militaris* song and silent decoys were equally attractive to cowbirds ($p=<.0001$).

k. Live singing male meadowlarks and silent decoys were equally attractive to cowbirds. For *defilippii* (k1) $p=.097$; for *militaris* (k2) $p=<.00004$.

The following general conclusions can be drawn from the probabilities associated with the above null hypotheses:

1. Whether from live males or decoys, songs of *P. militaris* were more likely to attract cowbirds, than were songs of *P. defilippii*.

2. For live *militaris*, males on utility wires and fences were equally attractive, while decoys with *militaris* song were more attractive on fence than on ground.

3. There was no significant difference in the effect of live male *militaris* and decoys with primary song, and both were more attractive than silent decoys.

4. Live singing male *defilippii* were slightly more attractive to cowbirds than were silent decoys, but decoys with *defilippii* songs were not.

These results confirm that at least on the study area, *M. bonariensis* is attracted to *militaris* but much less so or not at all to *defilippii*, and suggests that the vocalizations are of some importance not only in attracting the cowbirds but in allowing species discrimination by the cowbirds.

There are several ways in which this type of study might be greatly improved in the future. Although I usually timed the arrival of meadowlarks, I rarely did so for cowbirds. These data would be interesting (in a few cases cowbirds arrived before meadowlarks). In this set of studies I only occasionally noted the duration of the cowbirds association with the meadowlarks or decoys, and this is probably an important aspect of the host-parasite relationship. If cowbirds are not strongly attracted to *defilippii* and do not parasitize it regularly in the Saudade area, I would predict that cowbirds that do respond to *defilippii* would stay with it only briefly. With the equipment utilized the relative volume of *militaris* and *defilippii* songs differed in carrying power, this being modified by their position. For example, the playback of a *defilippii* flight song was greatly attenuated if the speaker was in

TABLE 27. Contingency tables analyzed for positive and negative responses of Shiny Cowbirds to live meadowlarks and decoys.

(Data are analyzed using Fisher Exact Probability, and the p values shown are two-tailed probabilities)

\+ Cowbird approaches to within 5 meters

\- Cowbird does not approach to within 5 meters

	+	-
a FOR ALL DECOYS		
with playback	43	128
no playback	4	53
p =.0034		
b1 FOR LIVE PEZITES		
Live ♂ on fence	44	96
Live ♂ on ground	6	73
p =.000043		
b2 FOR P. DEFILIPPII		
Lived on fence	23	71
Lived on ground	6	73
p =.0047		
c1 FOR LIVE PEZITES		
Lived on pole	9	24
Lived on fence	44	96
p = .81		
c2 FOR P. MILITARIS		
Lived on pole	9	24
Lived on fence	21	25
p =.152		
d1 FOR DECOY + 1° SONG		
Decoy on fence	32	48
Decoy on ground	9	50
p =.0024		
d2 FOR DECOY + MILITARIS SONG		
Decoy on fence	25	26
Decoy on ground	7	29
p =.0084		
d3 FOR DECOY + DEFILIPPII SONG		
Decoy on fence	7	22
Decoy on ground	2	30
p =.274		
e1 FOR PEZITES MALES		
Live singing ♂	59	192
Decoy + 1° song	41	88
p > .50		
e2 FOR MILITARIS SONG		
Live singing ♂	30	48
Decoy + 1° song	32	55
p > .50		
e3 FOR DEFILIPPII SONG		
Live singing ♂	29	144
Decoy + 1° song	11	73
p > .50		
f1 LIVE MALE ON FENCE		
P.militaris	21	25
P.defilippii	23	71
p =.020		
f2 FOR ALL LIVE ♂♂		
P.militaris	30	48
P.defilippii	29	144
p =.00045		
g DECOYS + 1° SONG		
P.militaris	32	55
P.defilippii	11	73
p =.00058		
h DECOY + DEFILIPPII SONG		
Primary song	9	43
Flight song	2	30
p =.258		
i3 SINGING VS SILENT DECOY		
Silent	4	53
defilippii 1°	9	43
p =.173		

(Table 27 con't)

		+	-
i2	SILENT VS DEFILIPPII SONG		
	Silent	4	53
	Flight song	9	43
	p = .33		
i3	SILENT VS DEFILIPPII SONG		
	Silent	4	53
	Any song	2	30
	p =.387		
j	DECOY ± MILITARIS SONG		
	Silent	4	53
	Primary song	32	55
	p <.0001		
k1	P. DEFILIPPII VS DECOY		
	Live singing ♂	29	144
	Silent decoy	4	53
	p =.097		
k2	P. MILITARIS VS DECOY		
	Live singing ♂	30	48
	Silent decoy	4	53
	p <.00004		

TABLE 28. Cowbird Responses to live Meadowlarks and to Decoys.

+ = cowbird approaches to within 5 meters of the bird or decoy.

N = total number of trials for which these data were recorded.

% = +/N(100) Percent positive Responses.

I. RESPONSES TO LIVE MALES SINGING FROM PERCH

Location of Perch	P. militaris			P. defilippii			Total
	N	+	%	N	+	%	%
On utility pole or wire	32	9	28.1	0	0	0	28.1
On fence post or wire	46	21	45.7	94	23	24.5	31.4
On grass clump	0	0	0	79	6	7.6	7.6
TOTAL FOR LIVE BIRDS	78	30	38.5	173	29	16.8	23.5

II. DECOY WITH OR WITHOUT PLAYBACK OF SONGS

Location of Decoy	P. militaris song			P. defilippii song			Total
Decoy on fence + 1° song	51	25	49.0	29	7	24.1	40.0
Decoy on ground + 1° song	36	7	19.4	23	2	8.6	15.3
TOTAL	87	32	36.8	52	9	17.3	29.5

III. ADDITIONAL TESTS

Decoy on fence + silent	57	4	7.0				
Decoy on fence with flite song				32	2	6.3	

the grass, although the song has good carrying capacity when given in flight. A study of this sort should more carefully regulate the volume of competing songs. Also I did not distinguish between the attractiveness of live militaris that were singing or not singing. In some cases cowbirds arrived near a militaris during a song bout and at other times when there was no song bout, but no usable data was obtained on this matter. In interpreting all of the responses to playback, one must remember that if meadowlarks arrived before cowbirds, it is likely that the latter would be responding partly to the live meadowlarks rather than to just the decoy. However, since the meadowlarks responding to decoys often did not sing, I have ignored this complicating factor in the above analysis.

OBSERVATIONS OF INTERSPECIFIC BEHAVIOR: MEADOWLARK AND COWBIRD

Since on most days observations of cowbirds were secondary to observations on meadowlarks, I unfortunately did not time or record the details of all sessions of association between the species. Particularly I usually did not time the associations between cowbirds and defilippii, and even for militaris my data are not a random sample, since they are based on only a few pair of militaris (6 pair) and these are pairs that I knew to

alter their behavior in response to the presence of cowbirds.

If cowbirds do have a strong preference for militaris over defilippii I would predict that in those cases (29 of 173 natural and 9 of 52 playback periods) where cowbirds did associate with defilippii, the distance between them would be greater and the duration of association less, than for cowbird-militaris interaction. I did not obtain data suitable for testing this prediction.

"PATIENCE"

For lack of a more convenient term, I will define as "patience" the ability of a bird to sit still and watch or outwait its potential host or parasite. Assuming that cowbirds must observe hosts building a nest and that the hosts must adjust their behavior so as to avoid having their nest discovered, "patience" is a virtue in the evolutionary sense of being an important adaptation.

Cowbirds, particularly females sat silently for long periods of time, within 1-3 meters of the meadowlarks. The cowbirds sat still with apparent disinterest, while the meadowlarks were perched on the fence or pole. If the latter flew to the ground, the cowbirds stared at the ground as if they were watching intently. It was

not possible for me to determine what the meadowlarks were doing, or whether the cowbirds were actually staring at and observing the meadowlarks, but it seemed that that was the purpose of the cowbird behavior.

After sitting more or less still on the fence for 5 to 10 minutes, the meadowlarks, particularly the female, might begin to preen, to give "nervous" outward flicks of wings and tail, or to give soft "chup" notes. Often the meadowlarks would sidle along the wire for a short distance or fly to the next fence post, a few meters away, with the cowbird sometimes following. The male meadowlark, if present, was usually the first to depart. Female meadowlarks usually left before female cowbirds, reflecting less "patience". Of 16 timed "patience" bouts the meadowlark left first in 12 cases (Binomial test, 2-tailed; p=.028; Siegel 1956:250).

I have already (see Chapter 7) referred to "patience" which female meadowlarks display when an intruder is present while they are trying to bring food to the nest. It is an assumption that the meadowlarks are reacting similarly when cowbirds are present, but certainly natural selection against parasitized individuals would operate in favor of such a reaction. In the 16 times bouts, I determined whether the "patience" of an interacting female meadowlark and female cowbird were correlated. When one bird left, the other was likely to

leave within about a minute, the female meadowlark to resume her activities, the cowbird to look elsewhere. Consequently, the high correlation between the patience-times (Kendall Tau = .784, z=4.236; $p<.00003$) is not surprising. Since the times are not independent, there is no point in comparing mean "patience-times". Mayfield (1961) noted that M. ater females spent long time periods watching hosts build nests.

In most cases, cowbirds flew within 30 seconds, after a meadowlark left the area. In approximately 1/3 of the cases the cowbirds followed the meadowlarks, while in other cases they moved to a new position along the road or made a long flight out of the study area. If the meadowlarks flew to the ground nearby, however, the cowbirds remained in all but two cases.

When both male and female meadowlarks were present, the cowbirds did not show apparent preference for either, and often sat between them. On at least six occasions, I noted that a singing male meadowlark, stopped singing, immediately after a cowbird joined it. On at least four occasions, I noted that a female meadowlark, which had been on the ground, flew up to the fence, when a cowbird flew to the fence nearby. These anecdotal data do not allow statistical analysis, but are consistent with the hypothesis that meadowlarks modify or interupt behavior when the cowbirds arrive.

Meadowlarks never showed any aggression towards cowbirds, their main responses being "patient" sitting or retreat. Even immediately following a display towards an overflying male Pezites, a territorial male, returned to its perch where a male and female cowbird were associated with his female. He landed, and paid no attention to the cowbirds, even when the female cowbird moved to within 1 meter of him. I never saw wild cowbirds engage in preening solicitation display discussed by Selander and LaRue (1961) and Selander (1964) (whereas a captive male M. bonariensis which I have raised, solicits vigorously). Thus the function imputed to this display by Selander and LaRue (1961) as a means of reducing host aggression, does not apply to the cowbird-meadowlark interaction, perhaps because aggression is not prominent to begin with.

THREE CASES OF COWBIRD-MEADOWLARK INTERACTION

Meadowlarks are seldom seen carrying nesting material for long distances (Marchant 1960, present study, among others). The two times when female defilippii were seen with nesting material, they were flushed from the proven or suspected vicinity of the nest. Female militaris were seen five times with nesting material, and in 3 cases cowbirds were present. On one occasion a pair of militaris flew across a pasture, the female carrying material, and landed on a fence where

they were joined within about 30 seconds by a female cowbird. On the second occasion, a male meadowlark was joined by a female cowbird, and about 15 seconds later the female meadowlark flew up from the field, with material. On another occasion, I saw a male and female cowbird and a female meadowlark with nest material, sitting on a fence. The first case represents a long flight with nest material, which is the only one I saw; another represnts what might be called interuptive behavior in the presence of a cowbird; the third cannot be classified. I believe that, like its relatives, P. militaris almost invariably gathers nest material on the ground near its nest, but perhaps it occasionally gathers material at a distance and flies with it to the nest site. This would certainly facilitate nest-finding for cowbirds or for predators, and selection should operate against such behavior.

Further details on these cases are given below to illustrate the responses of the two species.

CASE I. Saudade female YY/BB and her mate flew across a pasture and landed on a fence, and then almost immediately flew 50 meters down along the fence. Nesting material was conspicuous in the female's bill, and I noted that she regularly flew ahead of the male. Less than 30 seconds later, a female cowbird arrived from a different direction, and sat about 1 meter from the

female militaris. The male militaris flew an additional 30 meters to a song perch on a utility pole, where he remained silent for about 5 minutes before dropping down to the grass to forage. The female cowbird sat quietly, and after 18 minutes the female meadowlark increased her wing-flicking and chupping. Shortly the male meadowlark flew in and landed between the cowbird and the female meadowlark who sidled away from him. She then flew to the lowest strand of the fence, hopped to the ground, and about 5 seconds later returned to the fence, still with nest material. The male gave three alarm notes in quick succession, flew down the fence past the female who followed him about 50 meters into a short grass field, where she foraged for over 30 minutes, eventually dropping the nest material. The female cowbird flew back in the direction in which she had come after briefly "watching" the meadowlarks. Later I found the nest of this pair of meadowlarks, within 5 meters of where the female had been sitting on the fence. It was parasitized.

CASE II. Male YY/YY was sitting on a fence, and I saw a female Molothrus fly in and sit about 3 meters from him. Within 15 seconds, an unmarked female militaris apparently mated to YY/YY flew up from the fencerow with nesting material, and landed on the fence about 10 meters away. The female cowbird that had apparently been

watching her, now moved over to sit near her. The male meadowlark dropped off the fence to forage, but within about three minutes he returned to the fence and landed between the cowbird and his mate. After 8 minutes, during which time the male meadowlark gave occasional alarm notes, and the female became more nervous, the male flew off the fence out into the field. Two minutes later the female cowbird flew into the grass about 10 meters down the fence row. Judging by the cowbird's behavior, the female meadowlark,progressed back to her original position, from which I flushed her. I did not find the nest immediately, but ten days later I found it, well-concealed in a thistle, it contained four meadowlark and two cowbird eggs.

CASE III. Female YY/YB mated to Pezites militaris male YY/BB, was observed on the fence with nest material. She was accompanied by a pair of cowbirds. The three birds remained this way for nearly 12 minutes, towards the end of which period, the female meadowlark exhibited increasing nervousness. She flew about four meters down into the grass, about one meter out from the fence, where she was joined by her mate who flew from a utility pole used as a song perch. I could not see them, but the cowbirds remained in place and were perhaps watching the meadowlarks. The meadowlarks remained out of sight for 14 minutes, and then flew up without nest material,

toward the woodlot on the edge of the territory. The pair of cowbirds followed them almost immediately, and the four birds disappeared in the vegetation. I never found a nest near the site of this interaction, but 16 days later I found their nest with 3 cowbird eggs and 2 meadowlark eggs in a fencerow in the woodlot. Possibly the meadowlarks had actually attempted to nest along the fence and then moved to a new site. Alternatively the activity in the fencerow may have been a form of displacement activity, due to conflict engendered by the presence of the cowbirds.

In each of these three cases the female cowbird showed greater "patience" than the meadowlarks, but the latter showed additional types of evasive activity. Assuming that the meadowlarks were actively nest-building, they interupted their activity to sit still on the fence for 10 to 18 minutes. Their behavior suggested a conflict between a drive to continue their previous activity and a drive to interupt it in the presence of the cowbirds, but this inference requires verification. Simmons (1951 b) has suggested how such conflicts can give rise to seemingly irrelevant but adaptive behavior such as distraction displays.

It of course remains an assumption that the meadowlarks were nest-building, and the cowbirds were watching, but in the case of the three militaris seen with nesting

material, the assumption seems warranted. In the end the interuptive behavior was not successful since the nests of all three received cowbird eggs.

COWBIRD COURTSHIP

A possible benefit of cowbirds associating with meadowlarks would be that it affords a focus for pairing or at least for mating for the cowbirds. Usually however, only one cowbird was present, and they were almost always silent. Although I frequently observed the conspicuous courtship display of M. bonariensis (see Hudson 1920, Wetmore 1926) I did not see it when they were associating with meadowlarks. For example, the observation in Table 25 gives 11 cases of cowbird pairs not associated with meadowlarks, and courtship occurred 7 times, compared with no courtship in 8 pairs near Pezites, (2x2, Fisher 2-tailed p=.013). One of the latter pair flew together down the fence after the female meadowlarks had flown away. The cowbirds landed on a utility pole, and within about 30 seconds the male began to court the female with exaggerated flight display, ruff-out and bubbling song, described by Wetmore (1926). These observations suggest that even during periods of active courtship, such behavior is inhibited when in close proximity to the potential host, and further that attraction to meadowlarks is not primarily

for pairing.

However, the association between parasite and host during nest-building may play a role in synchronizing the reproductive activity of the parasite as Chance (1940) suggested for Cuculus canorus.

PARASITISM AND COWBIRD PRODUCTIVITY

My examination of the literature on cowbirds, particularly Friedmann's summary (1963) revealed that most host species are smaller than the cowbird. P. militaris is, however, substantially larger. Fiora (1934) gives weights of 110-117 gms for militaris males and 59-62 gms for male M. bonariensis. My pampas specimens of the former ranged from 85-95 gms, and 7 male M. bonariensis ranged from 50-62 gms (mean 54.6 $\pm$4.2). The maximum weight noted on a 3 year old captive male Molothrus bonariensis has been 59 gms. Therefore, unless the cowbird chick hatches several days before the meadowlark, the host's chicks are likely to mature and fledge along with or instead of the parasite. I did not make a systematic attempt to measure the impact of parasitism on productivity of P. militaris, since I interfered with many nests.

There was a marked discrepancey between the frequency of cowbird nestlings in militaris broods and cowbird fledglings in militaris families. In fact, I

never saw a militaris adult feed a fledgling cowbird, and none of the 20-25 families of young Pezites included a cowbird. This despite the fact, that a cowbird reached at least 8 days of age in a militaris nest on the Saudade study area and presumably fledged.

The discrepancy could be due to two factors:

1. My sample of nests was biased, and there were many un-discovered militaris nests that were not parasitized and that accounted for the fledglings, while parasitized broods did not fledge, either because of direct cowbird interference or because of predation.

2. Young cowbirds were preferentially destroyed by predators.

The first possibility can be only partially dismissed. On the study area I found most of the nests that could possibly have been present. Elsewhere I found some families of fledglings in areas where I found no nests, so I did not know the frequency of parasitism. Thus some of the families, e.g. the two found in Chubut, were in areas that seemed free of cowbirds.

The second possibility also probably operates. Elsewhere (M.S.3) I present evidence indicating that nestling Shiny Cowbirds beg more noisily and aggressicely than meadowlark young. Hudson (Sclater and Hudson 1888)

noted this and wrote that parasitized nests of certain species were revealed to Chimango Caracaras (Milvago chimango) and other predators by the noisy cowbirds. Some of the nests that I found were revealed to me by the begging calls of the cowbird nestlings. Ficken (1967) reported an instance where a fledgling cowbird begged from an inappropriate bird and was killed. Thus even if meadowlarks and cowbirds fledge together, the latter may be subject to more intensive predation.

Also it may be true that nests with cowbirds are more likely to be found by predators (and by humans) than unparasitized nests. Mayfield (1960) believed that Kirtland's Warbler nests parasitized by Brown-headed Cowbirds did not fare worse than non-parasitized nests, but his data belie this. The 58 parasitized nests suffered 3-fold more predation and 2.5-fold more overall loss than unparasitized nests, and the differences are significant when compared by Chi Square tests on 2 x 2 contingency tables ($p < .01$ and $p < .001$).

Another intriguing question pertains to the role of Zonotrichia capensis as host. The three cowbird fledglings I saw in Argentina, including one at Saudade, were attended by Zonotrichia and Gibson (1880) and Marchant (1960) mention that this is the only host that they saw feeding fledglings. One wonders whether cowbird fledglings from Zonotrichia nests behave

differently and survive longer.

In any event, somewhere along the way, the numerous eggs laid by M. bonariensis give rise to very few grown young. I have no details on productivity of M. bonariensis but data for the North American M. ater (e.g., Berger 1951, Young 1951) reveal a low overall productivity.

POSSIBLE ADAPTATIONS OF DEFILIPPII

Although I present data which show a much stronger response of cowbirds to P. militaris than to P. defilippii, I have relatively little information on the interaction of cowbirds with defilippii. This is partly due to the infrequency and brevity of the interactions.

P. defilippii occurs entirely within the range of M. bonariensis while much of the range of P. militaris in Patagonia is not occupied by cowbirds, and where they occur together in Patagonia, the cowbirds tend to occupy more mesic habitats. Assuming that the pampas population of militaris is as I believe, a relatively recent arrival (see Chapter 7), it may be that large scale contact between militaris and cowbird is more recent, while defilippii on the other hand may have a historically longer exposure to the parasite with concomitant greater opportunity to perfect adaptations

for avoiding parasitism. In addition, compared with the larger militaris, defilippii nestlings are more likely to suffer and lose in competition with aggressive cowbird nestlings, so that given equal frequency of parasitism, there would be more pressure on defilippii than on militaris, to perfect anti-cowbird defenses. However, it is not clear what adaptations other than nest-placement and perhaps more surreptitious behavior during nest building are involved. The fact that defilippii is basically a pampas species, grassland its natural habitat, means that cowbird parasitism would not necessarily be required to select for nest-placement in fields. However, it could at the same time select for nest-placement away from elevated perches. If militaris is a naive host its situation would be analagous to that of the Kirtland's Warbler with respect to the Brown-headed Cowbird. This warbler, currently suffering heavily from cowbird parasitism, shows no aggression toward cowbirds, makes many conspicuous trips to the nest with building material, and does not respond negatively to cowbird eggs (Mayfield 1960). Although not unique among cowbird hosts, it is of interest because its contact with the Brown-headed Cowbird is believed to be quite recent (Mayfield 1960).

Although P. defilippii has been reported elsewhere as a host for M. bonariensis, the zero rate of parasitism

in my study, albit based on a very small sample, suggests that at present it is winning the co-evolutionary struggle to perfect mutual adaptations for consummating or minimizing parasitism, at least where a more susceptible alternate host is available. Observations on militaris-bonariensis interactions in Patagonia, may help clarify whether low selection pressure, naievete or some other factors account for the susceptibility of militaris to parasitism.

SUMMARY OF NEST FINDING BEHAVIOR AND COUNTER-ADAPTATIONS

Based on my observations at Saudade, both male and female Shiny Cowbirds are likely to respond to the sight or sound of a meadowlark by approaching it and landing near it. The response is heightened if the meadowlark is singing a militaris song, however songs of non-meadowlark species were not tested. Cowbirds can sit for many minutes, apparently watching the activities of their hosts or waiting for them to visit the nest site. Meadowlarks have several behavior patterns which make the cowbirds' task more difficult. Mainly they are the same as anti-predator devices, and serve to inhibit nest-finding. They do not attack but behave surreptiously to avoid calling attention to nest-building activities. If the cowbird is nearby they may interupt nest building activity, and may sit patiently. The

cowbirds, however, are usually more patient and often the meadowlarks---apparently suffering a conflict between desire to build and desire to sit---return to their nest-building. It is not certain that cowbirds actually watch the meadowlarks building, but there is no evidence against this and it seems a most reasonable conclusion. If meadowlarks leave, the cowbirds also leave, but do not necessarily follow their hosts. Cowbirds may engage in courtship behavior before or after their association with meadowlarks, but when associating, such behavior seems to be inhibited.

I never observed cowbirds engage in what could be called random or systematic searches for nests, although I am not sure that such behavior would be readily recognizable if it occurred. An obvious disadvantage of such a search is that it might lead cowbirds to inappropriate nests---those belonging to an unsuitable foster species or those at the wrong stage of nesting cycle or even abandoned.

Perhaps an important advantage of approaching hosts that are singing, lies in the relation of song to the reproductive cycle. Territorial male meadowlarks sing most prior to incubation, with song decreasing thereafter, and since the probability of singing is highest in the pre-laying period, the time when the cowbird needs to contact its host, it can "assume" that a singing host

is at a suitable stage.

Cowbirds do occasionally lay eggs in abandoned nests, sometimes filling these with eggs which spill out on the ground (Berger 1951, Friedmann 1929, 1963, Hudson 1920) but such wastage is not usual. The nests involved in such reports are often very conspicuous nests of Furnariids which could be found by direct search, if no suitable nest building activity were observed. However, Pereyra (1933) reported two nests of Leistes m. superciliaris with 12 and 19 cowbird eggs, and there is a clutch of 10 cowbird eggs from a nest of L. m. militaris in the British Museum (Natural History) collection. I presume that such nests were not found by direct search, but once found were abandoned by the host, yet continued to attract cowbirds. In any case I found no evidence of very large numbers of cowbirds eggs in any Saudade nests (4 is maximum number), nor did Friedmann (1963) in northwestern Argentina. Clearly there is much more detailed observational work which can be profitably devoted to studying the interaction of the Shiny Cowbird and its hosts. Long term, daily, patient studies, such as those of Chance (1940) on the Cuckoo, would be very valuable, particularly if individually marked birds were involved. The coevolution of host-parasite adaptations could be clarified by such studies.

SUMMARY

1. I focused attention on nest-finding behavior of the Shiny Cowbird and on some counter-adaptations of its meadowlark hosts. Coevolution is basic to any host-parasite relationship.

2. I conducted field work during two breeding seasons on the southern pampas of Buenos Aires Province, where Pezites militaris nests were parasitized in 22 of 23 cases, while none of 11 completed defilippii nests were parasitized. None of the defilippii nests were within 5 meters of fences, while all but one militaris nest were close to fences or other elevated perches. The differential parasitism and nest-placement are both highly significant ($p < .00001$), and the possible relationship between these two features is considered.

3. Cowbirds arriving on the study area were often seen associating with meadowlarks (cowbird-meadowlark distance of less than 5 meters), and in most cases the meadowlark was a militaris. Despite the preponderance of defilippii on the study area (militaris:defilippii ratio = 5:21), I found that of 22 cowbirds associated with meadowlarks, 17 were associated with militaris ($p < .01$).

4. Playback experiments using a mounted male Pezites decoy, and songs of both meadowlark species were used to investigate possible differential responses of cowbirds. A decoy accompanied by defilippii song was no more attractive to cowbirds than a silent decoy ($p > .10$) while a decoy with militaris song was substantially more attractive than one with no song or with defilippii song ($p < .01$).

5. Observations on both meadowlark species during nest building, indicate that militaris is more often seen carrying nesting material than defilippii, and this may facilitate nest-finding by cowbirds.

6. Individual cowbirds may learn to associate with militaris after successes in finding militaris nests and may shun defilippii if they have failed to find nests after a long period of watching.

7. If host preferences are culturally transmitted, so that cowbirds are likely to parasitize the species that fostered them, there might be no defilippii raised cowbirds around to associate with defilippii.

8. Despite the high rate of parasitism on militaris none of the families of militaris fledglings that I encountered contained cowbird young, and there may be few militaris raised cowbirds to carry on that tradition.

The only cowbird young I saw on the southern pampas were being fed by Zonotrichia capensis, the main host over much of the cowbird's range.

Meadowlarks show interuptive behavior if they have a cowbird associating with them, and they may demonstrate considerable patience, and delay nest-building while the cowbird is present. In 16 time trials, however, I found that cowbirds had greater patience in 13 cases ($p < .05$), which suggests that it is ahead in this aspect of coevolution.

Several cases of cowbird-meadowlark interaction are discussed.

9. Aggressive begging by cowbirds, and conspicuous behavior in general, may make them easy targets for predators, and may account for the lack of fledged cowbirds in Pezites families, but not for the apparent differential success of Pezites-raised vs. Zonotrichia-raised cowbirds.

10. The greater susceptibility of militaris to cowbirds compared with defilippii, may reflect the distributional history of these birds. P. militaris, apparently requires elevated perches, and may have been unable to colonize the pampas, prior to the construction of farms and fences. It may therefore be naive with respect to the cowbird.

SECTION III. ANALYSYS OF VOCALIZATIONS Chapters 9 - 14

9. General Features of Vocalizations, Vocal Behavior, Variability, and Analytic Techniques
10. Primary Song Analysis
11. Flight Songs and Flight Displays
12. Call Notes
13. Female Song and Sex Chases
14. Playback Experiments and Trapping

This study did not focus on the behavioral repertoire of the meadowlarks, and I made no attempt to provide an "ethogram" for any of the forms. I did, however, devote much time to studying and recording their vocalizations, and as a by-product some observations on displays were noted. Many of the displays I observed, closely resemble those described by Lanyon (1957) for Sturnella, and some are characteristic of the Icteridae as a group (e.g., Ficken 1963, Orians and Christman 1968, Williams 1952).

Some displays, such as "bill-tilting" or "head-up" postures used in aggressive encounters, are commonly found not only in many icterids, but in other passerines as well.

I have focused on the following aspects of meadowlark songs and calls:

1. Comparison of primary songs, flight songs, and call notes among the meadowlark species.

2. Estimation of song repertoire size among the meadowlark males.

3. Descriptions of the contexts in which different vocalizations are given, from which one may with care infer their function.

4. Cursory survey of geographical variation in the components of Pezites militaris song.

5. Responses of males to playback of conspecific and hetero-specific songs.

No attempt was made to systematically study vocal dialects or many other aspects of vocalizations and communication.

CHAPTER 9

GENERAL FEATURES OF VOCALIZATIONS, VARIABILITY, VOCAL BEHAVIOR AND ANALYTIC TECHNIQUES

Vocalizations play important roles in avian communication, and the topic has received extensive attention in several books (Armstrong 1963, Greenewalt 1968, Hinde 1969, Thorpe 1961). Variability in song frequency, structure and temporal arrangement, choice of song types, and changes in intensity, provide the opportunity to convey information about the identity and motivation of the singer (e.g., Emlen 1960, Falls 1969, Ficken and Ficken 1967, Gill and Murray 1972, Marler 1956, Smith 1963). Lanyon (1957), Marler (1957), Schwartz (1972) and Stein (1963) among others, have considered the role of vocalizations in species recognition, and numerous recent studies have been conducted using playback experiments to examine the function of different vocalizations or their components (reviewed by Ewert M.S.).

In this section I use the following terms for discussing the structure of bird songs:

Call: a relatively simple vocalization, often monosyllabic.

Song: relatively complex vocalizations, often involving a variety of sound components. May appear in several contexts, but typically are given by males on territories.

Figure: on a sonogram, an element of a song separated from other elements by a time gap (the terms note or element are often used).

Syllable: may be part of an element, continuous in slope or otherwise discrete.

Phrase: a series of repeated figures, with no apparent temporal separation.

Click: a single figure, vertical in appearance, characterized by a short duration, with energy distributed more or less evenly over a large frequency span.

Buzz: a single figure characterized by a large frequency span, and rapid frequency modulation, with or without amplitude modulation.

BIRD SONG:

Terminology regarding bird song is somewhat confused, and several classifications have been proposed. Some classifications are contextual; for example, Borror (1961) discusses advertising song. But since a male may

be advertising his presence to a female, or his territorial possessiveness to other males, both categories are subsumed under advertising song. Lanyon (1957) adopted the terms primary and secondary song, which do not directly refer to context.

Hinde (1953) noted that there is great difficulty in interpreting functional or causal features of different vocalizations. A bird may use a variety of sounds in a single context or the same sound in several contexts (e.g., Smith 1969). Generalization from one species to even a close relative may prove risky. For example, Catchpole (1973) reports that the "advertising song" of Sedge Warblers (Acrocephalus schoenabaenus) serves only to attract females, while for the congeneric and sympatric Reed Warbler (A. scirpaceus) the songs serve also in territorial defense.

In this section I use the term "primary song" to refer to the characteristic songs given by male meadowlarks which appear to function in large part to define the territorial boundaries. These songs are given from a perch. I use the term "flight song", classified as one type of secondary song by Lanyon (1957), which are given regularly over a birds' territory, in flight, when the chief purpose of the flight is related to the song. One species, militaris, occasionally sings in flight, but the song is infrequent, not related to its territory,

formless and unpredictable. "Sex chases", another form of "secondary song", (cf Lister 1953, Lanyon 1957) occur with females closely pursued by males, the latter uttering a rather soft, formless, warbled song. This song has been classed as "rehearsed song" by Lanyon (1957). Other types of singing (e.g., female song, subsong, whispered song, rehearsed song) were heard during the course of field work, but will receive less attention here. The above categories are descriptive and partly contexual and can be applied clearly to the major meadowlark vocalizations I encountered in the field.

Since bird song plays an important role in avian reproductive biology, it is always tempting to determine the function of song. Primary songs are generally given in the context of territoriality, particularly early in the breeding season. They indicate the location of the territorial male and his territory's boundaries, and presumably indicate his tendency to defend. Studies with muted Red-winged Blackbirds (Agelaius phoeniceus; Smith 1972, see also Armstrong 1955) indicate that such birds are unable to retain their territories. Songs may also stimulate other males in the population (Darling Effect) or mates, leading to synchronization of reproductive cycles. Song frequency may indicate to females the mated or unmated status of the male (von Haartman 1956, Catchpole 1973), and once mating has occurred, may

serve to maintain the pair bond and to provide stimulation assuring synchronization of reproductive cycles.

In studying meadowlark vocalizations, I have attempted to determine what activities precede and follow song, the location of the male in his territory (particularly with respect to the female's position), and the bird to which the display is oriented.

VOCAL VARIATION IN MEADOWLARKS

A study of acoustic communication must take into account types of variability in vocalizations. I categorize these as follows:

1. INTERSPECIFIC. Birds, particularly oscines, have songs characteristic of a species. Species very similar in morphology may show marked differences in voice, particularly if they are sympatric. The vocalizations may serve to isolate them, and since birds often react much more strongly to autospecific than heterospecific song, vocalizations can be used to study their systematic relationships (lanyon 1969, Schwartz 1972). Vocalizations are sufficiently variable that they are generally non-conservative, and often one can detect similarities or convergence among unrelated species subject to similar sound environments (Marler 1957).

2. INTRASPECIFIC. Several categories contributing to within-species variability exist.

   a. Geographic variation.

      1. Broad-scale. Populations of a species may show defferences in songs (little sharing of elements) over great distances. These differences should be distinguished from dialects (Marler 1960). In this study P. m. catamarcanus and P. m. militaris showed such differences.

      2. Dialects. Differences may occur between populations separated by small distances. There should be much sharing of song elements or patterns within an area and little sharing between areas. Dialects are maintained by song-learning, and by breeding in the same locality where one was raised. Birds showing high dispersion should not have dialects. Dialects have recently received extensive investigation (see below).

   b. Within population.

      1. Song types. Song types should be distin-

guished from song patterns. The former may differ markedly in their structure (e.g., see primary and flight songs of bellicosa) and different song types may appear in different contexts as indicated by Ficken and Ficken (1969), Lanyon and Gill (1964), Morse (1970) and others. Some species, e.g., Chipping Sparrows and White-crowned Sparrows seem to have only one song type (marler and Issac 1960, Marler and Tamura 1962).

2. Individual variation. For any given song type an individual may have only one pattern which it repeats over and over (e.g., Blue-winged Warblers Lanyon and Gill 1964), or many patterns (e.g., Sturnella magna, Lanyon 1957; Vesper Sparrow, Kroodsma 1972).

   Patterns usually differ in the arangement of or choice of elements.

   For any pattern there may also be individual variation in the timing and duration of elements within the song. Adjacent individuals singing the same pattern may

show characteristic individual differences, or the differences may be masked by the individual variation of each bird.

The present study was not undertaken to investigate song variation, but in the course of studying characteristic vocalizations and determining repertoire size, some relevant information was extracted and is discussed below.

ANALYSIS OF VOCALIZATIONS USING A SOUND SPECTROGRAPH

Selected vocalizations were played into a Kay 6061 B Sound-Spectrograph, with a range of 85-16000 Hertz. Spectrographic analysis provides a visual display of the pitch and temporal elements of sounds, allowing more objective analysis than is possible otherwise. Man, being visually-oriented rather than acoustically-oriented, finds such analysis far easier to interpret and compare. Amplitude is less clearly represented on the spectrographs. By choosing narrow or wide band filters, one can pay closer attention to either the frequency or temporal components of the songs. Both types of analysis were employed in this study, but unless otherwise stated, most spectrographs were made with the narrow-band filter (45 hz).

In this section I will summarize the song types,

durations and frequency ranges of the different meadowlark songs. Although songbirds do not produce frequencies less than 1 khz, they can apparently hear them (Konishi 1969). Similarly, Thorpe and Griffin (1962) found ultrasonic components in bird song recordings and concluded that they were probably not important in communication. Most of the fundamental frequencies they investigated fell below 8 khz. The meadowlark vocalizations occur mainly between 1400 and 9200 hz. Although the buzz components of defilippii songs often seemed to reach the top of a sonogram scale (8000 hz) half-speed playback showed a clear cutoff, usually below 8400 hz. Therefore, I have relied on standard speed sonograms throughout with only occasional spot-checks when energy concentrated near 8000 hz.

CHAPTER 10

ANALYSIS OF PRIMARY SONGS

Primary song (see Lister 1953, Lanyon 1957) is used here to refer to the songs delivered by male meadowlarks mainly in the context of territorial display. Primary songs are often the loudest and/or most frequently uttered song given during the breeding season. A male hearing a conspecific primary song within its territory is likely to respond aggressively by approaching the singer and threatening it, while territorial boundaries are often delineated by males on two adjacent territories counter-singing their primary songs in close proximity. Such display bouts may involve exaggerated displays such as jump-flights of the meadowlarks (Lanyon 1957 and below)

MILITARIS PRIMARY SONG

General impressions: Songs of militaris are readily recognizable as such and distinguishable from those of other Pezites. Although the primary songs of both militaris and defilippii may end in a terminal buzz, that of militaris is louder, has the main energy located in the note (below 5000 hz), and shows a terminal decline in pitch. The modulation rate is slower. This gives the note a nasal rather than buzzy quality. The introductory

notes of a militaris song are often syncopated (irregular alternation in note and interval length) and many are diphasic (V shaped or inverted V shaped figures). Introductory notes of defilippii tend to be more simple in form.

In any song bout, militaris males tend to repeat the same song (identical to the ear) perhaps with slight change in intervals. Common variations include aborting a song (much more frequent than omitting introductory notes) or doubling a song. Doubled songs may involve repetition of the same song or combination of two song patterns. Abortive songs sometimes consist only of the introductory notes or only a single note.

Song bouts may consist of 1 to perhaps 30 songs and are terminated by a perch change (flying to join a female or engage another male or "spontaneous") or by periods of silence. Playback of a tape loop would often cause a singing male to stop briefly or a silent male to sing (see Chapter 14). Often the song changed and a male began to duet with the tape. A more detailed study might reveal song-matching, that is changing to a song type more similar to the playback tape.

Most males observed for more than an hour gave at least two song patterns. Male YY/BB, the one studied most intensively, gave 6 distinct song patterns (Plates 1, 2) in 6 consecutive song bouts, in a period of 90

minutes, and 9 distinct song types in a morning. However, recordings made over a two week period yielded only 1 additional song pattern. Male GG/GG had six song patterns recorded (Plate 38) in 1970 and 1 of these was recorded in 1971---the only pattern he was heard to sing. The present evidence suggests that militaris males probably have from 5-12 song patterns in their repertoire.

Short (1968) distinguished two song types in a militaris population 23 km west of Bahia Blanca. The types differed in average length and in organization of the introductory notes. Both the choice of notes and their arrangement differed in the introductory portion. Examination of primary songs of YY/BB (Plates 1-3) reveal long, short, doubled and abortive songs, which do not all readily fit into these song types. For example, fig. 1B (1.85 sec.) is a short song with a weak vertical note which seems to be an 'a' element, an ascending note (not classified) and a loud downward slurred whistle (element f) an 'a' element, and a terminal buzz. The pattern is very close temporally to Short's fig. 9C, albeit with different elements. A common feature of some YY/BB and other songs is the insertion of a 'c' element into the terminal buzz with no intervening shorter notes (fig. 1C). Plate 1D is a long song (2.25 sec.) with a pattern of note arrangement that seems intermediate between Short's two types.

Despite the abundant variability in the introductory portions of militaris song there does appear to be a bimodality in duration which supports Short's categorization of two song types. Whether there is a contextual or other difference remains to be determined.

DEFILIPPII PRIMARY SONGS

To the ear, primary songs within a defilippii population seemed very uniform. The songs are typically 1.23 to 2.0 seconds in duration. The two to five introductory notes are relatively short and simple figures, often pur whistles. All songs end with a 'rectangular buzz' which usually spans the entire frequency range of the song. The low frequency portion of the buzz is usually attenuated so that measuring the frequency span is difficult. The lowest frequency of any buzz is about 2200 hz, the highest about 8800 hz, although most songs span 2500-7800 hz. Energy distribution is quite variable from bird to bird but is often uniform throughout the buzz of a single song.

I did not document more than one song pattern in the repertoire of any marked male. However, two or more males may give patterns which were indistinguishable on sonograms. Male BB/WB (Saudade) was recorded both in 1970 and 1971, and there was no appreciable difference

in song (see Plate 13D, E). This bird had an extremely weak buzz note, audible only at close range.

Although I have not attempted to measure within- and between- population variability in primary songs, a comparison of songs from Saudade, Tres Picos, and Bahia Blanca reveals overall similarities (see Plates 12, 13), and suggests that there is no dialect formation. This awaits further study.

BELLICOSA PRIMARY SONGS

In the field I could distinguish two main classes of primary song which I referred to as regular and alternate. Primary songs almost invariably ended with a buzz, a rectangle figure, sudden in origin and termination, covering a range of about 5-6 khz, with maximum frequency range from 1800-9200 hz. The main energy was between 4-6 khz. In the regular song, two main types of introductory notes were more or less horizontal elements and longer descending elements (Plate 19). Typically a song was initiated with two short highpitched elements, two long descending elements, and then a buzz. Plates 19-24 show the great variability between males in the Bujama population, where almost every bird had its characteristic song. However, several marked birds (see Plate 50) were known to have 2-4 song

patterns. The alternate type song (Plate 23) began with two long horizontal whistles around 3-4 khz, lasting about 300-400 (first) and 200-300 (second) milliseconds. These were followed by one or two short high pitched notes and then a buzz. The buzz component was the same in regular and alternate type songs, and I never documented an individual singing both types. I concluded that what seemed to be an alternate song was actually just a variant of the primary song, sung by about 15% of the males. The song seemed to be confined to the northern and western part of the study area, for none of the marked males or their immediate neighbors sang this type.

Typical bellicosa primary songs last 1.2 - 2.0 seconds depending on the number of introductory notes and on the length of the buzz. Two of the marked males with two primary songs, each had one with a short buzz (<400 msec) and one with a long buzz (>450 msec). In both cases the short-buzz songs were the most frequently used. It is possible that these constitute song types, but no adequate evidence on this point was obtained.

PRIMARY SONGS OF LEISTES

Like defilippii and bellicosa, both forms of Leistes have primary songs that begin with a series of short, discrete, whitled notes and end with a buzz. The sample of songs presently available does not clarify the relationship between the two forms, militaris and superciliaris. There seems to be a tendency for superciliaris to have more complex introductory notes and for L. m. militaris to have the final introductory note lead directly into the buzz, with no intervening pause (see Plates 31, 32). The buzz of both forms shows complex frequency modulation, and there seems to be a greater tendency for numerous discrete frequency bands within the L. m. militaris buzz. This may account for the louder and harsher and more nasal quality which is apparent to the human ear. The buzz of superciliaris actually sounds similar to that of defilippii.

In duration, Leistes songs range from 1.4 to 2.5 seconds. The frequency range is generally 2500-10,000, with the main energy between 4000-7500 hz. The pattern of introductory notes is quite variable from location to location (e.g., 20 km apart in Surinam). In western Buenos Aires I recorded a song pattern very similar to that given by nearby Myospiza humerallis, and Lanyon (see Plate 33) recorded a similar pattern in Sao Paulo.

These songs are unlike those I heard on the southern pampas, but it would be premature to speak of dialects at this time.

SUMMARY OF PRIMARY SONGS

1. Primary songs of militaris are the most complex of the group. Single songs last 1.4 - 2.4 seconds, and further study may reveal the existence of two song types (see Short 1968) distinguishable by duration and perhaps by function. The energy range is 1600 - 9000 hz., and for most songs the entire frequency range is spanned by the terminal buzz. The buzz differs from other species in having most energy below khz and in slower modulation rate. The main energy concentration occurs between 3000-5000 hz. Each male had several song types, and the repertoire is believed to range from 5 - 12.

2. Primary songs of defilippii are simpler than militaris songs with a few simple whistled introductory elements. Primary songs end with a rectangular-shaped buzz which usually spans the entire frequency range of the song (2000-8800 hz). Energy distribution is quite variable from bird to bird. No bird is known to have more than one primary song pattern.

3. Primary songs of bellicosa were reminiscent of those of defilippii, that is they ended in a rectangular-

shaped buzz note. The duration of the primary songs is 1.2 - 2.0 seconds. For all birds the frequencies ranged from 1800-9200 hz, with the main energy falling between 4-6 khz. Two main song types occurred in the Bujama population, but no individual was documented singing both regular and alternate type (differing in introductory elements). The duration of the buzz is bimodal with many songs having a buzz < 400 msec in length and others having a buzz longer than 450 msec. Two of the marked males with two primary songs each had a long-buzz and short-buzz song, and these may constitute song types when further data are at hand. Several marked males had from 2-4 song patterns.

4. Primary songs of both forms of Leistes also have discrete introductory elements followed by a terminal buzz. The duration is from 1.4 to 2.5 seconds, with frequency range of 2500 - 10,000 hz, mainly 4000-7500 hz. The pattern of introductory notes is quite variable. There is a tendency for superciliaris to have more complex introductory elements and for L. m. militaris to have the last introductory element connected temporally to the buzz. The quality of the buzz also differs between the two forms although the consistency of the difference remains to be evaluated.

CHAPTER 11

FLIGHT SONGS

The role of song-flights or flight displays in avian behavior cannot be separated from the general role of songs and displays. It is perhaps trivial to note that flight songs are characteristic of open country species. Armstrong (1947) noted that birds of open spaces may overcome the problem of sound dispersal over their territories, by engaging in noisy and conspicuous flight. He noted that deficiency in song tends to be counterbalanced by conspicuousness in flight, and suggested also that display flights might serve to stimulate the female rather than merely to attract her. In this report I distinguish sexual chases and their accompanying vocalizations (Howard 1920, Tinbergen 1939, Lanyon 1957) from flight songs which appear to serve an "advertising" role.

I consider flight songs to be of two general types. The first type, characteristic of several of the meadowlarks and of Bobolinks and Lark Buntings (Calamospiza melanocorys), is an explosive, nearly vertical flight, usually brief in duration, which coupled with the black or black and red plumage, calls attention to the singer and renders it conspicuous both visually and acoustically.

The second type, characteristic of skylarks (Alauda arvensis) and pipits (Anthus spp.), are prolonged songs, lasting over an hour in some species, and consist of relatively weak indistinct songs that are difficult to localize and which do not call attention to the brown birds which often sing from heights exceeding 100 meters.

CONTEXT OF FLIGHT SONGS

The context in which flight songs occur can be inferred from several categories of information:

1. Seasonality with respect to the reproductive cycle.
2. Sex, species, and breeding condition of other birds present.
3. Orientation of the display with respect to other birds or to features of the territory
4. Preceeding events.
5. Subsequent events.

I attempted to record the following information for each flight display studied during certain observation periods:

A. Male involved

B. Date and Time

C. Immediate preceeding event

1) spontaneous or cause unknown.

2) flushed by observer.

3) elicited by neighbor or decoy tape.

4) elicited by stranger.

D. Initial position, flight path, terminal position.

E. Angle and distance of approach and descent components of flight.

F. Maximum height obtained.

G. Primary songs given before or after flight song.

H. Orientation of song with respect to female or neighbors.

Rarely was it possible to record all categories for any single song, so that on different days I concentrated on certain aspects of the flight song behavior. Often, because of distance, one cannot determine whether a neighboring male has elicited a response, nor is it always clear what happens when two males meet at a distant territorial boundary. Similarly females of many grassland species spend much of their time out of sight in the grass, and it is not always possible to keep track of their location without actually intruding on the territory and disturbing the birds.

FLIGHT SONGS OF S. MAGNA AND S. NEGLECTA

Lanyon (1957) noted that both species of Sturnella occasionally deliver their primary songs in flight, while both species also gave a distinct flight song, the vocal component of which was an ecstatic warble similar to the voice of the Bobolink. S. neglecta delivers the flight song regularly, sometimes 3-4 per hour, and the song may be heard from March through October (Lanyon 1957). S. magna rarely gives the flight song, and Lanyon (1957) noted it on only 13 days in three breeding seasons. Saunders (1952) indicates that the frequency of the flight song in magna may vary from year to year and place to place.

Lanyon (1957) did not find a clear relation between flight songs and particular aspects of territorial or courtship behavior, and he interpreted them as manifestations of "intense excitement". He observed it in situations of territorial defense, often in males returning to their territory after chasing an intruder, and in association with females. He noted the apparent structural similarity between the flight song and rehearsed song, and indicated that they may be part of a single phenomenon, differing only in intensity.

MILITARIS FLIGHT SONG

P. militaris is apparently similar to magna with respect to flight songs. For a given male, one may spend several days without seeing or hearing the flight song, although one male, RR/RR, gave three in three days. As in magna, the songs are unpredictable and I had difficulty recording them. Fortunately they may last 5 seconds or more, and I succeeded in recording some incomplete renditions (see Plate 52). The apparent context of these songs is indicated in Table 29. Most originated while the male was near the female, and may be interpreted as indicating sexual excitement associated either with frustrated or successful copulation. However, the actual events were never witnessed because the birds were invariably out of sight in vegetation. Occasionally a series of primary songs was given after landing, but only once was a primary song given within 10 seconds of takeoff. Unlike the flight songs of defilippii, bellicosa and superciliaris the flights were unstereotyped. Some were sometimes given entirely vertically with the bird rising to 30 meters or more, giving a loud or whispered warbling song during the ascent. At the peak the bird might level off and fly a long distance horizontally or might drop nearly vertically, and the second phase might be either with or without song. On

occasion I observed a militaris to hover briefly, for about two or three seconds with accentuated wing beats, at the peak before continuing its flight. The average frequency of flight songs per male was prabably less than three per week for all males, but for such an infrequent event one would have to obtain a very large sample of songs before determining a frequency or comparing individuals.

The race catamarcanus of northwestern Argentina, apparently has a much greater tendency to sing in flight. Along the Rio Santa Maria, near Amaicha del Valle, Tucuman, Lanyon recorded flight songs of male catamarcanus on 27 Nov. 1970. A pair of birds were collected and had enlarged gonads. Males engaged in frequent song flights, during which they uttered loud warbled songs (see Plate 37) very similar to those given by neglecta and bellicosa. The form of the song is similar to that given in flight by nominate militaris, but the frequency is more typical of neglecta. By the time I reached Tucuman in early January, there were no more song flights given over a period of four days of field work.

Since males of both races approached playbacks of the primary songs of the other race, and since there is no reason to question the overall similarity of catamarcanus to nominate militaris, it is interesting to

TABLE 29. Song flights of militaris.

DATE	LOCATION	MALE	PATH AND ORIENTATION	PRECEEDING EVENT	SUBSEQUENT EVENT
1970					
Nov. 12	Saudade	unm.	Vertical flight with song, then flew off about 100 meters at a height of >30 meters.	near group of 5 other ♂♂	unknown
Nov. 12	Saudade	GG/GG	Vertically up to 20m, then away 200 m to fence	in Stipa near ♀	gave three 1° songs
Nov. 12	Saudade	unm.	long horizontal flight, 10m up, for 300 m. to next fence.	♀ was 10m from origin	gave five 1° songs
Nov. 28	El Condor	BB/YY	Vertically up to 20m, then out of sight over 100m away.	2hrs of many primary songs Location of ♀ unknonw	unknown
Dec. 10	B37E	RR/YY	Arc up to 15m, after 45 min. absence	grass	to decoy, silent.
DEC. 11	BB7E	RR/YY	Arrives on territory in early morning with long horizontal flight.	unknown	feeds near ♀
Dec. 12.	BB7E	RR/YY	Vertically to 10m, then away about 100m.	leaves ♀	to fence, no songs
Dec. 12.	BB7E	RR/RR	Vertically up to 20m, then 100m away	Leaves ♀	unknown
Dec. 12.	BD7E	RR/WW	Long horizontal flight across territory toward singing decoy, then gives weak warble as he rises vertically over decoy	unknown	lands 10m from decoy, no songs
Dec. 13.	BB7E	RR/YY	Long horizontal flight at 30m up, more than 100m to decoy area, song lasted 5-6sec.	unknown	to decoy, no songs
Dec. 16.	Saudade	GG/GG	Arc up to 10m, and then down to pole	left decoy	on pole, no song
Dec. 16.	Saudade	GG/RR	Vertically to 20m., then horizontal flight silently for 100m to join female about 5m from decoy.	unknown	sits near ♀, then flies to decoy & begins songs.
Dec. 16.	Saudade	GG/BB	Low horizontal flight, 10m up for 50m	from ♀	to neighboring ♂ one primary song
Dec. 18	Saudade	GG/GG	Brief horizontal flight, 5m up, for 10m.	from ♀	to fence near decoy
Dec. 18	Saudade	♂6 unm	Long horizontal flight 10-15m up, for 200m	from ?	to decoy, 3 1°songs
Dec. 18	Saudade	GG/RR	Long horizontal flight 20m up, 100m long	from ?	to decoy, no song
Dec. 18	Saudade	GG/RR	Silent horizontal flight, 20m. to join ♀, then gives brief warble while sitting on fence next to her (rehearsed song)	from ?	with female
Dec. 25	22 km W of Medanos	unm	Vertical flight to 30m, then descends at steep angle,	leaves ♀	lands on fence 5m from female

TABLE 29. Song flights of P. militaris

Table 29 con't.

1971

Oct. 15[r]	LaValle	unm	Warbles from perches on two occasions	-----	-----
Oct. 18	BB7E	unm	Short horizontal flight to fence	in grass with ♀?	sang 1 min later
Oct. 18	BB7E	RR/GG	Long horizontal flight 10 up, 50+m long	from ♀	to fence, gave 4 1° songs
Oct. 19	BB30W	BB/WW	Vertically up to 20m, landing in bush	from ♀	sits over ♀, no song
Oct. 22	Saudade	YY/YY	Vertically up to 10m, directly over ♀	hovers over ♀	to fence over ♀ No song
Oct. 23.	Saudade	YY/BB	Short flight from fence to ground, <10m	singing on fence	joins ♀ in grass
Oct. 23.	Saudade	YY/BB	Short vertical flight to 5m, with subdued song, hovering over female	With ♀ in grass	Rejoins ♀ in grass
Oct. 23[r].	Saudade	YY/YY	two short flights from pole to grass to join ♀; one with "twitter" one with "warble" On second, he hovers over female with warble.	on pole	joins ♀ in grass Both fly to fence He gives 6 1°song
Oct. 28	Saudade	YY/BB	Long high arc to fence, up to 40m, and over 70m long (his first flight in 6 days)	with ♀ in grass	sings on fence
Oct. 31.	Saudade	YY/YY	Arcs up to 15m, hovers while singing for about 2 seconds, then lands on fence	in wheat perhaps with ♀	to fence near decoy
Nov. 2[r]	Pto Tombo	unm	Short horizontal flight 5m up, for 20m with weak song.	foraging on ground with young	sings in bush

unm=unmarked male

r = rehearsed song rather than song-flight

SUMMARY OF SONG FLIGHTS (some songs fit more than 1 category)

ORIGIN		DESTINATION		FLIGHT PATH	
Unknown	10	Unknown	3	Short horizontal	5
In grass, no ♀	1	To join ♀	9	Long horizontal	9
With female	13	To decoy	7	Vertical then down	6
With decoy	1	To song perch	2	Vertical, then long horizontal	7
On song perch	3	Primary songs	8	Short drop	2
				Hovers	1
				Rehearsed song	2

determine why one race frequently give songs in flight while the other does not. An attractive possibility is that the riverine marshes inhabited by catamarcanus are dominated by tussock grasses and bushes, 2-3 meters high, whereas the Patagonian woodlands occupied by militaris provide elevated perches 3-6 meters high. The greater use of flight displays by the population with lower perches is consistent with the generalized relationship between flight songs and open country. However, the difference in flight song output between magna and neglecta is not explainable on this basis.

DEFILIPPII FLIGHT SONG

P. defilippii gives a flight song as a regular feature of its display behavior, sometimes reaching a rate of 40/hour. Unlike bellicosa and neglecta the flight display of defilippii is accompanied by a short, non-warbled, song consisting of pure whistled notes and clicks (see Plates 14-18). To my knowledge, defilippii uses a warbled type song only in its sex chases.

The relationship between primary and flight songs is complex. Short (1968) heard more secondary or flight songs from defilippii than primary songs on one December day. At Saudade this was true on some days, but not on others. In 1970 the frequency of flight songs declined

more strikingly during the season than for primary songs. This may support Short's (1968) suggestion that the flight song functioned more in courtship, for he frequently saw it oriented over females.

In the field I had the impression that defilippii flight songs were more likely to be associated with territorial activity. A quantatative study of how different males used flight and primary songs is difficult since female defilippii are usually very inconspicuous, and it is possible that many songs that are actually oriented toward the female might be otherwise interpreted.

Most defilippii males had only a single flight song pattern, although a few had two. The main within-bird variability was in the presence and number of terminal 't' notes, and because of their low intensity, the apparent variability may have been an artifact due to varying distance from the microphone.

Flight songs of defilippii can be divided into an ascent, song, and descent phase. The angle of ascent is variable, usually between 30° and 50°. The ascent is accompanied by vigorous wing beats, and just before the peak the wings tend to be above the horizontal. At the peak they are thrown upward, the bird tumbles forward, and the wings are brought vigorously downward. The bird then descends with a few flaps, a long glide with wings

held more than 45° above the horizontal, and then more flaps before landing. The drooping wings at the peak are characteristic, and this event occurs just at the start of the song. There is considerable variability in length and angle of ascent and descent, but also in the display at the peak. For example, defilippii male RR/WW (Saudade 1971) usually kept his wings just below the horizontal without elevating them near the peak of the display. He held his body nearly vertical, thrust his wings forward, sang, and descended almost headfirst. The Triller (unmarked male, Saudade 1971) usually ascended at approximately 45°, and appeared to lean forward at the peak with a gradual transition from ascent to descent. These variations were characteristic of these males. Other variations appeared related to motivational states, since several males which typically had vigorous tumbles at the peak of their flight, occasionally behaved like the Triller, suggesting a low level of motivation. Observations on several marked males throughout the season would shed more light on these sources of variability.

Flight songs of defilippii were usually initiated from a grass clump, but occasionally began from the fence.

Although the flight song is quite different in structure from the primary song, the flight song pattern

is occasionally given from the perch. At Saudade, I heard a male defilippii, sitting near a male militaris, give several flight-type songs. On another occasion a warbled or "rehearsed" song was given by an apparently non-territorial male which was sitting about 15 meters from a decoy.

BELLICOSA FLIGHT SONG

Like defilippii, male bellicosa frequently give flight songs which seem to be a prominent feature of their behavioral repertoire. The bellicosa flight songs are bright musical warbles which seem to be indeterminate in length and variable in arrangement. The quality is very similar to flight songs of neglecta, to the songs given in flight by militaris and to sex chase notes of defilippii. The songs tend to begin explosively and are rich in steep slope elements (covering 4 khz or more in 100 msec or less). Frequently they contain improvisations around a primary song.

Although the flight songs seem unstructured, an individual may give an identical flight song several times in succession, even though the performance lasts more than five seconds. Both the within- and between-male variability arises from variation in the arrangement of figures, and many elements seem to be shared among

several males, (see Plates 27-30). A detailed study of the temporal organization of bellicosa flight songs is beyond the scope of the present study.

Most bellicosa flight songs started with vertical "tsip tsip" figures or with loud clear whistles as in neglecta (Lanyon 1957). Occasionally flight songs were aborted after only a few introductory notes. The flight songs often ended with a buzzy note which was frequently down-slurred or tapered toward the end rather than as in the primary songs. Analysis of these terminal buzzes reveals that their modulation rate is slower than in primary songs (approximately 120-140 hz compared with ±160 hz. for primary songs).

On two occasions males believed to be non-territorial were heard to give long, seemingly endless, warbled notes from a perch. One song lasted at least two minutes. Although essentially the same in structure as the flight song, these "rehearsed" songs were spiritless, and this observation confirms Lanyon's suggestion (1957) that there is a basic similarity between flight song and rehearsed song in meadowlarks, differing mainly in motivation. During sex chases, bellicosa males, like defilippii gave similar warbling notes.

My observation on the context in which bellicosa flight songs were given suggests that they are more restricted than those of defilippii (see below). This

may only reflect fewer non-meadowlark disturbances in the Bujama area. Flight songs were often given as males flew back and forth across their territories or changed position within territories. They were often given when males flew to a boundary to display against a neighbor and were apparently more often given when leaving such an encounter. Boundary encounters usually involved primary song duets, although occasionally two males would give parallel flight songs along their mutual boundary. Birds frequently gave flight displays when approaching or leaving a decoy or when flushed by the observer. Occasionally flight songs were given over females or after leaving a female, but this seemed to be exceptional. Flights were not given in relation to non-meadowlark intruders other than the observer. The contexts are given in Table 32.

A description of a bellicosa flight display follows: The song begins with the male on the ground or in a grass clump, often out of sight. The ascent is made with strong and rapid wing beats, and the plumage appears moderately sleeked as the male flies up at an angle of 45-60° (less often nearly vertical). At the peak of the flight it throws its wings upward into a V, tilts head and body forward, and delivers the song which begins at or just before the peak and continues into the early part of the descent, lasting 2 to 3 seconds, occasionally

longer. The height of the flight is usually less than 7 meters, but in nearly 10% of cases it was close to 10 meters.

The descent involves a few initial flaps, after which the bird keeps its wings set about 30° above the horizontal as it glides down into the grass. Shortly before landing, or if changing course, it begins to flap and may lower its legs. Its plumage appears normal rather than sleeked. The overall flight path is variable. The approach phase is most often straight, while the descent phase may continue on the straight line, may bend at an angle, or may double back. The latter occurs when a male flies from the center to the edge of his territory and then doubles back to the center.

CONTEXT OR FUNCTION OF FLIGHT SONGS

Beginning with a preconception that the flight song would be either a courtship or a territorial song, I found it difficult to arrive at a clear picture of its function in the field, for it seemed to be given under every circumstance imaginable. In many cases I noted on tape the apparent context in which the song appeared and these are summarized in the accompanying table. The categories are defined as follows:

A. Spontaneous: (=unknown). Flight song given with no apparent preceeding cause and no definable subsequent event, the bird usually disappearing into the grass somewhere in its territory.

B. Flushed: Bird flushed by non-meadowlark, usually by me, but occasionally by a vehicle, livestock, European hare, or Lapwing.

C. Female-related event: Flight song given over female, when flying to join female, when flying away from female, or flight "causes" female to approach and join male, or to initiate a sex chase.

D. Boundary-related event: Flight song given on way to or from boundary or along boundary, either with or without contact with neighboring male.

E. Flight related to intrusion by a meadowlark: Flight given while going to meet intruder or after chasing intruder, or flight given by intruder on way out of territory.

F. Flight directed at non-meadowlark intruder, usually pipits, lapwings, European Hare, Purple Martins.

The apparent contexts for flight songs in a sample of defilippii and bellicosa flight songs are compared in Table 31.

I also examined a second sample of bellicosa songs.

TABLE 30. Descriptions of 186 flight song displays from six male bellicosa at Bujama August, 1972. (Spont = spontaneous or unknown)

MALE	# of FLIGHTS	PRECIPITATING EVENT				HEIGHT (Range)	PRIMARY SONG*		FLIGHT SONGS PRECEEDING **		
		Spont	Flushed	Other ♂	Decoy Tape		Before	After	0-10	11-30	31-60
WR/GG	7	5	2	0	-***	15-20'	3	0	2	0	2
WR/BB	47	22	12	7	6	8-20'	17	1	17	4	15
WR/GR	11	5	0	4	2	20-25'	4	0	1	2	2
B"	26	14	11	1	0	15-20'	12	0	4	5	4
WR/BR	39	17	7	11	4	12-20'	14	4	3	6	12
D	6	5	0	0	1	15'	3	0	0	1	1
TOTAL	186	68	32	23	13	17.33 ± 2.94	53	5	27	17	36
PERCENT	(136)[a]	50%	23.5%	16.9%	9.6%		28.5%	2.7%	14.5%	9.1%	19.3%
							31.2%[b]		42.9%[c]		

* Primary song preceeding or following flight song within 20 seconds

** Flight song preceeding flight song within 0-10 sec. or 11-30 sec. or 31-60 sec.

*** - indicates no decoy tapes used during this period

a Precipitating event noted or sought in 136 of the 186 flights.

b 31.2% of flight songs were precceded or followed by primary song within 20 seconds

c 42.9% of the flight songs were preceeded by a flight song within one minute.

Table 30 presents the contexts and features of 186 flight songs observed for six adjacent males at Bujama. Primary songs preceeded 53 (28%) of these but followed only 5 (2%) within 20 seconds. My impression is that the latter figure is probably lower than average. For 136 songs I categorized the precipitating event as human disturbance, other male, decoy tape, or "spontaneous" (=unknown). Exactly 50% (68) of the cases appeared spontaneous.

Of this sample a total of 81 flight songs were given within one minute after a previous flight song. If one song did not influence the probability of occurrance of the next song, one would expect that 81/6 =13.5 of these songs would be given within 10 seconds after the previous song. Table 31 shows the expected and observed temporal distribution of these 81 flight songs.

TABLE 31 Expected and observed temporal distribution of 81 flight songs which followed within one minute of a preceeding flight song.

TIME INTERVAL SINCE PRECEEDING SONG (seconds)	NUMBER OF SONGS Expected	Observed	Chi square Contribution
1-10	13.5	27	13.5
11-30	27.0	18	3.0
31-60	40.5	36	0.5

degrees of freedom =2 Chi Square=17.0 $p<.001$

For these 186 songs, the mean estimated height was 17.33 ± 2.94 feet. Later in the season on 3 and 5 September, I noted details of 18 flight displays from different males with respect to approach distance, decline distance, and height. The vertical height of these displays was 16.22 ± 4.69 feet, not significantly different from the first sample. Table shows the mean values, and the correlations between the three components of the songs. None of the intercorrelations are significant at the .05 level.

FLIGHT DISPLAY CONTEXT: BELLICOSA COMPARED WITH DEFILIPPII

There is considerable overall similarity in the occurrence of flight displays for the two species. For both species about 25% of the flight displays noted appeared to be spontaneous (in some samples as high as 50%). More defilippii displays were oriented towards females, and more bellicosa displays were given in a territorial context. From a table of confidence limits around percentages (Rohlf and Sokal 1969) these differences are significant ($p<.05$) for female-related and ($p=<.01$) for territory-related activities (Table 32).

Care should be taken in interpreting these differences due to the fact that they were described on

TABLE 32. Flight song context for *defilippii* and *bellicosa* extracted from tape

	DEFILIPPII		BELLICOSA	
	#	%	#	%
TOTAL FLIGHT DISPLAYS	991		560	
FLIGHT DISPLAYS DESCRIBED	573		268	
Spontaneous (no apparent cause)	145	25.3	68	25.4
FEMALE RELATED	64	11.2	18	6.8
Approaching female	23	4.0	4	1.5
Leaving female	8	1.4	0	
Over female	19	3.3	8	3.0
Chasing female	14	2.4	6	2.3
BOUNDARY RELATED	255	44.5	145	54.1
To boundary	112	19.5	41	15.3
to encounter neighbor	53	9.2	29	10.8
around boundary	3	0,5	14	5.2
parallel flights	31	5.4	36	13.4
from boundary	45	7.8	4	1.5
from neighbor	11	1.9	11	4.1
from chasing intruder	--	---	10	3.7
INTRUDING MEADOWLARK	37	6.4	9	3.3
going to chase intruder	20	3.5	9	3.3
returning from chase	13	2.3	0	---
chasing heterospecific	7	1.2	---	---
OTHER INTRUDER				
Other bird	4	0.7	0	
Other mammal	2	0.4	0	
Flushed by observer (not included in totals)	26	4.5	13	4.9
To or from decoy	17	3.0	39	14.6
By intruding meadowlark	2	0.4	0	----

an a posteriori basis from tape recordings, and there was not necessarily a consistent pattern in description of events from season to season. However, they do bear out the general impression that bellicosa flight displays were not related to female activity. Moreover, some very strong flight responses were noted in bellicosa during playback tests, the birds almost always approaching or leaving the decoy with flight displays. This behavior was less frequent in defilippii.

LEISTES FLIGHT SONG DESCRIPTION

The overall pattern of the superciliaris flight song resembles defilippii. The most conspicuous and constant difference is the brief display at the peak of the flight, when superciliaris holds its wings and tail broadly fanned and slightly bowed upward so as to resemble a dish. Usually it holds this position for less than a second as it tilts forward and begins its song, but occasionally it actually seems to turn in a slight circle in this exaggerated position.

In any group of superciliaris the pattern of flight songs varies. The overall flight path may be straight, arched, or may even be a complete circle. Near the top of the flight the head may point downward with the wings only slightly above horizontal. During descent it keeps

its wings 60° or more above the horizontal and its legs dangle downward. In long descents it may flutter wings weakly. The height of displays vary from 15-60 feet. A series of 28 songs observed on 17 October near Tandil ranged from 25-60'.

Flight displays were given frequently in a territorial context, and occasionally in a context suggesting courtship behavior. Occasional flight displays were directed at other meadowlarks. On two occasions when a pair of militaris flew out into a field, the territorial superciliaris flew up, gave a flight song over the intruders, and then left. The militaris did not leave in either case.

COMPARISON OF DEFILIPPII AND SUPERCILIARIS FLIGHT SONGS

The general similarities in the displays of both species has been indicated above. To obtain quantitative comparisons of these displays I estimated the approach and decline phases and the heights of consecutive songs given by groups of defilippii and superciliaris males in wheat fields at Saudade on 25 October 1971. A single period of about 90 minutes was used and only wheatfield birds were chosen to minimize variability due to weather, time of day and habitat. To make the data independent I confined the analysis to one flight song for each individual. Since most of the birds were not marked, I

defined individuals by the territories they occupied, and moved around the perimeter of the wheat fields to minimize my chance of recording the same individual twice. This technique is effective over a relatively short period, but it becomes impossible to follow individuals after an hour or so unless they have characteristic songs.

I estimated the distance from start to peak (approach distance), from peak to landing (decline distance), and the height. Grid markers and utility poles provided reference points. Height categories were estimated as multiples of five feet. To determine whether my height estimate might be biased by the estimate of the previous flight, I determined serial correlation coefficients between the height of each flight and its predecessor. These coefficients were low for both species (.03 and .11) suggesting that at least one source of bias was not operating.

Either through estimation bias or through social stimulation a high flight song might be followed by a high flight song or for that matter by low ones. Sequential pairs of songs were categorized as HIGH-HIGH, HIGH-LOW, LOW-HIGH and LOW-LOW (high and low being defined with respect to the median value), and the data were analyzed in a contingency table only for this second order interaction. For superciliaris high and low songs

were independent (X^2=.51) while for defilippii high songs tended to be followed by high ones (X^2=13.6). It would be valuable to determine whether this results from increased social stimulation provided by higher flight songs.

Table 33 shows the mean and standard deviation for the three measures on both species, and a matrix of correlation coefficients and t-test values on untransformed data. Logarithmic transformation lowered the correlation coefficients slightly, but did not change their significance. The only interspecific difference of significance was the average height of the display which was greater for defilippii ($p<.01$). This is of interest since some of the highest displays I observed were by superciliaris (one estimated at 75 feet) and Hudson (1920) noted that it flew up to 25 yards or more. Within species the only significant correlation among the components was between approach and decline distances for defilippii, that is a long approach associated with a long decline.

TABLE 33

COMPARISON OF DEFILIPPII AND SUPERCILIARIS FLIGHT SONGS

SUPERCILIARIS n	mean	st. dev.		DEFILIPPII n	mean	st. dev.
31	27.71 ±	13.51	Approach	29	35.35 ±	32.68
31	27.06 ±	6.69	Height	29	33.03 ±	7.89
31	87.42 ±	52.09	Decline	29	75.90 ±	67.32

CORRELATION MATRIX

SUPERCILIARIS

DEFILIPPII	APPROACH	HEIGHT	DECLINE
APP	xxxx	-.014	.723
HGT	-.05	xxxxx	-.103
DEC	-.09	.06	xxxxx

t-matrix

APPROACH	HEIGHT	DECLINE
1.21		
	3.17 p<.01	
		.744

GROUP SIZE AND SONG OUTPUT IN DEFILIPPII

The belief that aggregations are important because of the opportunity for social stimulation has been propounded by Darling (1938, 1952) among others. One possible expression of this is that a bird is more likely to sing when in the presence of other singing birds than when alone. I repeatedly gained the impression that certain songs (particularly flight songs of bellicosa and defilippii were contagious (a problem to be studied in the future), and I also investigated the frequency of singing (songoutput/bird/minute) as a function of group size during roadside point censuses in Argentina. In view of the diurnal and seasonal influences on song output, a detailed study of this sort would require strict control of these variables. I noted a considerable difference in song rates in November and December, and in the present discussion, only data from November 1970 are included.

Figure 11 shows the linear regression of songs/bird/minute for 12 samples where defilippii were present. In each case the approximate group size was estimated and I made observations for 15 to 30 minutes. Since observations were made mainly during late morning and mid-afternoons, the values are lower than one would expect at the peak of singing in early morning. Moreover,

if significant temporal clustering of songs exists, it is possible that some of the samples could reflect this bias---either by catching or missing a song peak. An extension of this study with improved attention to sampling details would be valuable.

SUMMARY OF FLIGHT SONGS AND DISPLAYS

1. Flight songs and displays play important roles in the biology of many species of open country birds, wherein perhaps the elevation gained during the flight substitutes for the unavailability of elevated song perches.

2. Both species of Sturnella give flight songs, neglecta frequently and magna occasionally.

3. Like S. magna, P. militaris gives flight songs infrequently, and in that species they appear associated with moments of sexual excitement.

4. P. defilippii, P. bellicosa, and Leistes regularly give flight songs. In these species the songs seem to relate to territorial interactions among adjacent males. In defilippii I found evidence that the songs may attract females. A detailed account of the pattern of the flight display and of flight song sontexts is given.

5. The general aspects of the flight displays of defilippii and superciliaris are quite similar. At a distance it was not easy to be sure which species was displaying. This similarity may facilitate or be responsible for the apparent interspecific territoriality.

6. The flight song of bellicosa consists of a long series of warbling notes. The structure of the song is similar to the flight song of neglecta, to the occasional flight song of militaris, and to the songs used by several species (defilippii included) in sex chases. The flight songs of defilippii and Leistes are not warbled.

7. Among territorial males I found evidence for contagiousness of flight singing for defilippii and bellicosa. Data for 12 groups of defilippii males (4 - 30 males in a group) were analyzed by linear regression. The frequency of flight singing (song/bird/minute) increased with group size.

CHAPTER 12 MEADOWLARK CALL NOTES

Call notes differ from songs in being simpler in structure, often monosyllabic. Thorpe (1961:17) lists 10 categories of call-notes based on function, but his categories did not prove useful in the present study. Lanyon (1957) listed six call notes of *Sturnella* as follows:

1. "chupp" of *neglecta* and "dzert" of *magna*.
2. the whistle of both species.
3. rattle, roll and chatter calls.
4. "weet" call given in flight.
5. "tee-tee-tee" of female.
6. "zeree" and "dzert-tut" of *magna*.

These served as a basis for comparison with notes of *Pezites* and *Leistes*. In the present study I investigated the call notes of the different meadowlark species, attempting to delineate possible species-specific notes and to determine context or function where possible. I also obtained information on female vocalizations including songs, call notes, and particularly solicitation notes used to initiate sex chases.

MEADOWLARK CALLS

Lanyon (1957 et seq) has demonstrated that unlike their songs, meadowlark calls seem to be largely innate and function in reproductive isolation. Falls and Szijj (1959) reported that in an Ontario population, neglecta-type males gave magna calls. However, a definitive report was never published.

The following details on calls indicate an overall similarity among the meadowlarks with respect to some calls, while others appear to be unique. I recorded a greater variety of calls from defilippii than from militaris. Female defilippii and bellicosa utter distinctive notes (though similar to each other), but from female militaris the only distinctive call was the chatter heard on but one occasion (see below).

I could not discover whether females distinguished conspecific males on the basis of calls. Nor could I determine which member of the pair made the selection. Presumably it is the female, since I observed the willingness of defilippii males to pair with militaris female (although the converse was not noted). Lanyon (1957) also noted that males of Sturnella would pair with females of either species.

In the following section I treat a variety of notes for each species even though the context and meaning of

the notes remains unknown. Lanyon and Fish (1958) point out that for neglecta the basic "chup" note is quite stable over a wide geographic range. I found some variety in the "chup"-type notes within a population, and I have probably distinguished a greater variety of notes than is necessary to characterize the calls of the meadowlarks.

MILITARIS CALLS

1. "Chup" notes varied in intensity and dominant frequency and were uttered in a large variety of circumstances, particularly during threatening episodes. Plate 39 shows three such notes uttered by 1) a male facing-off with a silent decoy, 2) a male retreating from a territorial male, and 3) a male chasing an intruder. I could not record enough notes under such circumstances to indicate whether the apparent differences are consistent or not. The notes were usually 50-80 msec in duration, with a frequency range of 1400-6000 hz, the dominant frequency usually falling between 2000-4000 hz. The dominant frequency of these notes is much lower than for the biphasic notes of defilippii. Moreover, the militaris "chowp" call has energy nearly equally distributed during ascending and descending phases, unlike any defilippii call.

Three notes phoneticized as "chowp", "chup" and "typ" were analyzed from catamarcanus recorded by W. E. Lanyon at Amaicha del Valle (Nov. 1970). These were similar to those I recorded on the pampas. However, this note is somewhat similar among all Pezites, and appears also in S. neglecta (Lanyon 1957: Fig. 7). S. magna does not have a "chup" note, but other icterids may. For example, the "chuk" notes of Red-winged and Tricolored Blackbirds (Orians and Christman 1968) and of Boat-tailed Grackles (Selander and Giller 1961). Heard mainly from males, occasionally from females.

2. A loud, hollow-sounding "tyop" note was heard occasionally from males. It is a complex note 100-125 msec in duration with a frequency range descending from 7000 to 2000 hz. There appear to be two separate descending portions, the latter simultaneous with a continuous portion (frequency about 2000 hz). The call was heard several times, apparently in a territorial context, from males near decoys. It is apparently distinctive.

3. Female notes. A soft, high-pitched "see-see" note was heard during copulation sequences, but was not recorded. Since militaris females gave primary song duets with their mates (see below), and since the components were often hoarse and erratic (showing up as

"messy" sonographs) these songs may be considered analagous to those heard occasionally from female defilippii and bellicosa. Unlike those species, I did not hear any "jt jt" notes during initiation of sex chases, but I saw only a few sex chases for militaris and could have overlooked such notes.

4. A "chatter" (see Plate 48B) very similar to that of magna (see Lanyon 1957, fig, 9), was heard on one morning at El Condor when a female (perhaps more than one) gave the call three times. Each time she was near a male, but I could not observe their activities. I did not hear this note on the pampas, and it may be restricted to the western Argentine population, although I cannot imagine why this should be the case. Lanyon (pers. comm.) notes that in S. magna this call, given in response to the male, is essentially confined to the early part of the breeding season and could be easily overlooked thereafter.

Miscellaneous notes: Both sexes uttered soft "tsip" notes when foraging, and these seemed to be location notes. Soft "chk" notes sometimes given in flight by overflying birds may have been equivalent to the "weet" notes of Sturnella and of defilippii.

DEFILIPPII CALLS

On a phonetic basis I divided defilippii calls into two categories, the "chup" and its apparent variants and the "peet" and its variants. Other categories such as mobbing notes and female solicitation notes are also described here.

1. CHUP NOTES

a. "Chup" notes were frequently recorded from males and occasionally from females. These notes were very variable and fall into three general shape categories, the "chup" (Plate 40B), the "chek" (Plate 40B), and the "tup" (Plate 41E). It is possible that the next category is also only a variant of the "chup". The notes vary in duration from 30-60 msec. The main energy is concentrated between 3500-4500 hz, higher than militaris. The frequency range is restricted in the "chek", but spans 1800-7600 hz in the "tup".

These notes frequently indicate alarm or excitement, were uttered both in flight and on perches, and were heard from both sexes. Unlike militaris two males frequently engaged in long duets of "chup" notes. Frequently these series consisted of two different notes given by the same bird. Plate 40H shows notes of two males given in alternation.

b. "Pit" notes were also heard during periods of alarm or excitement. They were usually about 50 msec in length, with a frequency range of 2500-4500 hz, and were biphasic. They may be only a variant of the "chup". I did not record this note from females, (see Plate 40A).

c. "pesh" notes were very soft, short calls (< 50 msec duration) of 3000-4000 hz, which were uttered by both sexes in flight or by males on fences. No role could be ascribed to them, and they may only be low intensity "chups", (see Plate 40C).

d. "Tu" notes were recorded occasionally from males on fences, and an example of two males alternating such notes is shown in Plate 40H. The notes are actually biphasic, but almost all the energy is in the descending syllable. These are probably only variants of the "chup". Not recorded from females.

e. "Tsut" notes differed from "tu" notes in the terminal emphasis, and the lack of any sign of an ascending syllable. The duration was about 50 msec, and the frequency range about 2600-5000 hz. The call was heard from both sexes. In one case a male uttered it during mild alarm. It was often heard from females near the nest, when my presence interupted them, (see Plate 41A).

2. PEET NOTES

a. "peet" notes were loud, triphasic figures, usually given in pairs, by males during periods of excitement. They were approximately 70 msec in duration with a frequency range of 2500-6000 hz and main energy concentration between 3500-5000 hz, (see Plate 41D). Not recorded from females.

b. "Twee" notes were recorded rarely, and only from males. Plate 41B shows the completely ascending syllable, with a duration of 70 msec, and an energy range of 2000-6000 hz. This note had no counterpart in militaris or bellicosa. I did not hear it from females.

c. "Seet" notes were heard from both sexes, mainly males, during periods of excitement. They were pure whistled notes, constant in pitch, between 4000-5000 hz, and lasting up to 250 msec. They resemble the whistles of magna and neglecta, but are higher in pitch. Such notes were sometimes heard during sex chases or aggressive encounters. I did not note such notes for militaris.

d. "Kyēeyk" notes (Plate 41D) were heard infrequently, and only from males (usually when flushed by the observer or when confronted on territory by a decoy). The notes are biphasic, inverted U-shaped, with the dominant

frequency 7000-7400 hz and a duration of 100-120 msec. No similar call notes were heard from other species, although they may occur. The note is very similar to the introductory note used by some bellicosa males in primary songs, (see Plate 41C).

3. MOBBING NOTES

Adult defilippii, particularly males responded to distress notes of nestlings with high intensity, harsh call notes. It is noteworthy that I did not succeed in eliciting mobbing responses from militaris, and that bellicosa responded only mildly, while the response of defilippii was consistent for several pairs, involved particularly the male, and was among the most intense I have experienced for any passerine.

4. FEMALE SOLICITATION CALLS

a. "Jt-jt", (Plate 48A). This is one of two solicitation notes uttered by females at the time they elicit sex chases. Each component is brief (<25 msec) and has a frequency range of 1500-8000+ hz. These were sometimes given as a rattle during a sex chase.

b. "See-see-see" note (Plate 49) was also heard during initiation of sex chases and immediately prior to

copulation. The few females who gave male-type flight displays uttered long sequences of "see-see-see" notes. The notes are not pure whistles, have a duration up to 250 msec, and fall between 4000 and 8000 hz. They resemble the magna "zeree".

5. MISCELLANEOUS CALLS

a. "Tut-tut" notes were occasionally heard from females during periods of mild excitement. I did not record them. To the ear they resemble the terminal 't' notes of the male flight song.

b. "Weet" notes were occasionally given in flight by female defilippii, particularly when crossing foreign territories. It is not clear whether these were unmated females on all occasions, but in at least one instance this seemed to be the case, and the female was joined by a male who gave a flight song in her wake and then returned to his territory, while she circled around to join him.

The notes (Plate 49D) were generally given in series, had a duration of 75-100 msec and a frequency range of 2000-5500 hz. The song appears almost identical to the "weet" of magna (see Lanyon 1957, figure 8). Lanyon noted this call from both sexes of magna and neglecta given mainly by migrants in flight. However,

I have no record of the call being given by males. It is possible that militaris females also give a similar call, but I did not record it.

c. Other calls. Plate 36A shows a series of excited notes given by male RR/YY (Saudade 1971) during a sex chase. The first portion "tu-tsuk d-d-d-d-d" resembles a flight song with the whistle replaced by a "tsuk". It also resembles the "dzert tut-tut" of magna. This sequence was immediately followed by a "tsk tsuk ts ts tzeee", which also resembles a flight song, but has mainly harsh vertical, call-note type elements. These types of vocalization were heard in the same context as the warbled sex chase songs, and some males (for example RR/YY) might give either or might go from one type of song to the other. Yet it is difficult to determine whether these should be considered sequences of call notes or a song. If so, it would fall into the loose category of rehearsed song.

d. Plate 41D shows a series of high pitched squeaky notes given by one male confronting another in a boundary encounter. Plate 41E shows the whistled and warbled notes given during sex chases (considered separately under sex chases) or occasionally while chasing another male.

BELLICOSA CALLS

Plates 42 and 43 illustrate several of the call notes recorded from bellicosa. I group them into categories.

1. THE "CHUP" NOTE AND ITS VARIANTS

a. The "chup" was the most commonly heard call note and resembled "chup" notes of defilippii and militaris. However, visual comparison of sonograms showed that the bellicosa note was distinct in being monophasic, and essentially a long (50-80 msec click). The calls sometimes spanned the frequency range 1500-7000 hz, but usually there was a clear concentration of energy between 2500 and 3500 hz. Any variation in the dominant frequency changed the phonetic description in my notes. The call was given as an indication of apprehension or alarm when I approached a bird, and was often heard during territorial contacts between neighbors. Primary song duets were sometimes followed by a minute or more of "chup" calls delivered by the males. The call was sometimes heard in flight. A male "observing" a sex chase of an adjacent pair gave "chup" notes (Plate 43A). Male WR/GG gave the call in flight while chasing an intruder (Plate 43G). An unmarked male gave the call during a sex chase (Plate 42C).

b. Low intensity variants such as the "chip" and "chch" Plate 42D & E) were frequently heard. No unique context was ascribed to them, however, one male interupted long periods of low intensity rehearsed song (warbled from a perch) with "chip" and "chch" notes (Plate 43B).

c. The "cluk" note (Plate 43C) was uttered very frequently by both sexes in a flock that roosted on the study area. The call was given while flying to, settling in, and changing position within the roost. The energy in this call is more concentrated into a narrow range (4 - 5 khz) than in other "chup" calls. It is appropriate to consider this a contact call.

d. The "dzip" (Plate 43F) was uttered by some males in the same situation as the "chup". It may prove to be an individual variant. There is a slight temporal extension of the dominant frequency (mainly about 2000-3000 hz), giving a duration of 80 msec. It was sometimes given in flight and was recorded only from males.

2. STEEP-FIGURE CALL NOTES

a. "Tsyep" notes (Plate 43A) had a duration of about 150 msec sith energy distributed from 7500 to 2000 hz. It was heard only from males and was given in the presence of other males, females, and the observer.

The contexts could not be distinguished from those of the "chup" notes.

b. "Tseyu" and "tsu" notes (Plates 42H & 43D) closely resemble the "tsyep" but lack the staccato quality, apparently because of the terminal attenuation in energy. The call was recorded both during boundary encounters and male-female interactions. The superficially similar "typ" of militaris and "tsut" of defilippii have most of the energy concentrated in the last part of the note and the bellicosa note therefore appears distinctive.

c. An unmarked male intruding on an occupied territory gave "tzut" calls (Plate 43G) which closely resemble the "chup" but are of lower intensity with strong attentuation of higher frequencies. It thus appears as a steep-slope figure.

d. A "chip" note uttered during a long sequence of warbling "rehearsed" song appears to be a steep-slope figure (Plate 43B).

e. A "tip" note (Plate 42G) uttered by both sexes had a duration of about 50 msec, and a fairly even energy distribution over the 3500 - 5500 hz range.

f. A very soft "sh" note (Plate 42F) heard occasionally from demales flying into or out of territory, was similar

in form to the "tip" but lower in pitch (2200 - 3600 hz).

3. FEMALE SOLICITATION NOTES

a. "Jt-jt" notes similar in sound to those of some defilippii females were delivered in rapid succession (usually doubled or tripled), as females flew up at the start of a sex chase. The notes were also uttered during the chase, more frequently than by defilippii females. The duration was 30-50 msec, and notes were repeated about 200 msec apart (Plate 42A).

b. Harsh, buzzy "scree scree" or tzee seet" notes were occasionally given in the same context as "jt jt jt" notes. Also on the rare occasions when female bellicosa gave male-type flight displays, they uttered an ascending series of two to four "scree" notes (Plate 42B).

4. MISCELLANEOUS NOTES

a. "Pfit tit" notes were occasionally uttered by males in flight (Plate 43E). These are biphasic notes uttered in pairs, the first somewhat lower in pitch than the second. Duration of each note is 50-70 msec, and the frequency range is 1800-7800 hz with the main energy between 4500 and 7000 hz. Although several calls of militaris and defilippii are biphasic none have the

energy concentrated at such high frequency.

b. Occasional buzz notes, essentially identical to those of primary song were heard from various males on occasion. They may even represent aborted primary songs.

c. Occasional soft whistled notes heard, but not recorded, were phoneticized as "wit" or "weet". These were heard occasionally from males, more often from females, and were usually given in flight. They resemble the "seet" calls of defilippii and similar calls of magna.

d. On one occasion I heard, but did not record, a note phoneticized as "dzert", apparently given in mild alarm by a female. The note was accompanied by quick partial fanning of the tail and was given only once. It would resemble the "dzert" of S. magna.

LEISTES CALLS

My recorded material of calls from both forms of Leistes is very scant, (see Plate 44). The following notes have been graphed.

1. "Tsuk" notes given by a male superciliaris while flying to the fence to land near a neighboring male. The bird landed and gave a primary song, and shortly after it left the fence with a flight song. No displays

were noted while the bird was on the fence, (Plate 44A).

2. "Tup" note given by a L. m. militaris male in Surinam, while posturing in front of a decoy. The main frequency is 1500-3000 hz and the duration was 160 msec. It is very similar to the "chup" of neglecta (Lanyon 1957, fig. 7.), and is both longer in duration and more restricted in frequency range than the "chup" notes of Pezites.

3. "Tsu" note of L. m. militaris (Plate 45C) is similar in shape, pitch and duration, to "chup" notes of defilippii but is unemphasized and has a hissing quality.

4. "Chlk" is a more clearly disyllabic note recorded from L. m. militaris. It has a frequency range of 1800-8000 hz and a duration of 140 msec (Plate 44D).

5. "Wsst" is a harsh alarm note (Plate 44E) recorded from male L. m. militaris. In shape it resembles the "twee" note (Plate 41B) recorded from defilippii but the quality is quite different.

6. "Teyu" and "tyop" notes were recorded from males of both forms under a variety of circumstances. There appears to be considerable intraspecific variation. Plate 44F, G and H illustrates three notes recorded from L. m. militaris males in Surinam. Notes of this

sort seemed to indicate mild alarm and seemed also to be given when birds arrived at new perches. The notes are more complex than similar notes of Pezites. The frequency range is 3 - 6 khz, and the duration ranges from 100 - 150 msec.

The presentation of call notes for Leistes is more incomplete than for the species of Pezites that I studied. It appears that Leistes has a greater number of calls which are long in duration (>100 msec) than does any Pezites. The close resemblance of the Leistes "chupp" to neglecta "chup" is of particular interest.

COMPARISONS WITH CALLS OF STURNELLA MAGNA AND NEGLECTA

The following comparisons are based on figures 7-9 in Lanyon (1957).

1. I did not hear any male vocalizations comparable to the roll or chatter. One female militaris uttered a definite chatter, and female Leistes and defilippii occasionally fused 'jt jt' notes into a chatter or rattle, though I never heard this from bellicosa.

2. The "weet" of female neglecta has a shape similar to the "twee" of male defilippii, but the "weet" graphed for female magna is almost identical to the "weet" notes given mainly by overflying female defilippii and perhaps

other meadowlarks as well.

3. The neglecta "chup" has a direct counterpart in the "chup" notes heard from all three species of Pezites. The "tyew" note of bellicosa males has a slight resemblance to the magna "dzert".

4. The "zeree" note of magna is approached by some of the excited whistled notes given by male defilippii and also by the "see" notes of female defilippii. The "zeree tut-tut" and the "dzert tut-tut" are similar to other sex chase notes of defilippii, the 'tut' notes being equivalent to the terminal 't' notes seen on graphs of defilippii flight songs.

5. The "chupp" of neglecta is closely approached by the "tup" of Leistes.

Although interesting in pointing out differences among species, I suspect that such comparisons are spurious where similarities are concerned. For a simple figure with only one to four syllables, there are only a few possible products, and the same note may have different function in two different species.

I found that most call notes appeared in a variety of circumstances and that for any circumstance different notes might be given (sometimes in the same sequence). Perhaps many of the variants which I noted, reflect only

differences in intensity, as I have indicated for the defilippii "chup".

When captured, adults and older nestlings or fledglings gave loud, harsh "zhreet" notes (and perhaps others as well, which are typical distress notes or high intensity alarm notes) (Driver and Humphries 1969). I did not record these, but the calls are probably common to many passerines with no specificity. Only defilippii adults (particularly males) responded to these vocalizations. However, the begging notes of a hungry Shiny Cowbird nestling attracted a pair of militaris which were themselves caring for nestlings---the approach was accompanied by soft "chup" notes rather than by mobbing notes.

SUMMARY

1. For Sturnella, Pezites and Leistes there is overall similarity in calls, particularly the "chup" note, probably reflecting their close relationship.

2. The "chup" note of militaris differed from those of defilippii in the lower dominant frequencies (below 3 khz for militaris and above 3 khz for defilippii). Notes of defilippii had a tendency to be biphasic, whereas militaris notes were not. The note of bellicosa was a long click, with a more extensive frequency range than

for militaris. A "tup" note of L. m. militaris was longer in duration and more restricted in frequency than any of the Pezites notes, and resembled the "chup" of neglecta.

3. "Chup" notes were given in a variety of circumstances involving mild alarm, "nervousness", or territorial aggression. For each species there were several variants, which may on further study be found to have contextual significance.

4. Geographic variation in call notes was not examined in any detail. P. m. catamarcanus call notes were not different from those recorded on the pampas or in Patagonia.

5. A variety of "peet" notes was heard from defilippii, particularly during periods of excitement. These triphasic notes were recorded only from males, and no counterparts were noted for militaris.

6. Various steep-figure calls were recorded from bellicosa during boundary encounters and male-female interactions. These notes resemble some calls of both militaris and defilippii except that the energy was distributed more evenly over a wide range of frequencies, and only bellicosa used such calls often.

7. Several calls were recorded only in flight. These include a soft "sh" uttered by territorial female bellicosa, "kye-yk" notes uttered by male defilippii when flushed, "pesh" notes uttered by both sexes of defilippii, and the "weet" given by female defilippii in flight. The latter note resembles notes of magna and neglecta given during migration.

8. Soft notes were occasionally heard from militaris males and females when foraging, and these may represent contact calls. They were not heard from the other species which may reflect inadequate sampling or that members of a pair do not try to remain in contact when foraging.

9. The present study did not reveal whether females might distinguish conspecific males on the basis of call notes, but there are species distinctive characteristics which would allow this to occur.

10. On one occasion a female militaris uttered a chatter very similar to that of magna. It is possible that such calls were overlooked since in magna they occur mainly early in the season. Future studies of meadowlark vocalizations should clarify the distribution of such notes since Lanyon found them to be prominent in Sturnella. Females of Leistes and defilippii

occasionally uttered a long series of rapid "jt jt" notes which sounded like a chatter or rattle, but no such notes were heard from bellicosa.

11. For defilippii and bellicosa females frequently elicited sex chases by taking off from the territory and uttered repeated notes, for example the "jt-jt" or "see see" of defilippii. Such notes were not recorded for militaris.

12. The call repertoires of Leistes were inadequately explored. Several notes had close counterparts in Pezites; others did not. The "wsst" alarm note uttered by male Leistes superficially resembled the "twee" of defilippii but was uttered in different context and with different quality. Calls of Leistes tended to be longer in duration than those of Pezites, while the "chup" bore a particularly close resemblance to that of neglecta.

13. Some call notes of Pezites, particularly those uttered in flight or during sex chases or territorial confrontations, appear to be high intensity fragments of rehearsed song, while others appear similar to introductory notes of primary songs. One such note given by defilippii is similar to the "zeree" note of magna.

14. Mobbing notes were given consistently by defilippii adults, particularly males, in response to the high intensity alarm calls uttered by nestlings that I was handling. In similar situations bellicosa adults responded weakly and inconsistently, and militaris adults tended to remain at a distance and to utter "chup" notes indicative of alarm.

CHAPTER 13 FEMALE SONG AND SEX CHASES

In oscines song is primarily a male phenomenon. Thorpe (1961) noted that in sexually dimorphic species, female song was exceptional, although probably commoner than formerly supposed. He considered it aberrant behavior indicating an hormonal imbalance. Kern and King (1972) produced song in female White-crowned Sparrows injected with testosterone, and they reviewed the several other published reports of song induction by androgen injection. Nice (1943), Armstrong (1963) and others (see Kern and King 1972) have reported female song to be more than occasional, and recent studies have shown that female-male song duets are particularly common in species inhabiting dense vegetation.

Lanyon (1957) noted that female Sturnella rarely if ever sing. In the present study two types of female "song" were noted. Female militaris frequently gave primary-type songs, usually in duets with the male. Female defilippii and bellicosa occasionally gave male-type flight displays accompanied by female-type calls. Whether these vocalizations are biologically important or merely represent a "spillover" of androgen production at the height of the breeding season remains to be determined. The direct relation between androgen production and vocaliztion can be inferred from Kern and King

(1972) wherein estrogen injection produced copulatory trills and increased receptivity of the female but did not produce song.

FEMALE MILITARIS

Male and female militaris spent much time in close proximity. Often when a male approached a neighbor or a decoy, he was joined by the female, and frequently his songs were followed by similar songs from the female. In some cases the female songs were very similar to those of the male while in others they were merely single harsh notes. Females rarely sang spontaneously (no instances noted with certainty), but they very often gave their songs while flying to join the male or while leaving. Often a series of duetting would terminate when the female flew during her last song.

Although my records are incomplete, I have notes (Table 34) on some circumstances during which females joined their mates (or presumed mates). Females duetted with males in 2 of 11 natural border disputes, in 13 of 24 responses to decoys militaris song, and in 9 of 57 spontaneous song bouts (no territorial or decoy encounter). The frequency of response during playback differs significantly from the other circumstances (2 x 2 contingency table, $G=19.2$, $p<.0001$). It seems

TABLE 34 SOME EXAMPLES OF SINGING BY FEMALE MILITARIS

1970

21 Nov.	BB7E	Spontaneous duetting of a pair of militaris. The male sang, followed about 1 second later by the female who sang a similar song but more buzzy in quality. After two such duets the pair flew to the ground and foraged in the bunch grass. The male was trapped about an hour later (RR/RR).
11 Nov.	BB30W	One hour after being trapped male BB/BB sang in response to playback, and the female joined in after landing in the grass about 5 meters from the male. Her song was similar to that of the male but she only sang once and was not recorded.
11 Nov.	BB12N	A female sitting about 3 meters from a silent male gave a buzzy primary type song.
28 Nov.	El Condor	Two pair of militaris were recorded duetting. In each case the female songs were similar to those of their mates. Seven of 25 male songs of male A were followed by female songs, and 6 of 25 of male B songs were followed by female songs. Female B led her mate on a sex chase giving a primary song in flight. After landing the male engaged in two very

TABLE 34 (cont'd.)

		long song bouts totalling at least 64 songs of which the female followed 9 times.
9 Dec.	Saudade	Male GG/YY gave a primary song which seemed to attract his female who flew toward him. When they flew off together the female gave a partial primary song. Later female duetted with 4 of 10 male songs.
18 Dec.	Saudade	Unmarked female of GG/RR arrives with primary song given in flight as she joins her mate at a singing decoy.
19 Dec.	Saudade	Unmarked female of GG/RR gives two primary songs on fence alone. Male is not in view. He is very aggressive towards singing decoy.
18 Dec.	Saudade	Unmarked female of GG/RR flies in to join her mate as soon as he begins singing in response to a decoy. She duets with him.
1971		
23 Oct.	Saudade	Male YY/BB attacking silent decoy then sings. Female duets with male in 27 of his 34 songs. Two of her songs were given in flight.

TABLE 34 (cont'd.)

26 Oct.	Saudade	Female YY/BB joins male who is countersinging with decoy and duets with her mate.
27 Oct.	Saudade	Female YY/BB joins male who is at decoy and sings with him, although decoy is silent.
		Female flies in with song to join male who is near silent decoy.
26 Oct.	Saudade	Male YY/BB sits silently with silent decoy for 17 min. Begin playback of militaris primary song. Female immediately flies in and sings with male when he gives his first response song.
27 Oct.	Saudade	Male YY/BB sitting at silent decoy and singing. Female flies in and begins singing in response.
28 Oct.	Saudade	Male YY/YY not at decoy; female flies in to join him giving a primary type song in flight.
28 Oct.	Saudade	Male YY/YY duetting with tape and female following male, in about 3/4 of his song.

TABLE 34 (cont'd.)

19 Oct.	BB30W	Two hours spent recording this male BB/BB who was accompanied by two females. One female did not sing at all though she spent most of morning close to him. A second female flew in and sang with him once near a border.
15 Oct.	La Valle	Unmarked male gave several long song bouts over a three hour period. Female duetted occasionally in two of these bouts and spent most of her time foraging on the ground, often below the male.
15 Nov.	Saudade	After I trapped male YY/BB a strange bird arrived. He sang once from wire; female answered. He flew down to join her. Thereafter they appeared to be mated.

likely that the continuous stimulation from the playback, which does not yield to the male's aggression, may be a greater stimulus than that experienced under natural conditions, and this may encourage female song.

FEMALE DEFILIPPII

On rare occasions, female defilippii gave flight displays which were very similar to those of the males, except that the vocalizations were similar to the solicitation notes. On 25 October, the unmarked mate of P. defilippii male RR/YY (Saudade 1971) repeatedly gave such flight displays. Often on the descent, she elicited a sex chase from the male who gave only two flight songs during the morning, but spent most of his time chasing the female. On one occasion, the female terminated a sex chase by breaking away from the male and going up into a flight display. The male landed 50' away from her, and then gave a rapid series of three flight displays in about 30 seconds, which were not oriented over the female. At the peak of her activity this female (presumably only one female was so engeged on this one morning) gave 14 flight songs in 26 minutes. Only one display had been noted in her territory the preceeding day, and only two were seen the following day.

Only two other defilippii females were observed to give more than one such flight display, while three gave a single display (all were unmarked birds). Thus it seems that such female displays are given by only a few individuals, probably at the peak of their cycles. In form the displays differed from those given by males in that wing-dropping at the peak was not noted.

FEMALE BELLICOSA

Female bellicosa frequently flew up to leave a territory or initiate a sex chase giving a three-part buzzy call (see Plate 46, 47), phoneticized as "tz-tzee-TZEeee", with energy gradually ascending, the main concentration occurring at about 6 khz. The same notes were occasionally given by females during flight displays.

Only one bellicosa female, an unmarked bird in territory F gave flight displays regularly. The pattern of her flight was almost identical to that of a male, and it was not recognized as a female flight at first. At the peak of her flight she uttered the harsh three note sequence, performed a typical tumble, and then landed in the grass. She did this at least 12 times on the morning of 6 September, but only three times on the following morning. This presumed pair did not engage in sex chases during this morning, and I finally

collected the bird (A.M.N.H. specimen No. 822024) and verified that she was a female with enlarged ovaries, and yolks of 4 mm and 7 mm.

SEX CHASES

Hinde (1953) believed that sexual chases of male Chaffinches represented attempts to copulate by force, but might also have a stimulating effect on the female since females often solicited just after such a chase although not before hand. Tinbergen (1939) and Lanyon (1957) reported that females actively elicit sex chases. Although I could rarely discern the events immediately preceeding a sex chase, I also found that in most cases the female seemed to invite the male to chase by giving a series of soliciting notes---in some cases notes similar to those given when soliciting copulation. I observed sex chases at least once for each form of meadowlark studied, but only in defilippii and bellicosa did I observe them frequently. Whether this is due to different phenology, or whether militaris actually has a lower frequency of sex chases remains to be ascertained.

Sex chases were a characteristic feature of the courtship period and were seen many times on certain mornings. It was not uncommon for a presumed pair to engage in several such chases in an hour. The songs were typically initiated by the female who got up with solicitation notes phoneticized as "jt jt" or "see see" (Plated 48A). To my ear the notes had an "imploring" quality. The male followed, usually remaining slightly below and behind the female, but occasionally actually touching her as if trying to force her down. The pair would pursue a rapid flight over a tortuous path, usually less than 5 meters off the ground. A flight typically lasted 20-40 seconds (but often longer), and often extended beyond the presumed territory where the pair might be joined by other males. Sometimes the female would break away, circle higher, and fly away from the territory, perhaps eliciting flight displays from other males. If the female returned to the territory the male might or might not land next to her. The fact that members of a pair would often land apart suggested that the chase was more of a courtship ritual than an attempt to force copulation, which is consistent with the fact that chases were generally initiated by females.

Females were sometimes silent during the sex chases, but often they uttered the "jt jt" or "see see" notes. I never documented one female giving both types of notes. Males usually gave excited notes during the chases. Some were squeaky (Plate 36D) in character, some resembled modified flight songs, while others were slurred and warbled notes (Plate 36E) similar to the flight songs of neglecta, bellicosa, and the Bobolink. Occasionally similar notes were given while chasing intruding males. For example, I twice observed RR/YY give excited squeaky notes as he chased intruders and once he gave a flight song while chasing a superciliaris and then returned to his territory with a typical warbled song. This dual use suggests that the notes reflect excitement and are not specific to a context. This is consistent with Lanyon's suggestion (1957) for similar notes of Sturnella.

BELLICOSA

Bellicosa engaged in sex chases somewhat less often than defilippii, but the events were very similar. Females initiated the chases uttering either 'd-d' or "scree-scree" notes, similar to those of defilippii females. Males uttered either squeaky or warbled notes, the latter closely resembling the flight song.

MILITARIS

Perhaps because they were already mated when I arrived, I saw few sex chases involving militaris. On 18 December 1970, at Saudade, male GG/RR gave a weak song while chasing a female in a low twisting sex chase. On 19 October 1971, at BB30W, male BB/BB was on a fence over a female who was feeding. I flushed her and the male gave chase while the female lead him on a low twisting flight which carried them out of sight. They were joined by another male and both males gave weak warbled notes. On neither occasion did I hear any notes from the females.

SUPERCILIARIS

Females of this species were seldom evident, and in some cases I never saw them on territories defended by males. The first sex chase I observed was near Tandil on 17 October 1971 where a male chased a female in a typical though brief flight. He broke off, flew up and gave a flight song. However, I was too far to hear whether either bird vocalized during the chase. At Saudade I noted only two sex chases, and on one of these I heard excited warbled notes. For L. m. militaris I observed a sex chase at Upata, Bolivar, Venezuela on 6 May 1970, but was too far to hear whether any notes were

used. In this case the male chased two females and was followed by a third.

MAGNA AND NEGLECTA

Lanyon (1957:38) describes sex chases for Sturnella which appeared to be integral parts of the courtship process. These flights were initiated by the female, were low tortuous flights, and often lasted several minutes. The birds were usually silent, although males occasionally uttered phrases of "rehearsed song". Occasionally more than one female was involved, while neighboring males would frequently join the chase when a pair passed over the territory. These "aerial duets" are clearly the same as those observed for defilippii and bellicosa and probably for militaris and Leistes as well. Lanyon (1957:38) cited several other references which indicate that this behavior pattern is widespread among Icteridae.

SUMMARY

1. Female song in oscines is uncommon, can be induced by injection of androgens, and is believed to be abnormal behavior reflecting a "spillover" of high androgen levels during the peak of the reproductive period. Female call notes and notes used to elicit sex chases were described in the previous chapter.

2. Female militaris frequently joined their mates and sang with them. They regularly duetted giving a song pattern similar to that of their mate or different. Female notes were buzzier than male notes, but were quite recognizable as song. Such duetting was heard during territorial encounters, visits to a decoy, or spontaneous bouts of primary song. Females were never heard to sing alone. Such primary singing is very unusual for icterids and has not been noted for other meadowlarks.

3. Females of defilippii and bellicosa did not duet with their mates (nor accompany them silently), but on rare occasions a few females indulged in flight displays similar to male displays. For both species the female vocalizations were quite distinct from those of the males, being harsh buzzy notes rather than whistled or warbled notes. This behavior involved only a few females

and occurred on only a few days. It is interpreted as reflecting the high androgen spillover effect, if such an effect is real. Such behavior has not yet been observed for other meadowlark species.

4. Sex chases were noted frequently during the early part of the breeding season. The chases appeared to be initiated by females taking off and giving solicitation notes (distinct from pre-copulatory notes). Males then followed in close pursuit often uttering excited warbled notes (sometimes referred to as rehearsed song). This behavior pattern occurs in all meadowlark species and is widespread among the Icteridae. It appears to function both in pair-formation and in pair-bond maintenance prior to incubation. It reaches a peak in the egg-laying period, probably associated with copulation.

CHAPTER 14

SOUND PLAYBACK EXPERIMENTS ON SPECIES "DISCRIMINATION" TESTS AND TRAPPING

With technological developments in portable sound recording and playing equipment, "playback experiments" have become very popular in studying bird behavior, ecology, and relationships. Ewert (M.S.) has recently reviewed the variety of techniques, purposes, and analyses reported in the literature, and has pointed out some of the sources of confusion which arise when two different techniques are compared. He has stressed the differences between one and two speaker playback (dual-playback) techniques, and has noted the disadvantages of using a visual stimulus during playback experiments.

I employed both mono- and dual-speaker tests, although the latter were confined to bellicosa studies in Peru. Unless otherwise stated all playback studies involved a mounted militaris decoy or a plastic facsimile of one. I noted several categories of response, such as closeness of approach, whether a flight song was given during the approach, frequency of approaching vs. leaving (or re-orienting), frequency of singing, frequency of physical attack. Although in many cases I noted the time

preceeding the approach or attack, I found these to be very variable. The main problem is that meadowlarks frequently spend part of the time feeding outside the territory, and they may not be available to approach the decoy until some unknown period after the test has started.

TRAP TIME

Trapping attempts, using playback and decoys, can be treated as a variant of playback studies, particularly for evaluating motivational levels, since a higher motivation or attack tendency is necessary for a bird to enter a trap than to attack a decoy. I deal with these tests in this chapter.

MONO-SPEAKER METHODS

A decoy was placed in a prominent position (on fence, grass clump, or stick) in the territory of the bird to be tested. I attempted to place the decoy about 2/3 of the way from the presumed center to the presumed boundary of a territory, although both of these estimates were very crude. I found that males, particularly militaris would move beyond the area that they defended to attack a decoy (an "intruder") until repulsed by a neighbor.

Decoys remained "silent" from 5 to 10 minutes before

starting playback. Various protocols were used in these initial experiments, including autospecific-hetrospecific-autospecific or hetrospecific-autospecific-hetrospecific sequences. In some cases, autospecific sequences included flight vs. primary songs. The sequence in which songs are presented can influence responses, and since in the present series, only the initial song was chosen at random, the usual statistical tests of comparing strength of responses within tests would be inappropriate.

I have employed here the more crude and conservative method of predicting the expected frequency of responses from the amount of time the total test population was exposed to different kinds of songs. Thus if 25% of the test minutes involved autospecific primary songs, one would expect 25% of each response category to occur during autospecific primary song playback, if all the stimuli are equivalent.

DUAL SPEAKER METHODS

The two speakers were set up about 50 meters apart in a bellicosa territory and were connected to two tape recorders by about 75 meters of cable so that I could operate them from a blind (=car). The territories studied were all adjacent to the dirt road from which I did most of my work. For decoys I used two plastic statues painted to resemble male Pezites. These were placed on stakes about 50 cm tall over the speakers.

Each experiment began with 10 minutes of silence after I returned to the blind. Then the two test songs were begun at approximately equal volume, the assignment to each speaker being at random. After 5 minutes, the speakers were switched, and after five more minutes the playbacks were stopped. After another 10 minute silent period the playback was resumed with the same speaker arrangement as at the end of the first period. Again the speakers were switched midway through the 10 minute period. Another 10 minute silent period was followed by a third 10 minute test period with the same speaker alternation as in the first period. This was followed by a final 10 minute period of silence.

Thus each bird received 30 test minutes and 40 silent minutes, and a positive response involved three re-orientations, one during each test period.

I scored the dual-speaker tests as follows:

Approaches song during first 5 minutes of each test period (no score if bird had approached that speaker during control period; 2.5 in first min, loses .5 for each minute)	=0-2.5
Reorients to other speaker when song is switched after five minutes (within 1 minute =5, loses 1 for each minute)	=5 or less
If bird remains closely associated with this speaker during silent period	=1
If bird remains at same speaker, at start of next test period	=1
Attacks decoy during test period (if no attack during silent period)	=3
Departure from a speaker to leave test area	=-1
Departure from a speaker to other speaker, except during first minute or 6th minute of a test period	=-2

The maximum number of points would be gained by a bird showing no interest during first silent period, approaching song A within first minute and attacking, reorienting to song A within first minute and attacking, remaining at that speaker, etc. Maximum score = 3 x 14.5 = 43.5 points. Although complex, these scores proved easier to apply than measurements of time and distance.

PLAYBACK -- MILITARIS

Early in the 1970 season I used a tape loop of catamarcanus made in Tucuman by Lanyon, or a recording made at Saudade by me. However, for the playback tests I used a recording of a Bariloche male (El Condor BB/YY, made by me on 28 November), (see Plate 39A). This "foreign" song was chosen because some species have differential reaction to near-neighbors vs. non-near neighbors, vs. birds from different dialect areas, (Lemon 1967, Milligan and Verner 1971, see also Ewert M.S.). To avoid variation in response that might occur if a song from the pampas was used, the Bariloche song was employed.

All playback tests were conducted with a decoy---a stuffed male militaris. The first series of tests of 24 pampas males revealed that there was a little difference in initial response to a decoy whether accompanied by silence, or by militaris or defilippii song. This is partly due to the small sample size, but also reflects the strong response to silent decoys. The results are summarized in Table 35. In 275 minutes of silence, there were 13 approaches compared with 13 for 180 minutes of militaris song. There was only a slightly lower approach rate to a defilippii song (.046/minute) compared with a silent decoy (.047/minute). However, there were

TABLE 35 . Results of 24 playback tests to male militaris in the Bahia Blanca-Saudade area, using a "Bariloche primary" loop with a militaris decoy.

Response Category	Score Value	Number	Test SILENT	Vocalization MILITARIS	Employed DEFILIPPII
Number of minutes tested			275	180	65
Approaches within 10 meters	1	28	13	13	3
Approaches within 1 meter or crosses (no attack)	2	4	0	4	0
Starts primary song bout	2	27	10	10	5
Physical attack on decoy	3	10	6	4	0
Leaves decoy	-2	15	9	3	3
Total Score			33	47	7
Score/exposure minute			.12	.26	.10
Approaches/minute			.047	.072	.046
Departures/minute			.033	.016	.046
Approach/Departure Ratio			1.44	4.33	1.0
Attacks/minute			.0218	.0222	0

nearly 50% more departures from the defilippii than from the silent decoy (.046 compared with .032/minute). The departure rate from a militaris decoy was .016/minute, or about 2.5 times lower than for the defilippii decoys, and more than half of these departures were to accompany the female. In other tests a militaris male lingered at a decoy for more than 30 minutes while a militaris loop played and then left shortly after a defilippii song was substituted.

Perhaps the most useful measure of response was the approach/departure ratio which was 4.33/1 during militaris playback but was less than 1.5/1.0 during defilippii playback or silent periods.

There was also a marked difference in the attack rate, six of which occurred during silence (.028/minute) and four during militaris song (.0222/minute), while none occurred during defilippii song. Although in this respect the silent decoy appears to provide almost as strong a stimulus as the decoy with militaris song there were some striking differences. Once a male arrived, it might vanquish a silent decoy within 30 seconds, often with only a brief display, while a singing decoy often elicited extensive posturing as if it took more courage to attack a singing decoy. Moreover, a male would usually leave a silent decoy as soon as it had been knocked over, while a singing decoy would continue to

provide a stimulus, even though the decoy dangled upside down from the wire fence.

Clearly the visual stimulus of the decoy is a very important part of the present experimental series, and Ewert (M.S.) has noted the disadvantages of using decoys in playback tests.

Finally, it is probably significant that two males which strongly responded to defilippii song were in an area with no defilippii neighbors, while three militaris with many defilippii neighbors showed no response at all to the heterospecific songs.

PLAYBACK -- DEFILIPPII

Data are available on 31 playback tests for male defilippii believed to be defending territories. Several formats were used in the experiments, although all started with a silent decoy for 5 minutes. Experiments alternated auto-specific song and silence at 5 minute intervals, auto-specific and heterospecific song, and autospecific flight and primary songs, and the experiments lasted from 15 to 65 minutes. I did not attempt to make a rigorous test of the relative responses of males to different songs under different experimental conditions, but only to ascertain that there was a difference in response to auto-specific, heterospecific songs, and to silent decoys, (Table 36).

TABLE 36. Results of playback tests to *defilippii* males.

			TEST VOCALIZATIONS EMPLOYED			
			SILENT	DEFILIPPII SONG		MILITARIS
			Control	flight	primary	1° song
Number of Minutes Tested			462	88	362	270
Percent of total time			(39.1)	(7.4)	(30.6)	(22.8)
RESPONSE CATEGORY	Value	Number				
Primary song given	1	88	27	2	28	14
Flight song given	1	60	23	9	15	13
Approach + flight song	2	24	4	3	15	2
Departure + flight song	1	15	4	3	1	7
Silent approach	1	26	4	0	21	1
Silent departure	-2	15	5	2	4	4
Physical attack on decoy	3	3	0	0	3	0
Total Score			56	16	96	31
Score/exposure minute			.12	.18	.27	.11
All approaches			8	3	36	3
All departures			9	5	5	11
Approaches/minute			.017	.034	.099	.011
Departures/minute			.019	.057	.014	.041
Approach/departure ratio			.89	.60	7.2	.27

I have therefore restricted the analysis to comparing the proportion of different responses to each of these experimental conditions, based on the proportion of time that each condition pertained. Examination of individual experiments revealed that different males differed markedly in their frequency of vocalization, and in the persistence of response. A strict statistical evaluation would require different experimental design, preferably restricting each male to a more limited number of responses.

The results shown in Table 37 demonstrate that defilippii were significantly more likely to approach the decoy, while an autospecific primary song was playing, than under other conditions. Experiments 32-37 comparing flight and primary songs, show that although a male was more likely to give a flight song during a flight playback than at other times, it was more likely to approach during a primary song playback.

For each response category, the expected number of responses to each of the four playback situations (silence, def-p, def-f, mil-p) could be predicted from the total number of responses and the percent of the total time that test birds were exposed to each stimulus. The observed distribution of response was compared with these expected values by response category (df=3). The G-statistics for primary and flight songs were 6.04 and

TABLE 37 . Six experiments comparing defilippii responses to conspecific flight and primary songs. (expected values computed where sample exceeds 10). [expected values in parentheses, df=2].

CATEGORY OF RESPONSE	SILENT	PRIMARY	FLIGHT	TOTAL	G	Prob.
Minutes	80	70	45	195		
% of total time	41%	35.9%	23.1%	100%		
Flight Songs given	2(6.1)	3(5.4)	10(3.5)	15	13.0	<.005
Approach with flight song	0	2	1	3		
Depart with flight song	1	0	1	2		
Silent approach	2	5	1	8		
Silent departure	0	1	2	3		
Total flights	3(8.2)	5(7.2)	12(4.6)	20	13.3	<.005
Total approaches	2(4.5)	7(3.9)	2(2.5)	11	4.1	>.10

4.01 respectively, neither being significant. Thus flight and primary song responses were given equally under all four test conditions. However, although not statistically significant it is interesting that silent decoys and def-p decoys received more primary than flight songs, while militaris song received the same number of flight and primary song, and the def-f decoys received 9 flight songs and only two primary songs. Only 88 minutes (7.4% of total time) involved the flight songs, so that this discrepancy may become significant if greater attention is devoted to testing flight songs.

There was no significant difference in silent departures ($G=.09$), but the other categories of response revealed differences. Flight approaches occurred mainly in response to primary song playback or flight song playback ($G=14.1$; $p<.005$), while flight departures occurred mainly after an approach to a militaris song ($G=9.96$; $p<.025$). Silent approaches occurred almost exclusively to defilippii primary song ($G=29.5$; $p<.001$). Physical attacks on the decoy and also successful trapping occurred only with defilippii primary song. However, the attack rate (.008/min.) was lower than for militaris responding to autospecific song (.022/min.).

Although not apparent in the table, there was a tendency for some individuals to respond repeatedly to any stimulus while others did not respond at all. There

may be considerable interbird variation in tendency to respond to militaris playback, perhaps depending on exposure to militaris. A detailed study of this problem would require more attention to independence of responses by limiting the number of tests per individual.

In view of their observed interspecific territoriality, I attempted to test defilippii responses to supercilaris primary song. The responses were either weak or negligible, even when the defilippii was close to begin with. This may be due in part to the distortion of the high frequencies of the superciliaris song by the equipment employed. However, I did not notice a tendency of defilippii to respond to real superciliaris primary song, while they did seem to respond more to superciliaris flight songs. Unfortunately, no bellicosa recordings were available in 1971 to test defilippii responses.

PLAYBACK -- BELLICOSA

Playback experiments were particularly important in evaluating the relationships of *bellicosa* since it is not sympatric with any other meadowlarks. Single and dual speaker tests were used, and the following categories of vocalization were tested:

bellicosa	primary and flight songs	(bel-p or bel-f)
defilippii	primary and flight songs	(def-p or def-f)
militaris	primary song	(mil-p)
neglecta	primary song	
magna	primary song	
Zonotrichia capensis	song	

Dual speaker tests were confined to territories of marked males. Each male was tested twice, in August and/or September, with at least a week between each test.

The protocols used were as follows:

	Speaker A	Speaker B
10 minutes	silence	silence
5 minutes	bel-p	test song
5 minutes	test song	bel-p
10 minutes	silence	silence
5 minutes	bel-p	test song
5 minutes	test song	bel-p
10 minutes	silence	silence
5 minutes	bel-p	test song
5 minutes	test song	bel-p
10 minutes	silence	silence

Test Songs Chosen	Trials
militaris primary	3
defilippii primary	5
bellicosa flight	1
defilippii flight	2

bel-p = *bellicosa* primary

On each test the assignment of A and B to the speakers was done at random by toss of coin.

In the single speaker tests a greater variety of songs and sequences was employed, and the results are shown in Table 39.

TABLE 38. Results of 11 dual speaker tests with *bellicosa* males.

	RECORDING TESTED AGAINST PRIMARY SONG	POINTS SCORED Bel-p[2]	Test Song
1	militaris primary song	38.5	0
2	defilippii primary song	22.0	2.0
3	defilippii primary song	6.3	2.9
4	defilippii primary song	19.0	4.0
5	militaris primary song	27.3	1.0
6	bellicosa flight song	21.3	6.5
7	defilippii primary song	28.3	1.0
8	defilippii flight song	17.7	0.5
9	defilippii flight song	9.5	0.5
10	militaris primary song	19.6	0
11	defilippii primary song	39.4	1.0

RATIO BETWEEN RESPONSE TO CONTROL & TEST SONGS	
defilippii flight song	10.6/1 [b]
defilippii primary song	27.2/1
militaris primary song	c
bellicosa flight song	3.3/1

a = all songs were tested against a *bellicosa* primary song

b = ratio is low because in these tests birds had low overall response to control tape

c = no response to militaris primary song

TABLE 39 . Results of single speaker playback tests to male bellicosa at Bujama.

	TEST VOCALIZATION						
	Silence	bellicosa p	bellicosa f	defilippii p	defilippii f	militaris	neglecta	Total
Number of Tests		18	16	12	8	17	4	71
Tests with weak positive response		4	4	3	0	2	1	14
Tests with strong positive response		9	3	0	0	0	0	12
Tests and (%) with no response		5	9	9	8	15	3	49
% tests with no response		28%	56%	75%	100%	88%	75%	
Number of minutes of test exposure	310	240	195	120	80	145	40	1130
% of total time of exposure	27.4	21.2	17	10.6	7.1	12.8	3.5	
Categories of responses observed								
primary songs given	43	7	8	9	3	7	2	79
flight songs given	8	6	8	2	1	1	1	27
approaches with flight song	4	14	9	1	0	1	2	31
departure with flight song	5	9	4	0	0	1	1	20
silent approaches	7	5	0	0	0	1	0	13
silent departures	5	1	2	0	0	1	0	9
physical attack on decoy	1	5	0	0	0	0	0	6

DISCUSSION

There was no evidence of a bellicosa response to songs of Zonotrichia capensis, S. magna or neglecta, or P. militaris. Like defilippii, bellicosa showed little tendency to make close approaches to silent decoys which is perhaps related to the fact that they often tolerate non-territorial males foraging in their territories.

There was a low but real tendency to approach decoys with defilippii primary songs, presumably due to the overall structural similarity in their songs. Despite the variability in the songs within species, there is probably enough between-species difference to allow species discrimination by primary song, but in the absence of sympatry such discrimination has perhaps not been selected for. Unfortunately I did not have a sample of bellicosa songs in 1971 for testing defilippii. There was no tendency to approach defilippii flight songs which are very different from bellicosa flight songs.

The short, relatively low-energy primary songs, and the long, high-energy flight songs of bellicosa provide very different stimuli in playback tests. An adequate study of the different responses to these two song types would require many more tests with more males under a variety of circumstances, preferably with dual speaker protocols. Only a few flight song tests were done in

my study, and there appeared to be a different response, although the number of tests is inadequate for statistical stury. A territorial male seemed more likely to respond to a flight playback with a flight song, seemed less likely to approach the speaker closely, showed little tendency to respond with primary song, and tended to leave sooner. These results are not surprising, since males often approached a common boundary with a flight song, and then immediately began primary song duets across the border. Clearly a more detailed study is called for.

PLAYBACK -- SUPERCILIARIS

On several occasions I attempted playback experiments with superciliaris at Saudade. Tests were always equivocal because of the inconsistent responses of males to autospecific voices. The main problem was that much of the energy in superciliaris primary songs is between 6000-10,000 hertz, beyond the optimal range of equipment used. It also appeared that the large militaris decoy with the extensive red area on the breast, might be inhibiting or intimidating the superciliaris males. In later experiments I masked part of the red by pinning brown paper over the lower breast, and in future tests of this species I would use a superciliaris decoy.

OBSERVATIONS ON THE TRAPPING OF MEADOWLARKS

During this study a large proportion of time was devoted to capturing birds for color marking. I treat these attempts here as a special case of playback experiments. In all cases a trap contained a mounted specimen of a militaris male and was accompanied by a tape-recorded playback loop of some song. Although I experimented with a variety of traps, two main types were used (see figure 4). The collapsible triangular trap could be used only on the ground while the bird-cage trap, purchased locally, fit snuggly between adjacent strands of the wire fences. These traps differed substantially in shape, dimensions and particularly in the size of the door, factors which no doubt influence the reluctance of meadowlarks to enter. Although a small trap entrance might dissuade a male from entering, the smaller dimensions of the bird cage trap, allowed males to get much closer to the decoy, and presumably more excited. This seemed to compensate in part for the small door, although no detailed comparison was performed.

COMPARISONS OF TRAPPING SUCCESS

In the few cases where I prolonged trapping attempts for more than one hour, I was not successful, and in general I discontinued trapping attempts after an hour (or less in cases where males failed to approach). There are many variables which influence whether a male will enter a trap. The most important of these are: stimulus value if the decoy-playback combination, fearsomeness of the trap, position of the trap in territory, stage of breeding cycle, recent experience of male with respect to other territorial encounters, and other events occuring during the trapping attempt.

Since many things combine to produce success or failure, I have decided to consider only those trapping attempts which were successful. I found a greater tendency for failure late in the season, but, remarkably, I did not find that males who approached traps rapidly (< 2 min.) were more likely to be trapped than males who were slow in approaching. Also, despite the greater visibility and shorter approach-times and distances when traps were mounted on the fence, I found that militaris males were more likely to enter a trap on the ground. Perhaps the ability to walk completely around the trap is important, but observations of traps placed in the open, indicate that males spent almost all the time directly in front of the trap entrance, the direction

the decoy was facing.

The case of militaris male YY/BB illustrates the problem. This male was trapped and color marked on 21 October, and I spent over three weeks observing it. Starting on 11 November, I made seven attempts to live trap it, placing the trap in different positions within its presumed territory. Finally, on 15 November, I succeeded in capturing it, with the trap placed 25 meters from the nest.

This bird had had the opportunity to become trap-shy, and it had spent nearly six hours in close proximity to the trap without entering it, but on the successful try, it approached in less than two minutes, and entered the trap in 10 min. 35 sec. (close to the average for first captures for the species). This experience bore out my impression that if trapping were going to be successful, it would usually be successful early.

DEFILIPPII

Male defilippii were trapped at Saudade (n=15) and at Bahia Blanca (BB7E) in October 1971 and November, December 1970. Table 40 summarizes the approach-time and trap-time data for these three periods. In view of the decline in display frequency and territorial defense activity with season, one would predict that the maximum

response to trapping attempts would occur early in the breeding season and that both the approach-times and trap-times, as well as failure rate would increase as the season advanced. The data were compared by month with the Mann-Whitney U tests (1-tailed since the direction of change was predicted). The differences between October and November were not different, while the differences from October or November to December were significant ($p<.05$).

I assumed that the two years could be merged, and I numbered days consecutively from 18 October = day 1, to 15 December = day 49. I compared the total time (approach + trap) to the days using the Kendall Tau test for correlation ($tau=.305$, $p=.032$). This shows a significant increase in the total trap time as the season progressed. Comparing approach-time to trap-time also showed a correlation ($tau=.559$, $p<.001$).

MILITARIS

Twenty male militaris were trapped at various locations in Argentina. Table 41 summarizes the approach-time and trap-time data for these three species. For both time categories inter-month comparisons were made with the Mann-Whitney U test. Only one male was trapped in December, so no meaningful comparison can be

made with that month. However, values for November were significantly longer than for October.

The correlation between day and total trap time was positive (tau=.427, p=.004), and there was also a significant correlation between approach time and trap time (tau=.531, p<.0007).

BELLICOSA

At Bujama, I trapped seven male bellicosa in July and August, with most of the birds captured in a two day period (18-19 August). Table 41 summarizes the approach-time and trap-time data. No meaningful comparison can be made with the seasonality. There was also no correlation between approach-time and trap-time (tau=-.144; p>.35). Although less responsive than militaris, male bellicosa had lower approach-time than did defilippii. Trap-times were similar for bellicosa and defilippii and were significantly longer than for militaris.

TABLE 40. Approach-time and Trap-time results for 23 captured *defilippii* males.[a]

MONTH	N	APPROACH TIME Mean	S.D.	TRAP TIME Mean	S.D.
October 1971	10	7.75	± 5.85	12.49	± 8.05
November 1970	7	7.21	± 6.40	17.47	±13.85
December 1970	6	21.21	±13.89	30.43	±20.78
Combined Total	23	11.10	±10.34	18.68	±15.25

MATRIX OF MANN-WHITNEY U Scores to compare months with respect to trap time and approach time.

TRAP TIME	APPROACH TIME OCT.	NOV.	DEC.
OCT.	---	U=32	U=10 p<.025
NOV.	U=28	---	U= 7 p=.026
DEC.	U=14 p=.05	U=13 p=.15	---

a= the times noted in this table are a biased sample of responding males, since males responding but not trapped are excluded from the table.

TABLE 41. Approach-time and Trap-time results for 20 captured militaris males.

MONTH	N	APPROACH TIME Mean S.D.	TRAP TIME Mean S.D.
October 1971	8	2.72 ± 2.37	8.46 ± 5.08
November 1970	11	4.12 ± 4.14	10.88 ± 5.09
December 1970	1	12.4 ±	25.1
Combined Total	20	3.98 ± 3.94	10.62 ± 6.01

MANN-WHITNEY U TEST Comparison of Times by Months

		U	P
Approach	Time	36	p>.30
Trap	Time	27	p>.10

COMPARISON AMONG THE THREE SPECIES FOR TIME COMPONENTS OF TRAPPING

SPECIES	N	APPROACH TIME mean S.D.	TRAP TIME mean S.D.	TOTAL TIME mean S.D.
militaris	20	3.98 ± 3.94	10.62 ± 6.01	14.62 ± 9.39
defilippii	23	11.10 ± 10.34	18.68 ± 15.25	29.78 ±24.33
bellicosa	7	5.31 ± 5.53	15.17 ± 6.99	20.49 ± 9.13

MATRIX OF MANN-WHITNEY U COMPARISON AMONG SPECIES

APPROACH TIMES (2-tailed probabilities)

TRAP TIME	MIL	DEF	BEL
MIL	---	U=86 p=.002	U=42 p=.132
DEF	U=110 p=.004	---	U=39 p=.042
BEL	U=42 p=.132	U=64 p>.40	---

DISCUSSION OF TRAPPING

Trapping has an advantage over other playback techniques, in that the trap introduces an obstacle which only birds with a high level of aggression are likely to overcome. In view of the many sources of trapping-failure, I make no attempt to compare successful with unsuccessful trials, but the successful trials can be analyzed to some extent. The approach-times and trap-times proved very variable, but militaris was quicker in approaching and entering traps than either bellicosa or defilippii. This accords with its greater responsiveness in playback experiments. It would be valuable to investigate whether the lower aggressiveness of defilippii and bellicosa relate to their social structure (relatively small, regularly spaced territories), to phsiologic variables in the small samples used, or perhaps to the stimulus complex itself, since the decoy used was actually a militaris.

It would be most valuable to relate aggressive behavior to social structure in birds, and some progress has been made for the Laridae (e.g., Cullen 1960).

SUMMARY OF PLAYBACK AND TRAPPING

1. Playback experiments, involving the broadcasting of various acoustic signals allow one to experiment with avian behavior and to define the various functions of the signals and responses of the birds.

2. Both single and dual speaker experiments, in all cases accompanied by a mounted decoy, were used in this study. During trapping attempts a decoy was placed in a trap and appropriate song broadcast, and these attempts are treated as special cases of playback tests. The presence of the trap provides a fearsome obstacle so that obly a strongly motivated bird will enter to attack the decoy.

3. P. militaris males showed a strong tendency to approach and even attack silent decoys (without a trap). Attack tendency was enhanced by militaris song and reduced by defilippii song. Trapping was only successful with militaris song.

4. P. defilippii males responded less strongly than militaris, but approached the decoy significantly more often when autospecific song was broadcast. Autospecific primary song was more attractive than flight song. Physical attacks and successful trapping occurred only with defilippii primary song.

5. Despite occurrence of interspecific territoriality between *defilippii* and *superciliaris*, I could not demonstrate cross-responses to vocalization, perhaps because of the technical limitations of the equipment.

6. *P. bellicosa* males responded weakly to silent decoys. Responsiveness was not enhanced by playback of *militaris* song, was slightly enhanced by *defilippii* song, and greatly by *bellicosa* primary song. Flight songs of *bellicosa* were less attractive than primary song.

7. Responsiveness, particularly during trapping attempts, declined appreciably through the season reflecting physiological changes in aggressiveness associated with the breeding cycle.

8. During much of the season natural territorial encounters were infrequent. The playback techniques introduced a high level of artificial territorial challenges.

9. Species differed in aggressiveness with *militaris* males having a greater tendency to attack decoys. This may reflect the different social structure of this species (large dispersed territories) compared with the more grouped territories of *defilippii*, *bellicosa* and Leistes. Further work on the sociobiology of these

species would be revealing.

SECTION IV. TERRITORIALITY AND DISTRIBUTION

15. Introduction, Technique and Species Accounts

16. Dispersion and Coloniality

Mapping so-called "territories" or utilized spaces of meadowlarks often proved difficult even with marked individuals. All data for unmarked individuals, even those obtained over a period of a few hours, are tenuous for reasons indicated earlier. Nonetheless it was possible to make some composite maps indicateing the approximate territorial relationships on the various study areas. From these maps, ignoring the uncertainty with which they were constructed, it is possible to measure the size of the territory or utilized space (see below for distinction and relevant techniques). The estimates derived from such maps have some value, as evidenced by the consistent order of magnitude and should be useful until better ones are obtained.

In this section I also examine the pattern of dispersion of Pezites. I recorded superciliaris on only one of the point censuses discussed in this section, and I therefore omit it from further consideration.

CHAPTER 15 MEADOWLARK TERRITORIES

INTRODUCTION

Territoriality is a central principle in the study of avian biology, and some of the most conspicuous attributes of birds (e.g., their bright color patterns and their voices) are involved in the maintenance of their territories. Armstrong (1947), Huxley and Fisher (1948), and Nice (1933, 1941) among others provide historical reviews of the concept in ornithology, noting that the first mention of territoriality dates back to a publication by Olino in 1622. Bernard Altum provided a synthesis of the concept in 1869 (Der Vogel und Sein Leben, cited by Mayr 1935), in which he discussed the maintenance of territory in terms of assuring an adequate food supply for the adult and young birds. Howard (1920) published a somewhat broader account of territoriality, the first major report in English, although neither author gave a strict definition of territory.

The most widely accepted definition involves the concept of "defense of an area", first stressed by Nice (1933) and amplified by Noble (1939). Emlen (1957) stressed that within its territory a bird maintains dominance via aggression, and that the bird is not actually defending anything in many cases.

Various authors (e.g., Emlen 1957, Jourdain 1921, Lack and Lack 1934, Mayr 1935) have criticized Howard's presentation of territoriality, and Tinbergen (1936) suggested that territory (in the sense of an area) was inadequate to account for much observed aggressive behavior. His argument was to some extent semantic, since he restricted his notion of territory to a static space with no temporal change. He stressed that "territorial" behavior was directly related to the sexual bond, and this is operationally useful, since in many birds such behavior declines markedly later in the breeding cycle (e.g., Lanyon 1957; Peek 1971; Stefanski 1967; Stenger and Falls 1959; Wiens 1969; Yarrow 1970; Young 1951). This has also been reported for the male Three-spined Stickleback (Gasterosteous aculeatus) by Wooten (1972) and no doubt for other organisms as well.

The above discussions of territoriality were hindered by lack of a generally acceptable definition, and Brown (1964) pointed out that such arguments are largely irrelevant in evaluating the evolution of the many different kinds of territory. Brown and Orians (1970) provide the basic generalization that territoriality can be interpreted as the defense of any environmental resource, and that such behavior will evolve in those cases where defense of the resource is economically feasible and advantageous. The diversity of territorial

systems can be understood when the time-energy budgets are determined, and they consider speculation on the function of territory as unproductive. This is reasonable since the function of territoriality or of any ecological, behavioral, or morphological adaptation, is ultimately to improve fitness.

Major reviews of the literature on avian territories include those of Hinde (1956), Brown (1969), Brown and Orians (1970), and Orians (1971). The essence of territoriality lies in defense of a resource, and Nice (1941) distinguished six types of avian territories:

A. Mating, nesting and feeding ground for young
B. Mating and nesting only
C. Mating station only
D. Nest site only
E. Winter territory
F. Roosting territory.

It seems reasonable to add an additional category, defense of mate, as in Rosy Finches (Leucosticte tephrocotis atrata) where French (1959) found males defending a moving space around their females. Also defense of a finite "individual space" (Conder 1949) around oneself can be considered a territory, and birds may often defend food resources as well.

Although the Nice classification is useful, the

categories mentioned are not necessarily discrete, nor are they necessarily constant for a given species. Although the type A territory, often believed to be the commonest system, may predominate among North Temperate passerines, it may not be common elsewhere. Moreover, the usual dichotomy between territorial and non territorial species should be replaced by a concept of a continuous gradation in the size of space defended around a nest which may vary from zero to very large, and attention should focus on the circumstances under which defense occurs, and the nature and proportion of activities conducted in the defended area.

DESIGN OF STUDY

In any study of evolutionary ecology one would like to compare organisms with and without a particular attribute to determine the function or advantage of the attribute. This would allow one to make predictions about the circumstances favoring the occurrence of the attribute. Carrick (1963) and Snow (1956) noted that measuring the selective value of territoriality would require a comparison of the breeding success of territorial vs. non-territorial within the same species, whereas for most species, probably only one type of male behavior pattern will be encountered. Possible exceptions include the behavioral polymorphism reported for

the Ruff (Philomachus pugnax) by Hogan-Warburg (1966) and others, and the different territorial regimes reported for the Seaside Sparrow by Post (1974) in different habitats.

I approached the problem as follows:

1. For each species I attempted to learn the nature of the territorial system.

2. For each group of meadowlarks encountered I obtained at least a crude census and density estimate and tried to relate this to habitat. I particularly tried to compare militaris territories on the pampas and in Patagonia and defilippii territories in wheat and grass.

3. In a few cases I noted the change in apparent size of territory or utilized space with season.

4. I attempted to relate utilized space to territory.

SIZE OF TERRITORY OR UTILIZED SPACE

The distinction between utilized space (Stenger and Falls 1959) or activity space and territory is that the latter is defended while the former is only occupied. The various techniques used to measure these areas may measure one or the other, but usually not both. Perhaps the most useful means of estimating a bird's use of space is to plot a time-area curve where the position of the

bird is mapped periodically, either for every 2 or 5 position-changes or at given time intervals. At first area increases rapidly with increasing number of observation points, but eventually the curve flattens out and approaches an asymptote. Failure to achieve such a plot is evidence that the bird is probably not confining its activities to a discrete space, or that observations are inadequate. This technique, popularized by Odum and Kuenzler (1955) has various modifications and applications. It relies on a law of diminishing returns, which allows one to predict how many observations are needed to determine the occupied area. Using this technique they demonstrated that for several species the size of the territory or home range declined during the breeding season.

An alternative method measures territory specifically, when one plots on a map the points where male-male encounters occur, and the perches where males repeatedly sing. This can be very time-consuming, since activity along a particular border may be low if the neighbor on that border does not participate in border challenges. Moreover, there is evidence that in some species (Weeden and Falls 1959), but not others (Belcher and Thompson 1969) individuals may "learn" the voices of neighbors, and respond less to them than to voices of strangers. Thus once territories are established,

defense along boundaries could diminish.

Another technique is for the observer to move into the area occupied bu a bird and flush it repeatedly, noting the area which it covers. This method was used by Wiens (1969) and has the advantage of providing many data points in a short time period. In my own experience, this method gave excessive estimates of occupied area, since birds would fly beyond the bounds of their own territories, and their neighbors, perhaps also frightened by the observer, would not chase them from an area that would normally have been defended.

METHODS

On each study area I made some estimates of the utilized space or territory size of meadowlarks. The techniques employed varied, depending on place and purpose, and the exact technique will therefore be discussed when the results are presented. In order to minimize the effect of seasonal change in territory size, any given measurement is based on observations made within no more than a 48 hour period. Longer observations on the same bird are treated in discrete 48 hour categories and show the temporal change in territory size.

The two basic techniques referred to below are:

TECHNIQUE 1. For a given time period, all position changes of a bird are mapped. (estimates utilized area).

TECHNIQUE 2. For a given period all song-perches, territorial encounters and flight displays are mapped. The latter are often oriented parallel to a territorial border and provide useful information even if the territorial neighbor is not nearby. (estimates territory).

Often the two techniques could be applied simultaneously. Data were assembled into composite maps which attempt to show the location of several males with respect to one another. It is often difficult in such cases to be certain of the position for boundaries and corners.

The results on territory size are considered separately for each species.

MEADOWLARK TERRITORIES

S. magna and *S. neglecta*

Lanyon (1956a, 1957) described territories and territorial behavior of *magna* and *neglecta*. He found no marked differences between the species. Territories of the two species were similar in size (3-15 acres) and were maintained solely by males. An individuals' terri-

TABLE 42

Literature reports on territory sizes for meadowlarks (hectares)

CITATION	STURNELLA NEGLECTA			STURNELLA MAGNA			BOTH SPECIES			STATE
	n	mean	range	n	mean	range	n	mean	range	
Kendeigh (1941)	4	8,2	3.8-12.1	--	---	----	-	---	----	Illinois
Lanyon (1957)	-	---	----	--	---	----	2.6-3.1		1.1-5.6	Wisconsin
Weins (1969)	5	2.2	1.6- 3.1	18	2.1	1.6-2.9	-	----	----	Wisconsin
Schroeder (1974)	-	---	3 - 5	--	---	-----	-	----	----	Colorado

(all reported figures have been converted to hectares)

torial behavior fluctuated during the breeding season, but some degree territoriality was manifest until the young had fledged. He noted that territories were not constant but changed in size and/or shape due to pressures from neighboring males, female activity, habitat changes, and probably also due to changes in the male's own aggressiveness. He noted that territories shrank in size as new males arrived. This accords with Tinbergen's findings (1939) that Snow Bunting territories were not static in size, but changed with the arrival of new males, aggression increasing as territory size decreased. Lanyon doubted that food was limiting during the breeding cycle and indicated that territory size was probably not related to food. I have found only a few reports estimating sizes of Sturnella territories, and these are summarized in Table 42.

P. militaris

I examined meadowlark territoriality on the pampas and in less detail in Patagonian scrub vegetation and in the grape arbors, and riverine marshes of western Argentina. On the pampas, militaris territories were almost always arranged along fencerows and utility lines. Elevated perches seem to be required by militaris and if utility poles and lines were not available they used woodlots. On the Saudade plots most breeding and singing

activity was confined to the fencerows, although the birds foraged in the fields.

For the most part, therefore, militaris territories were linear, although if there were a cross fence, the birds activity might occur along both fences. Territorial encounters with neighbors occurred only at the ends of the territory, and even there were rarely observed. Except for the ends of the territory, the next neighbors would be along the next fencerow, often more than 1 km. away. Territorial activity in the center of the territory was directed against intruders.

As indicated below there was no strong interspecific aggression between militaris and either defilippii or superciliaris although the three species are quite similar. Although militaris-militaris interactions also were infrequently observed, militaris males were extremely vigilant in defending and in vanquishing a stuffed decoy. At Saudade, I attempted to retrap male YY/BB for breeding purposes. Its female was just beginning to re-lay, and I often saw them foraging in a short grass field. Over a three-day period I was unsuccessful in trapping the bird, or even eliciting an attack against the decoy, when it was placed in the open field where the birds foraged. However, I succeeded subsequently with the trap placed near the fence, although the two trap positions were less than 50 m

apart. In other territories, I also experienced failures with traps in the field followed by success near the fence, though clearly more data would be needed to substantiate this.

In view of the infrequent occurrence of territorial encounters, it proved difficult to distinguish the utilized space from the defended space. A characteristic of militaris behavior is that a pair of birds would frequently make long flights away from the center of activity, often disappearing from view. They might remain absent for an hour or more, and I did not succeed in determining whether they were consistently going to one locality or whether they defended the distant locality. Often the flights exceeded 500 meters, and the activity space utilized by militaris is therefore much greater than the area known to be defended by them.

On the Saudade study area the militaris males ranged along 300-400 meters of road frontage, and pairs were active as much as 100 meters from the road. Excluding the long flights away from the road, the area utilized on a given morning was approximately 2-4 hectares. For male GG/GG and YY/BB (Saudade 1970 and 1971) I was able to note activity centers over a period of more than four weeks, and the shifts noted were related to the location of active nests in their territories.

At Bahia Blanca (BB7E) militaris were active over much of the fields, but it proved much easier to elicit aggressive responses and to trap males along the few fences than in the open field. At Punto Tombo where up to five males held territories around a water tank, the areas occupied appeared approximately circular, and probably exceeded 4 hectares (over a three day period), but without marked birds it was impossible to follow individuals and document their activity.

The same limitation applies to the grape orchards of San Juan and La Rioja and to the riverine marshes occupied by catamarcanus. And in each the shape of spaces mapped for individuals did not appear to be linear. At Villa Union, La Rioja, one male dominated a grape orchard 2.5 hectares in extent and also defended adjacent patches of Prosopsis and Tamarix. Another male defended an orchard of slightly over 1 hectare and a large part of the adjacent woodland. Near Tinogasta where three males defended areas around a 6 hectare orchard, most of the singing activity occurred in the rows of introduced Populus surrounding the orchards, while birds foraged in the orchard and in the surrounding grasslands, and sometimes disappeared into the low woodlands adjacent to the orchards.

Thus it is mainly on the pampas that the territories and activity spaces assume a linear shape, and the

proportion of time spent along the road or fencerow, probably depends on whether the male is engaged mainly in singing or in feeding, and whether nesting is occurring. Figures 12, 13 and 14 illustrate militaris and defilippii territories mapped at Saudade and BB7E.

P. defilippii

Unlike militaris, defilippii males appeared more or less regularly spaced over a field. Only two or three of some forty activity spaces straddled a road, although many of the utilized spaces bordered a road. Also defilippii males did not use elevated perches, even when available, and only one individual was ever seen to land on a utility wire (unmarked male #1 at BB23N) (see also Short 1968).

Judging from the occurrence of many territories in one field and none in nearby fields of similar vegetation, it seems proper to treat this species as loosely colonial. Whether the clustering related to primary social attractiveness or to some inapparent feature of the habitat, remains to be determined.

I was not present at the time territories were first established, but I found that the newly arriving males filled in spaces in fields where earlier arrivals were defending territories. I did not observe the process by which the filling in occurred, or whether established

males were tolerant of new arrivals or eventually abandoned vain efforts to drive them away. I did note that by the middle of the season, far fewer birds were present, both at Bahia Blanca and Saudade, as if many individuals were unseccessful at obtaining mates and ten departed. Since in a few cases, marked individuals were present both early and late, it seems likely that it was mainly unsuccessful birds that departed, although some birds may have bred early and departed with their brood. This matter is merely speculative at this time, however, Lanyon (1957) noted that failure to mate might result in failure to maintain a territory.

Territories are maintained by primary and flight songs, and male activity spaces coincide more closely with defended area than do the spaces of militaris. I found that both the activity spaces and the territories fluctuated during the season, and one example of change in size and shape for a single territory is shown in figure 15. The fluctuations are dramatic early and late in the season, but also occurred over a period of a few days during the height of the season. This made it difficult to map territories even for marked individuals since their willingness to defend a given point varied from day to day.

I assembled the recorded positions for adjacent defilippii males, both marked and, where possible,

unmarked, into composite maps based on two or three days. The areas were measured with a compensating polar planimeter, and in most cases the areas were within the range of 4000-6000 square meters. I noted that the mapped areas seemed to fill almost all the available space, and they are so indicated in figures 12 - 14. However, when I studied individual males for long periods ($>$ 2 hrs) I found that territories were usually 5000-8000 m^2. I conclude that some of the males noted on the study area were transients which attempted to defend territories but departed during the period of observation ----remaining only long enough to be mapped.

An example is provided by observations on the "triller" whose distinctive song allowed me to map over 200 perch changes. I noted 114 consecutive perch changes on which figures 16 and 17 are based. Table 43 notes the increment in territory size which occurred during these 114 changes. Twenty one of the 114 positions were "external" (that is they served to enlarge the observed activity space), and most of these were directly related to a boundary encounter, so it seems reasonable to refer to the entire mapped area as a territory.

I used the "triller" data (the largest consecutive sample I obtained to evaluate the position points-area curve procedure suggested by Odum and Kuenzler (1955). I found that there were several times during the morning

TABLE 43 Increments in territory size per observation (The Triller, defilippii). Only those observations that increased the territory size are listed. Maximum polygon technique was used.

Observation Number	Increment to area	Cumulative area
3	1376	1376
4	615	1991
7	281	2272
10	116	2388
11	221	2609
12	37	2646
16	592	3238
17	195	3433
25	41	3474
30	371	3845
32	155	4000
33	30	4030
35	772	4802
40	818	5620
59	248	5868
61	75	5943
77	469	6412
79	263	6675
80	300	6975
100	120	7095
111	605	7700
114	Terminated	

when the increment to the area curve seemed to approach an asymptote. At each of these times I would have considered the observations sufficient to document the territory size. The cause of the irregularity involved changes in the activity emphasis during the course of the morning. This irregularity was demonstrated by dividing the territory into four quadrants (from the center point of the east-west and north-south axes). If activity was evenly distributed, the % of positions in each quadrant should correspond to the % of area or of perimeter in that quadrant. The activity deviated from this expectation ($G=28.2$, $df=3$, $p<.001$).

The total area included by the first 114 position changes was 7700 m^2, and after about 200 position changes it reached just over 9000 m^2.

P. bellicosa

The study area covered approximately 10 hectares. The meadowlarks did not establish territories in freshly plowed fields, and more were found in grassland and marshes than in cultivated cropland. Although the marshland with its risk of flooding might seem hazardous, the excellent opportunity for nest concealment in the dense vegetation, particularly in Salicornia and Distichlis was probably of importance since in cultivated areas, suitable nest sites were few----mainly dense grass clumps

between the fields.

The nearest group of meadowlarks was near Bujama Baja, 4 km. to the north, but the observed clustering was obviously due to the discontinuous vegetation, for these area were separated by barren dunes. Within the available vegetation it seemed that the areas might be saturated, so it is not possible to speak of clustering in the bellicosa population I observed.

I attempted to estimate the utilized space of bellicosa males on several different days over a six week period. The results of the observations are summarized in Table 44. Some individuals were studied frequently, others only once. Interpretation of these data must be limited. The amount of time devoted to observations differed from day to day and territory to territory, and this accounts in part for the overall low values obtained on 5 September. Peripheral territories might have larger activity spaces, since there would be no neighboring male to limit ones activity. This seemed to be the case for unmarked males 1, 2 and 3, but not for unmarked male J who had no neighbors constraining it, yet moved about very little when studied on 19 August. (The numbers and letters applied to unmarked birds, actually apply to the territories in which such birds occurred. In some cases the stability of songs recorded in the territories confirm that only

one bird was involved).

There is scant evidence that this utilized space increases with season. This is best shown for male WR/GG. The sudden jump in utilized area for WR/GR on 6 September reflects the disappearance of a bird from territory F, which was defended on 4 and 5 September.

In considering utilized space one would have to add any distant areas, such as cornfields, visited by the birds during the observation period. Such visits were less common in the early part of the season than in September when the corn was ripening and the birds were nesting.

Perhaps the most interesting aspect of the data is the relatively small areas occupied by a bird on a given day. Only 3 of the observations (exceeding 2 hours) gave areas greater than 6000 m^2, while 3 areas were smaller than 2000 m^2.

For the most part the activity spaces tabulated in Table 44 correspond with the territories, that is boundary encounters frequently marked the position changes which I used to measure the spaces. I examined the defended area of WR/BB on three successive days, 4, 5 and 6 September (see figure 15B). The territory sizes were 3058, 2915, and 6065 m^2 over a 3 hour period, and these are about 90-100% of the activity spaces for the same periods. (The size of the spaces are influenced

Table 44. Daily activity spaces of male bellicosa at Bujama. (see text)

Individual	Aug 19	Aug 21	Sep 4	Sep 5	Sep 6	Sep 8	Sep 28	Sep 29
WR/GR	1720							
B						3350		
WR/BB	2825		3360	3265	6065		2455	
B"	2480			2240			2875	4410
WR/GG	2675	3400		3770		3850	5055	7165
WR/YY	1800			2190			2995	
E	2040			3170			3355	
WR/GR	3370		2350	2850	5820	6625	3075	
F'				2425				
G				3600				
G'				3270				
Dist				3000				
D"				2375				
J	1510							
						Sep 7		
1						6890		
2						5575		
3						4485		
Mean	2302		2855	2923		5322	3158	5788

(all activity spaces measured as square meters)

as much by the activity of neighbors as by the bird under observation). In this respect, bellicosa resembles defilippii more than militaris.

Both flight and primary songs are used by bellicosa in delineating territory. Primary song duets were a conspicuous event and were noted more often than for defilippii. On numerous occasions I noted that a second male would begin its song just after the first male began the buzz note terminating its song. Sometimes 5 or 6 songs of 2 or 3 males would be linked without a break.

Occasionally I observed physical faceoffs between birds at a boundary, but I did not observe physical contact nor the jump-flights which were noted in defilippii and superciliaris. It is possible that these take place in dense vegetaion or that they were overlooked because of phenology (peak occurrence prior to my arrival), but, it is possible that they do not occur regularly in bellicosa.

Often two birds would give sequential flight songs parallel to each other, which I presumed to demarcate their common boundary. Males approaching and departing from encounters or from my decoys often gave flight songs.

L. m. superciliaris

This species resembled defilippii in its tendency to nest in loose colonies, and it often associated with defilippii, territories of the two species intermingling with essentially no overlap. Interspecific territoriality was apparent in the consistent interspecific aggression which served to maintain the non-overlap. However, when mapping was extended over a period of several days (as on Area A at Saudade) I found that the territorial boundaries shifted and the non-overlap was obscured, even though it was clear cut on any given morning.

I was not successful in getting superciliaris males to respond consistently to decoys with superciliaris song probably because the equipment used was inadequate to handle the high frequency range of their songs (much of it above 6 khz).

Although this species did most of its singing from the grass and fences, males were less reluctant than defilippii to sing from elevated perches, and I saw several singing from utility wires. I also observed L. m. militaris singing from trees and poles in Venezuela and Surinam.

L. m. militaris

A territorial interaction between two male L. militaris was observed 22 km west of Paramaribo (2 April 1972). One male was sitting in a bush when a pair of Leistes arrived on a nearby fence. The first male flew at these birds and then landed on the ground just below them, and the new male dropped to the ground about 1 meter away. There followed a series of brief up-flights, with the birds sometimes leap-frogging over one another as they moved along a very narrow line, often within a body-length of each other. Both on the ground and during the up-flights, their heads were pointed almost vertically upward. For about three minutes the sequence was interupted by a period of foraging and facing-away, during which the birds remained within a few meters of each other. Then the exaggerated posture and jump flights were resumed. The total distance covered was estimated at 100 feet (30 meters). The 2nd bird terminated the sequence after about 10 minutes leaving with a flight song.

The entire sequence of events was similar to one I observed between two defilippii males, and also to events described by Lanyon (1957).

SUMMARY

1. Territory plays a prominent role in the life of meadowlarks, although unanticipated variation in the nature of their territoriality was found. For militaris I found a linear distribution of territories on the pampas, although in other habitats they assumed a more or less polygonal or circular shape. The utilized space was oten much greater than the defended area, and if one excludes primary song, I occasionally had days when no territorial defense was apparent. Although the territories approximate type A (mating, nesting, feeding), the birds in some cases make long forays beyond the limits of their defended area. Birds did not feed with territories of another pair. Territories of defilippii were often small (1 hectare) compared with militaris (2 hectares), and were usually regularly arranged over the grasslands. They would be considered type B territories in many cases since much food for nestlings was obtained off the territory. I found that bellicosa territories were similar to those of defilippii.

2. Territorial defense involves both primary and flight songs in bellicosa and defilippii and probably in superciliaris as well. P. m. militaris does not use flight songs in territorial defense, although

catamarcanus may.

3. Territories of militaris and defilippii overlapped extensively. The non-overlap of defilippii and superciliaris territories will be considered in a later chapter.

4. Observations of the "triller" position vhanges, revealed several instances where the area increment was negligible over several position changes. Using the area/observation curve technique, one might prematurely conclude that observations were sufficient to delineate the activity space.

CHAPTER 16 COLONIALITY AND DISPERSION OF MEADOWLARKS

COLONIALITY IN RED BREASTED MEADOWLARKS

The distribution of militaris on the pampas appears to be regular, limited only by the availability of elevated perches. Populations of bellicosa were obviously clustered in response to the very restricted available habitat. On the other hand, the dispersion of defilippii and superciliaris appear to represent clustering, due to sociality, and these aggregations can be considered loose colonies or grouped territories. I would consider them colonial if the clusters arise out of social attraction to conspecifics rather than out of mutual response to a desirable environmental feature.

Aggregation can be disadvantageous in fostering aggressive interactions and interference or in attracting predators, but is often necessary where nesting or food resources are clumped. Moreover, it may be advantageous in improving anti-predator effectiveness and perhaps also in social facilitation of reproductive behavior. These factors have been examined in icterids (e.g., Orians 1961, Horn 1968, 1970, Robertson 1972). These authors found no evidence for social facilitation or the Darling Effects (after Darling 1938) but Collias et al. (1971) have found social stimulation advantageous in aviary studies of finches. I mention this debate because

of considerable anecdotal observations of contagiousness of flight displays among the Red-breasted Meadowlarks. Figure 18 shows that male defilippii in large groups sing proportionately more than those in smaller groups. Since flight songs are used not only in territoriality but in courtship (see Chapter 11), it seems likely that social stimulation may be significant in the meadowlark "colonies". Future investigation can include analysis of the temporal relationships among flight and primary songs for different size and spacing patterns as well as studies of productivity and predation in different colonies.

Data suitable for testing the dispersion patterns were obtained in point censuses conducted along roadsides on the pampas in 1970 and 1971 and on a systematic census of the Saudade area in October 1971. Results are shown in Tables 45 and 46 and in figure 19. In 1970 the stops were made at 10 km intervals without regard to habitat and lasted for at least 10 minutes. Counts were made mainly in mid-morning and late afternoon. The second sample included 44 stops at 10 km intervals. In 16 of these locations I judged the vegetation to be unsuitable, mainly because of habitation or recent plowing. The remaining 28 stops included 12 dominated by pastures (mainly Stipa sp.) and 16 dominated by wheat.

Table 45 gives the occurrence of the two species in each of the samples. The number of plots on which a species occurs is its frequency. Whether the two species attract each other or respond similarly to habitats or whether they repel each or respond oppositely was examined in 2 x 2 contingency tables---the null hypothesis underlying the test being independent distribution.

POINT CENSUS RESULTS

In both the 1970 and 1971 samples militaris and defilippii distribution was consistent with the null hypothesis of independence ($p > .10$). Both species occurred with similar frequency in the area northeast of Bahia Blanca, but defilippii was more numerous. Considering only points where the latter was present, the average group size was 8.93 compared with 1.93 for militaris. North and West of Bahia Blanca, one was more likely to find militaris, but group size was of the same order of magnitude as in the 1970 sample. Both species were somewhat more common in areas with wheat than in areas with Stipa, but the differences were not significant.

TABLE 45. Occurrence of militaris and defilippii in roadside censuses in southern Buenos Aires Province.

	Usable Census Points	militaris +	militaris −	militaris N	militaris Ave.[c]	defilippii +	defilippii −	defilippii N	defilippii Ave.[c]
November 1970[a]	66	29	37	56	1.93	31	35	277	8.93
October 1971[b]	28	20	8	31	1.55	10	18	105	10.50
Wheat	16	11	5	19	1.72	6	10	68	11.33
Pasture	12	9	3	12	1.33	4	8	37	9.25

a=areas north and east of Bahia Blanca b=areas west and northwest of Bahia Blanca

c=average based on areas where present (Ave.=N/+).

THE SAUDADE SAMPLE

I superimposed an 11 x 13 grid of 1 km squares on a map of the Saudade area, and censused this area in October 1971 over a five day period. The census was accomplished by jeep and horseback, by working along each "line" (at 1 km intervals). In addition to covering the transect lines themselves, I counted males approximately 500 meters to either side. This amounted to a singing male census. The counts were made in late morning (09:30 - 11:30) and in mid-afternoon (15:30 - 18:00) in an attempt to achieve standardization. Davis (1965) pointed out the critical factor of time of day in such censuses, and Slagsvoid (1973) has discussed many of the complex problems of interpreting such data. For one thing, I noticed that when I censused my own study area in this manner, I recorded only about 3/4 of the bird known to be there. Thus as density estimates the figures given below are underestimates. Despite the obvious limitations, the data provide useful information on clustering.

The census area and approximate location of males of the three species, are shown in figure 18. Habitat that was either unsuitable (woodlands or freshly plowed fields) or invisible (hillcrests or swales) is indicated by cross-hatching, and the 143 grid squares are thereby reduced to 102 squares for analyses. On this area I

counted 48 militaris, 254 defilippii and 60 superciliaris.

By inspection, I found three large clusters of defilippii and superciliaris and additional clusters of defilippii and I gained the impression that both species had a clumped dispersion pattern on the area. The distribution of militaris appeared more regular and seemed to follow roads.

I tested the dispersion patterns for goodness of fit to expected values if the birds were distributed at random. The 11 columns of the grid map were treated as 11 subsamples and, before correcting for unsuitable area, one would expect to find approximately 1/11 of each column if they were either regularly or randomly distributed. Table 46 lists the columns, number of available squares, percent of total area and expected values for each of these subsamples. The observed values for each and the goodness of fit by chi square test are also shown. The probability that if regular or random dispersion existed the observed patterns might arise by chance are $p>.10$ for militaris and $p<.005$ for defilippii and superciliaris.

The 102 usable grid squares were examined for the number of squares with 0, 1, 2, 3... individuals of a given species. The resulting distributions were tested for goodness of fit to a Poisson distribution, and probabilities of $p>.50$ for militaris and $p<.005$ for the

TABLE 46. Distribution of three meadowlark species on Saudade grid map compared with expected distribution in 11 map columns (goodness of fit test and chi square).

COLUMN	AVAILABLE SQUARES	% of Total area	NUMBERS OF PAIRS OBSERVED & EXPECTED					
			militaris		defilippii		superciliaris	
			Obs	Exp	Obs	Exp	Obs	Exp
A	13	12.7	6	6.1	43	32.3	2	7.6
B	5	4.9	2	2.4	47	12.4	4	2.9
C	8	7.8	8	3.7	14	19.8	0	4.7
D	11	10.8	5	5.2	14	27.4	30	6.5
E	12	11.8	3	5.7	36	29.9	13	7.1
F	10	9.8	7	4.7	22	24.9	0	5.9
G	5	4.9	1	2.4	17	12.4	7	2.9
H	12	11.8	10	5.7	10	29.9	0	7.1
I	10	9.8	2	4.7	33	24.9	1	5.9
J	8	7.8	2	3.7	10	19.8	2	4.7
K	8	7.8	2	3.7	8	19.8	1	4.7
Total	102	100.	48		264		60	
p			>.10		<.005		<.005	

Test of the null-hypothesis that each species is regularly or randomly distributed. p is the probability of observing the existing dispersion pattern by chance, if the null hypothesis is true for any species.

others, were obtained.

Finally, since militaris was distributed along roads which ran parallel to the chosen columns (by and large), I also tested it for goodness of fit to 13 subsamples of rows. Again the results are consistent with a regular or random distribution ($p>.20$).

The Saudade data were used to test the impression that superciliaris and defilippii are likely to be found together. The null hypothesis that the two are distributed independently was tested in 2 x 2 contingency tables, and the analysis was extended to include militaris as well. The results (see Table 47) for defilippii vs. superciliaris are quite consistent with independent distribution ($p>.90$). With respect to militaris, the dispersion of defilippii is consistent with repulsion ($p=.014$) while dispersion of superciliaris and militaris appeared independent ($p=.122$).

It is necessary to point out that this last method is severely influenced by quadrat size. It is quite possible that if one used some other quadrat size, association might be demonstrated. This limitation has been pointed out by Pielou (1969) and has been discussed in detail by Poole (1974).

In this census, since I utilized all available roads, I was less likely to miss militaris than the other species. Thus the census results underestimate mainly

TABLE 47. Concurrence of three meadowlark species at Estancia La Saudade

(2x2 contingency tables tested for independence by Fisher Exact Test. The p value is the two-tailed cumulative probability that dispersion patterns are independent.
Each species can be either present or absent on 102 grid squares)

		MILITARIS Present	Absent	Total
DEFILIPPII	Present	13	38	51
	Absent	26	25	51
	Total	39	63	102
	p =.014 (suggests repulsion)			

		SUPERCILIARIS		
DEFILIPPII	Present	6	45	51
	Absent	7	44	51
	Total	13	89	102
	p >.90 (suggests independence)			

		SUPERCILIARIS		
MILITARIS	Present	2	37	38
	Absent	11	52	63
	Total	13	89	102
	p = .122 (independent)			

the values for *defilippii* and *superciliaris*.

SUMMARY

1. Several lines of evidence suggest that *defilippii* nests in loose colonies. I found clusters of territories in one area while a nearby area of very similar appearance (to me) had no birds. Such clustering is particularly apparent when wheat fields are concerned because of the artificial uniformity of this habitat.

2. On the pampas *militaris* appeared to be regularly distributed while *defilippii* and *superciliaris* were clustered. The evidence from Saudade is consistent with the hypothesis that the species are distributed independently of each other.

3. Problems of sampling bias due to linear distribution of *militaris* and variable flight song activity of *defilippii* and *superciliaris* are discussed.

SECTION V. ECOLOGICAL ASPECTS OF SYMPATRY

Chapters 17 - 21

17. Introduction and Habitats
18. Foods and Foraging
19. Morphometric Analysis and Ecogeographic Variation
20. Multivariate Search for Character Displacement
21. Interspecific Territoriality

In this section I consider the ecology of meadowlarks in Argentina with respect to sympatric coexistence on the pampas. The discussion focuses on differences in habitat selection and food utilization, and the external morphology of meadowlarks is analyzed in relation to differences in ecology. Univariate and multivariate analyses reveal no evidence of character displacement or convergence. Two species maintain interspecific territoriality.

CHAPTER 17 INTRODUCTION AND HABITAT

ECOLOGY OF SYMPATRIC MEADOWLARKS ON THE PAMPAS

The discovery of three similar species breeding together in local sympatry on the pampas, raises the question of how they coexist. Assuming that they are potential competitors, one would derive from the competitive exclusion principle two alternative predictions:

a) one or more species would be eliminated, as evidenced by allopatry in the absence of environmental discontinuity (cf Terborgh 1971)

b) spatial, temporal or ecologic displacement would occur to minimize niche overlap.

Where species occur in local sympatry one can examine their spatial distribution to see whether they follow a vegetation mosaic, and particularly whether the usual range of habitats selected by a species has been narrowed. If both species have the same habitat preference, yet only one occupies the preferred habitat while the other is apparently "forced" into less suitable habitat, one has a type of competitive exclusion. Murray (1971) has viewed the origin interspecific territoriality in this light (see Chapter 21).

In an area that is homogeneous, interspecific

territoriality could minimize competition, thereby lowering selective pressure for morphologic character displacement. If the territories or activity spaces of two species overlap, then niche compression may occur by change in the size and type of prey or method of feeding. Lack (1971) discusses these alternatives with respect to many avian groups, and he traces the history of the competitive exclusion concept in ornithology back at least to Steere in 1894.

In temperate grasslands the opportunity for temporal and spatial separation is limited. Interspecific territoriality (or more extensive exclusion) should prove common, and Orians and Willson (1964) and Willson (1967) emphasize the relation between avian interspecific territoriality and simple habitats.

In this chapter I consider the preferred habitats and song perches, foraging methods, and food of the red-breasted meadowlarks. Although these help to understand the probable ecologic realtions among them, the most important species differences in this case are morphological (see Chapter 19). The three species that are sympatric on the pampas differ markedly in size, each being about 75% the weight of the next heaviest species. The overall size differences are not, however, reflected in wing or bill differences, for militaris and defilippii are very similar in these dimensions.

MEADOWLARK HABITATS

All meadowlarks are primarily grassland birds, but their habitat preferences are not identical. Lanyon (1956b, 1962) considers the complex habitat preferences of *Sturnella magna* and *neglecta* in North America. Short (1968) noted some differences in the habitats utilized by *Leistes* and *Pezites*. Wiens (1969) provided a detailed method for characterizing grassland vegetation and providing exact descriptions which would be useful for ordinating habitats and for making rigorous comparisons among species. He included *Sturnella* in his study. Cody (1966, 1968) made much simpler habitat descriptions when he tried to compare North American and South American grasslands, with respect to foliage height diversity and avifaunas.

In my field work I characterized grasslands by the dominant vegetation, by the height of the majority of the vegetation, and by the percent of ground cover. The presence of particular features such as scattered bushes or bunch grass was noted. Each field, surrounded by a fence, was usually homogeneous, and artificially I would treat each field as a habitat. I was able to make crude but rapid descriptions of many habitats and to learn at least those which were unsuitable for one or another species.

MILITARIS HABITATS

Over its extensive range, militaris occurs in a wide variety of habitats including grape orchards, tussock grass marshes, desert scrub, forest edge, coastal dunes, and pampas. Since males generally sing from elevated perches it is not surprising that almost all militaris territories had some perches of 2 m or more. I relate the preference for elevated perches to the absence of a flight song, and it is perhaps significant that the race catamarcanus, which inhabits tussock grass marshes which generally lack perches above 2 meters, frequently gives flight songs.

On the pampas, militaris territories were related mainly to fences and artificial plantations, although this restricted the number of pairs present. In some cases, e.g., at Saudade, all of the leangth of a road was defended by militaris, while open field was not. Although the birds foraged in fields, they were less likely to defend area in the field, and I demonstrated this with playback experiments.

Along my transects through Patagonia, I found that militaris generally required at least 20% ground cover, and some bushes over 2 m tall (unless there were utility poles). If cover was less than 20%, the occurrence of scattered bunchgrass might render an area suitable.

Fencerows with thistle, mustards, and other vegetation were attractive, no matter what grew in the adjacent fields.

Completely barren ground was of course unsuitable. Much of Patagonia is covered with low bushes (< 1 m tall) and has less than 10% ground cover. Grass is either sparse or absent. Such areas are avoided by militaris. However, in low-lying areas one occasionally finds grassy areas watered by moist seeps, and these are sometimes occupied by militaris. Where scrub vegetation exceeded 1 m but was widely spaced (> 10 m apart) one was not likely to find militaris.

In western Patagonia, one finds a grassy steppe, similar to North Temperate desert grasslands. The broad expanses of grass are not suited for militaris, but the birds occur on slopes which are more mesic and contain clumps of low trees. I found militaris on the edge of Fuegian forest and even within it where there was open parkland, and Navas (pers. comm.) indicates that such areas are regularly inhabited by militaris.

In San Juan and La Rioja, I found militaris almost exclusively in grape orchards. These are under 3 m in height, but are often surrounded by tall trees, particularly Populus spp. from which the birds sing. I did not find any nests, but the orchards are unkempt and usually have an abundant grassy understory.

In central Catamarca, where I first encountered birds approaching catamarcanus in color, I found meadowlarks in riverine marshes of tall tussock grass. As one ascends the Quebrada of Humahuaca in Jujuy, the tussock grass diminishes, and by the time one reaches the true altiplano (> 3600 m) at Abra Pampa, there is essentially no suitable habitat.

I was not able to discern what factors combine to restrict militaris to the southern part of the pampas. As I drove northward and eastward from Saudade, there was no change in the distribution of utility poles and plantations, but there were no militaris in evidence. The aspect of the vegetation (most of it artificial anyway) was no different to my eye. It seems unlikely that competition with defilippii, the pampas species, could be important, since in my experience, that species also decreases north of Saavedra and east of the Sierra de la Ventana. Perhaps some subtle difference in agricultural practices is important in influencing the distribution of these meadowlarks at present.

Short (1968) reognized that militaris regularly used elevated perches while defilippii did not. In my census of the Saudade area in 1971, I succeeded in demonstrating the reliance of militaris on fencerows (see figure D-1).

DEFILIPPII HABITATS

The common denominator of defilippii habitat seems to be grassland. It was found in wheat, barley, alfalfa, close-cropped pasture, and a variety of natural and disturbed grasses. In pasture it required a scattering of taller grass clumps which were almost invariably Stipa spp. It also occurred in fields of pure Stipa Ambigua as at BB7E. It occupied grasses from 8" to about 24" tall (20-60 cm), but was occasionally found in wheat up to 30" (75 cm) tall. However, at the time of habitat choice the wheat would have been much shorter. Most fields occupied by defilippii had close to 100% ground cover, although in some cases ground cover was as low as 75%, particularly if scattered clumps of bunch grass were available.

In areas where defilippii was common there were many seemingly suitable fields which were unoccupied, engendering the impression that the species was loosely colonial. Where it occurred near monte it seemed to avoid the edges of the woodland, but data suitable for demonstrating repulsion were not obtained.

BELLICOSA HABITAT UTILIZATION

At Bujama a variety of habitats was available including freshly plowed fields, several crops, Distichlis fields, and marshes of Distichlis, Salicornia, Scirpus, Phragmites and Typha, (see figure 10, and account of Study Area). The native Huarango tree was reduced to a single grove and to small strips along the roads. A row of tall casuarinas bounded one corner of the study area. There were two rectangular plots of corn, and part of the marshland was bounded by dunes. Areas utilized by bellicosa included the cropland, grassy fields, and the Salicornia and Scirpus marshes. Trees and dunes provided song perches and much feeding was done in the corn fields.

Although I confined my attention almost exclusively to a small group of birds near the bend of the road, I did make a crude census of males (based largely on flight songs) throughout the valley. The distribution of apparently territorial males is indicated on the map (figure 10). White areas include cultivated fields and plots of short grass. I estimated 36 territorial males in approximately 140 hectares of cultivated land east of the road, and about 45 territories in about 40 hectares of marsh west of the road. Fields that were recently plowed or sown did not have territories centered

on them, and this accounts in part for the discrepancy in density.

Several impressions are worth mentioning. In the cultivated areas and along roads, males frequently sang from elevated perches such as trees or dunes. In the marsh, where elevated perches were not available, males delivered primary song only from grass clumps. It would be valuable in future studies to compare sizes of territories and or utilized space, behavior, and frequency of flight and primary songs and success between these two groups of males (cf Post 1974).

I did not find any difference in the apparent size of territories in the Scirpus and Salicornia marshes. The greatest density seemed to occur in the Distichlis fields and the Distichlis-Salicornia boundary near the bend of the road.

Birds whose utilized area included recently plowed or sown fields, did not seem to defend these, but tolerated other birds (particularly in flocks) foraging in the fields. In one instance, I was able to demonstrate that male WR/GG showed a greater response to decoy and playback in the Distichlis area than in the recently sown field---it proving impossible to trap it in the latter habitat.

SUPERCILIARIS HABITAT

I encountered superciliaris at relatively few locations, and its habitat preferences appeared to resemble those of defilippii with which it sometimes associated. In 1971, when it was common near Saudade, I found that it preferred somewhat taller grass than did defilippii, shunning grass less than 15" (38 cm) tall. I also found it in 30-36" (75-90 cm) tall wheat. It may occupy wetter habitats than does defilippii, but on the pampas I found it in well-drained fields. For instance, at Saudade, where it had a choice of lush grass and marshy ground near the lagoon, some 20 pair occurred in wheat beginning about 100 meters from the shoreline, on ground that was dry. Moisture alone was perhaps not the main feature involved in habitat selection. It is possible that heavy rains occurring earlier in the season might have rendered the marsh too wet. Similarly, in Corrientes, where I encountered superciliaris near Ita Ibate, they were in dry fields, although extensive marshes with varying relief are available throughout the region.

In Trinidad, I found L. m. militaris in wet savannas and rice fields, rather than in grasslands, but on the Venzuelan llanos I found it in very dry grassland. However, in the latter area, which is subject to inunda-

tion in the rainy season (personal observation), breeding had not begun. Haverschmidt (1968) and French (1974) mention pastures, rice fields, and wet savannahs, indicating that Leistes uses a wide variety of open-country habitats.

SUMMARY

1. The habitat preferences of red-breasted meadowlarks were examined in various parts of their ranges. Most species occurred in several distinct plant associations, but some characteristics were determined for each species.

2. P. m. militaris required elevated perches, more than 2 meters tall, and was less dependent on continuous grass cover than other species.

3. P. defilippii occurred in various grassy or grass-like associations, requiring at least 75% ground cover and preferring vegetation in the 20 - 60 cm range.

4. L. m. superciliaris was similar to defilippii in preference for grassland, but appeared to tolerate and perhaps to prefer somewhat taller grass (40 - 80 cm or 90 cm). Its reported preference for marshy habitats was not apparent on the pampas, but may be valid for L. m. militaris.

5. P. bellicosa nested at higher density in marshy areas than in cultivated fields, probably due to the availability of nest sites.

CHAPTER 18 FOODS AND FORAGING

MEADOWLARK FOODS AND FORAGING

Partitioning the food resources of a community is one means of maintaining stable coexistence of similar species. A large number of papers have been published on resource utilization, but it suffices to say that when two potential competitors become sympatric, narrowing their range of food utilization is a possible means of coexisting. Morphological correlates of such dietary differences include differences in bill length, for birds with longer bills are supposed to eat a greater proportion of large food items (Hespenheide 1966, Schoener 1971). Cody (1968b) has emphasized that in grassland birds different feeding behavior may be important in reducing competition. Many reports have shown that different species (or sexes) utilize different feeding stations, (e.g., MacArthur 1958, Ligon 1968, Jackson 1970). and others have shown that sexes utilize different parts of the territory for feeding (e.g., Robins 1971, Martin 1974), but Cody (1968b) emphasized the rate of feeding progression. His paper is relevant because P. militaris figured in several of his South American studies. He shows (1968b:113) the feeding progression of several species in terms of average progression rate,

and duration and frequency of stops, and these appear to be distinct for each species in the communities he describes. This behavioral attribute has been worked into a comprehensive theory of competition in avian communities (Cody 1974). However, it is not indicated whether the observed progressions are averages over many birds under many conditions or merely represent observations on a single bird in a single community.

Although I intially intended to study the foraging behavior of meadowlarks, I found it almost impossible to do so. Birds were seldom in view when feeding, and even when in view they did not remain in view for long. Only on road shoulders and mudflats (as at BB30W) did I have prolonged opportunity to study foraging progression, and these are clearly atypical feeding stations.

I did succeed in watching militaris male YY/BB for several minutes on 12 November 1971, and I recorded the feeding progression. The number of feet moved per second ranged from .38 to .94 (compared with .1 derived from Cody's figure). Time stopped was more constant at 50-69% (compared with less than 10% observed by Cody), and the number of stops per minute ranged from 4-8 (4 reported by Cody). The only inference I can draw from these limited data is that progression rates are very variable and would require extensive study, and that for meadowlarks such study will have to be done by telemetry. I

can agree with Cody, however, that militaris is generally a slow, deliberate forager.

An unmarked male defilippii observed on 13 November, was studied for almost three minutes, and the two samples yielded a progression rate of .13-.23 feet/second, 36-58% of time stopped, and 3-8 stops per minute. I did not, however, gain the impression that defilippii is more deliberate than militaris, which the above data suggest.

Since feeding progression probably varies with the kind of food utilized and the substrate, it is difficult to see how it can be utilized separately from these variables which are both more direct measures of niche separation.

Although my study of foraging was thwarted, I can make some general comments based on both wild birds and birds studied in the aviary at the Kalbfleisch Field Research Station.

All meadowlarks species studied did most of their foraging in tall grass. I often saw militaris feeding in roadside ditches and on road shoulders or in other semi-open areas. I seldom observed defilippii feeding in the open. At Bujama, I saw bellicosa foraging on freshly tilled fields. One male seemed to specialize in unearthing potatoes, and examination revealed that it was feeding on potato rather than insects within the potato. This habit has also been reported on the

Falklands (Pettingill 1973). I also observed them feeding on corn borers which they extracted from nearly ripened corncobs. I made no observations on the feeding of Leistes.

Two male and a female defilippii hand-reared from about 5 days of age, and a male bellicosa purchased in a market, were observed on several days in September-October 1973 in outdoor aviaries. The aviaries were mowed prior to the study, and observations were made from a platform nearly 2 meters high. Nonetheless it was often impossible to see what the meadowlarks were actually doing.

Gaping is known to be an important mechanism for feeding by meadowlarks (e.g., Beecher 1951), and I noted that both male and female defilippii used gaping. Gaping was done in soil, particularly after hard probing efforts had loosened the soil, but mainly it was done at the base of grass plants or in clumps of grass litter, to separate the strands.

I noted that bellicosa seemed to do more probing in the ground than defilippii, but the significance of this remains to be evaluated under field conditions. All birds frequently used their feet to grasp and move a bit of ground cover or in a treading fashion to spread ground cover, The treading was done one leg at a time.

In the pens bellicosa ate insect larvae and seeds

about equally, while defilippii ate mostly seeds. These observations are probably not meaningful since the birds were supplied with supplementary food and water. It is interesting that despite the abundance of artificial food and the fact that the birds had been kept in indoor flight pens for a year or more, they spent much time foraging. It was also interesting, to observe that bouts of foraging were interupted by aggressive encounters and by rest periods. In the latter case, birds would crouch down between grass clumps, stretch heads forward, and perhaps sleep. Such interuptions lasted 2 to 20 minutes.

In view of the pronounced sexual dimorphism in the red-breasted meadowlarks, I tried to discern whether there were concomittant foraging differences. None were apparent in the aviaries. The only field observations relate to militaris pairs and to bellicosa feeding on corn borers. In the case of the latter I saw no differences in feeding behavior.

On several occasions I noted that female militaris foraged more rapidly than accompanying males, even when I knew that the female in question did not have young. However, female energy requirements differ from male requirements during the egg-forming period and also during incubation, when the female must gain all her food in a brief time period.

A more significant difference is that in three sets

of observations, females foraged exclusively on the ground and at the base of grass clumps, while males regularly stripped grass seeds or other seeds from plant heads. One militaris male actually climbed up on a clump of grass, seized an overhanging mustard plant seed head, pulled it down, held it with its foot, and tried to grasp the seeds. It soon fell off, however.

In the aviary, male bellicosa and defilippii regularly took stems, and worked the stem laterally through the bill, stripping off and swallowing the small seeds. The female did this only once. Both sexes, however, eat grass in this fashion, chewing the stem to pulp and swallowing as the grass moves laterally through the bill. This is important, since militaris and bellicosa often had much plant material (other than seeds) in their stomachs. It remains to be determined whether females are actually less likely to take seeds from grass heads. The fact that males are longer and can reach at least 20-35% higher, may make it more feasible for them to feed on aerial foods. Other aspects of sexual dimorphism will be considered below.

MEADOWLARK FOODS

Sturnella magna and neglecta: Data are provided by Beal (1895), Knowlton and Maddock (1943), Bent (1958), among others. These sources indicate that meadowlarks take a wide variety of invertebrate food and seeds. Knowlton and Maddock (1943) found that 35% of insects taken were Coleopterans 21% Lepidopterans, and 19% Orthopterans. Knowlton and Harmston (1943) and Rivers (1941) stress the importance of crickets in the diet of neglecta.

P. m. falklandicus: Primarily insectivorous, but also eat new potatoes. Frequently seen probing in earth for grubs and flipping over cow hips with their bill (Pettingill 1973).

P. m. militaris: In Tierra del Fuego, Crawshay (1907) reported that all specimens contained Coleopteran larvae. Stone (1927) reported that in Chile birds were largely insectivorous but also ate grass and fruit, and Goodall et al (1957) include seeds, fruits, bulbs and crustaceans in the diet.

Castellanos (1934) notes that in cornfields, militaris ate mainly insects and their larvae, and not corn.

P. defilippii: A specimen from Ensanada (Buenos Aires) contained insects and vegetable fragments. Another pair contained small beetles, and a male from Tolosa (Buenos Aires) contained caterpillars and grass seeds. The specimens were all taken in February and March (Marelli 1919). Aravena (1928) reported 3 specimens from Buenos Aires; one taken in October contained only insects (including Curculionid beetles). Two specimens taken in March contained 20% insects (beetles) and 80% seeds.

P. bellicosa: Philippii (1936) found that stomach contents of a series from northern Chile had entirely green vegetation.

Leistes m. militaris: Haverschmidt (1968:386) reports spiders, Curculionid beetles, Orthopterans and seeds in an unstated number of stomachs. A specimen collected by Chapin at Tocuman, Panama in August (Princeton #12840) contained grass seeds, orthopteran femur, and a beetle larva.

L. m. superciliaris: Marcelli (1919) reported caterpillars in a specimen from Punta Lara (Buenos Aires). Aravena (1928) reported on three specimens from Buenos Aires. One taken in November contained Carabid beetles, Lepidopteran larvae, seeds, and alfalfa awns, with

about 37% insect matter. A December specimen contained 100% insects, and a February specimen had 100% seeds, including thistle.

METHODS AND RESULTS OF STOMACH ANALYSES

As soon as possible after collection, stomachs were sliced in half and stored in 10% formalin. For the present analysis I determined mainly the percent of insect matter by volume in the moist contents. Results are shown in Table 48.

On the pampas, Orthopterans figured heavily in the diet of defilippii. Insect larvae, which form the bulk of material carried to nestlings, were present in many stomachs. When grain was ripe, it formed a large part by volume of the meals of all birds, except females who were feedling young. Birds showed considerable variability in the number and size of stones found in their stomachs, and late in the season, a few feathers (presumably those molted by the bird) were found in several stomachs.

The sample I obtained is relatively small, and particularly female defilippii and superciliaris are inadequately represented. Nonetheless the following tentative conclusions can be drawn.

1. militaris males and females were generally similar in the amount of insect matter consumed, although on any day and place there was mauch variation. However, at Tinogasta, the small sample obtained revealed an almost significantly greater amount of insects in the females than in males. There is also a slight suggestion that on the pampas, the amount of insects consumed may increase during a season. Also militaris generally had more herbage and seeds than did defilippii.

2. No between-sex comparison is possible for defilippii but within the sample of males there is a tendency to eat more seeds in December than in November. This probably reflects only the availability of both wheat and grass seeds as the season progresses.

3. The three specimens of superciliaris were all predominantly insectivorous, although one had consumed some wheat as well. The three specimens reported by Aravena (1928, see above) illustrate that the diet can vary from 100% insects to 100% seeds, over a short period of time.

4. A significant difference in the percentage of insect material was found in the bellicosa series. Almost the entire series was obtained in late September, and males averaged 11.25% insects while females averaged

51.67% insects (Mann-Whitney U=1, two-tailed probability = .020).

5. At Saudade there was overall similarity in the foods consumed by the three meadowlark species as to type. For example, seeds consumed were mainly wheat, mustard, or unidentified grass. All three Species consumed wheat, while militaris showed a greater tendency to eat the latter two foods. Insects were predominantly Orthopterans (mainly nymphs) and beetle larvae. No differences in the size of femurs was noted in stomachs from the three species, while the larval material was too digested to compare.

It is likely that all three species can and do take a large variety of material and that choice is dictated largely by availability. That some individuals may specialize, at least over a period, is indicated by the great variability within samples, (for example, 0% insects in one male and 90% in another at Tinogasta, 4 January 1971). Although there is a tendency for defilippii and superciliaris to be more insectivorous than militaris, there is no reason to suppose that this is effected by competition and narrowing of niche, (indeed the long bill of militaris led me to predict that it would be insectivorous while superciliaris would be granivorous).

TABLE 48. Comparisons of Meadowlark Stomach Contents with respect to percent Insect Matter by Volume.

	% INSECT MATERIAL		
	Sample	Mean S.D.	Range in %
bellicosa ♂♂	4	11.25 ± 13.14	0 - 30
bellicosa ♀♀	6	51.67 ± 28.57	25 - 95
superciliaris ♂♂	3	75.0 ± 13.22	60 - 85
superciliaris ♀♀	---		
defilippii ♂♂	9	65.0 ± 25.92	25 - 95
defilippii ♀♀	1	60. ---	60
militaris ♂♂ pampas	7	44.28 ± 34.93	5 - 90
militaris ♂♂ N.W.Argentina	11	40.90 ± 38.91	0 - 95
All militaris ♂♂[a]	19[a]	41.03 ± 35.67	0 - 95
militaris ♀♀ pampas	5	27.00 ± 22.80	5 - 50
militaris ♀♀ N.W. Argentina	6	46.70 ± 31.62	5 - 95
All militaris ♀♀	11	37.73 ± 28.55	5 - 95

a = includes one bird from Junin de los Andes

Certainly during the summer when grass seed is available, it is unlikely that there is any meaningful competition for this superabundant food resource. Earlier in the season, I judged grasshoppers to be superabundant (although I did no formal sampling). I did not follow meadowlarks to their off-territory feeding areas where they obtained most of their beetle larvae so I do not know if competition may occur there. However, at Bujama, I sampled corn for the number of corn borers, and judged that it also could be considered a superabundant food source (see appendix 3). My findings thus agree with Lanyon (1956:487) who doubted that food supply is a limiting factor for Sturnella during the breeding season.

SUMMARY

1. Partitioning of food resources, equivalent to narrowing of ones niche, allow coexistence of potential competitors. No clear evidence of such partitioning between sexes and species was demonstrated, lthough contrary to Cody's studies, foraging behavior could not be adequately studied.

2. All meadowlark species foraged almost exclusively on the ground in grass. For militaris males occasionally climbed up on grass clumps to reach seed heads.

3. Gaping was observed in most species and was either directed at the ground or at vegetation. It was not noted for Leistes, but observations of that species cannot be considered adequate.

4. Literature reports on meadowlark foods are summarized.

5. Observation on captive birds are reported.

6. Stomach contents were analyzed for all specimens, with at least a volume comparison of plant and insect matter.

7. All species showed considerable variability in food taken, although some individuals seem to specialize on one kind of food or another.

8. Females tended to be more insectivorous than males, perhaps related to the feeding of young. This was most pronounced in the sample of bellicosa.

9. A large amount of leafy material was found in militaris stomachs, and captive meadowlarks were observed eating grass.

10. On the pampas, defilippii showed an almost significantly greater tendency to be insectivorous compared with militaris.

CHAPTER 19 MORPHOMETRIC ANALYSIS AND ECOGEOGRAPHIC VARIATION

This chapter covers the following topics:

Choice of Variables and Methods
Results by Population
Discriminant Analysis
Meadowlark Weights
Ecogeographical Variation and Wing-lenght Regression
Shape Indices

The tables and graphs of data are given in Appendix IV. All original data and basic statistics are filed in the Department of Ornithology, American Museum of Natural History.

The morphometric study of specimens of meadowlarks, occupied a large part of the time spent in the present study. There were three main problems to be examined by this aspect of the study.

1. Clarification of the systematics of meadowlarks with respect to geographical variation and species boundaries.

2. Delineation of ecogeographical variation in morphology.

3. Investigation of possible morphological character

displacement. The original univariate study was supplemented by a multivariate analysis to enhance the possbility of detecting character displacement.

CHOICE OF VARIABLES AND METHODS

The study was restricted to external measurements obtainable on standard study skins. A detailed morphological examination of internal morphology, particularly the musculoskeletal features involved in feeding, would be particularly interesting in examining species similarities among meadowlarks. Moreover, C. J. Ellis (personal communication) has recently found some differences in the syringeal anatomy of bellicosa, militaris, and magna based on specimens I sent to him. However, such lines of investigation were beyond the scope of this study.

In addition to measuring the wing, tail, bill and tarsus length, I also measured the width and height of the bill at the anterior angle of the nostril, and the culmen length. Several ratios between the above measurements were also analyzed.

Wing Length: Measured as the arc, from the bend of the wing to the tip of the longest primary, with the wing flattened against the ruler.

Tail Length: From insertion of central rectrices to tip of longest rectrix. Tail wear was noted on a scale of 0 to 4 and in some cases more than 10% shortening could be effected by wear alone. I initially assumed that tail length would be extremely variable because of wear, and I planned to eliminate birds in classes 3 and 4 (>3 mm of naked rachis). However, many samples were composed entirely of birds in very worn plumage, so that comparisons for wear class would have resulted in very small samples. Since there was no way of determining the distribution of wear within each class it seemed impossible to correct obtained lengths for wear. Therefore I chose to ignore wear, to hope that the distribution of worn and unworn birds might be similar for different popularions (not the case), and to accord little significance to tail length. As it turned out, the coefficient of variation for tail length was almost invariably greater than for wing length and tarsus, but was frequently lower than for bill length. My interest in this character relates to its possible use as an indicator of body size. It is harder to ascribe adaptive significance to tail length, than to wing, tarsus and bill, particularly in taxa where there are no signals on the tail (unlike Sturnella which has conspicuous white corners).

Bill Length: Measured to nearest 0.1 mm from anterior angle of nostril to tip of upper mandible.

Tarsus Length: Measured to nearest 0.1 mm from notch on posterior side at proximal end of tibiotarsus, to the triangular scute which is the last undivided scute at the base of the middle toe. For each specimen this was the most difficult measurement to obtain, mainly because of the positioning of the legs during preparation. Moreover, there was considerable variation in the length of the triangular scute which led me to predict that tarsus length would be an unreliable character. Nonetheless, even in small populations it consistently had a low coefficient of variation.

Bill Height and Width: Measured to nearest 0.1 mm across anterior angle of nostril. The height was measured perpendicularly to the gape. Many specimens could not be utilized because the bills were not properly closed. If there was no gap between the mandibles I elected to measure it, even though experience with my own fresh specimens showed as much as 1 mm of possible error due to incomplete closure.

SELECTION OF SPECIMENS

I attempted to obtain representative material from all parts of the ranges of red-breasted meadowlarks, and also subsequently large locality samples. The low coefficient of variations found in specimens of L. m. militaris males from the Rio Tapajos and from the mouth of the Rio Andira, and in male P. militaris specimens from El Bolson, from the southern pampas, and from Catamarca, indicate the value of such local collections for statistical analysis. I examined specimens from the following collections:

American Museum of Natural History
Field Muesum of Natural History
British Museum of Natural History
Carnegie Museum
Museum of Comparative Zoology
Princeton University
United States National Museum
Peabody Museum (Yale)
Louisiana State University
University of Michigan
Cornell University
Florida State University

South American Museums

Museo de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires

Museo de Historia Natural de Montevideo, Uruguay

Museo de Historia Natural "Javier Prado", Lima, Peru

Museo Departmental de Historia Natural, Cali, Colombia

Coleccion Ornitologica Phelps, Caracas

STATISTICAL METHODS

Measurements for all populations were analyzed for normality using the statistical program UNGROUP in Sokal and Rohlf (1969). With few exceptions data showed a close fit to the normal curve and no transformations were used. Descriptive statistics were calculated for all forms (raw data and statistics are on file in the Department of Ornithology, American Museum of Natural History), but in this report only summary statistics for large geographical areas and subspecies are considered.

Size is an important and difficult problem in dealing with morphological variation, and it is measured indirectly. Kendeigh (1969), among others, has discussed the use of weight and/or wing length as measurements of "size", the former bring subject to considerable daily and seasonal variation, and the latter to a variety

of selective pressure and environmental factors. In the following discussion, I will consider wing and/or tail length as synonymous with size within a single taxon.

RESULTS BY POPULATION

P. militaris males: 19 groups and 285 specimens.

Birds from Chile and the pampas were smaller than birds from southern, western or northwestern Argentina. There is a north to south (small to large) cline along the coast of Argentina, and a less-marked cline in Chile. In western Argentina birds are larger both southward and northward of Mendoza. The race *catamarcanus* has the longest wing length, but it is very closely approached by nominate and intermediate specimens from central and southern Catamarca. Birds from the Falklands and Tierra del Fuego are next largest with respect to wing lengths.

Several shape variables were of interest. Birds from Chubut had longer than average tails (Tail/Wing ratio = .76). Falkland island birds were unusually long-billed while birds of northwestern Argentina had particularly narrow bills.

For Chilean birds, from northern Chile to Tierra del Fuego, there was a strong cline in size (reflected by wing length), but there were very few birds from

latitudes 42-54° so that evaluation of the cline is hampered. There is an interesting cline in bill length and width, but not in bill height as one goes southward in Chile.

P. militaris females: 7 groups, 110 specimens.

As with males, the largest specimens (wing and tail length) are those from northwestern Argentina and the Falklands, and the smallest are those from Chile and the pampas. Chilean birds were longer-tailed but not longer-winged than those of the pampas. Falklandicus had a longer bill than catamarcanus, although the latter was otherwise larger. Birds from Chile and the Falklands had proportionately long bills. The north to south clines were significant for both the Argentine coast and Chile.

P. defilippii males: 5 groups, 64 specimens.

All characters seemed very homogeneous over the range of this species. Despite the lack of between-group variation, the coefficients of variation were not low, indicating that the groups established by me were probably artificial. This is one form where the separation of breeding and non-breeding specimens could be of interest since there is apparently erratic post-breeding movement over the pampas, rather than defined north-south migration.

P. defilippii females: 4 groups, 40 specimens.

With respect to wing, tail and tarsus, birds from southern Buenos Aires province were significantly smaller than those from furhter north. The biological significance of this anomalous finding, remains to be determined.

P. bellicosa males: 5 groups, 147 specimens.

Groups used were from Ecuador, northern Peru, central Peru, southern Peru and Chile, and the Andes. Birds from the Peruvian Andes are significantly larger than those from other areas. Along the coast there is size increase both northward and southward from the area of Lima. Birds from Ecuador have shorter (not significantly) wings than those from southern Peru and Chile (along a gradient of 17° of latitude). Thus in this low-latitude region the main environmental gradients relate to altitude.

P. bellicosa females: 6 groups, 54 specimens.

The same groups were used, except that montane specimens were broken down into groups from Ecuador and Peru. In general the smallest birds were from Ecuadorian lowland locations, the largest from Ecuadorian montane locations ($>$ 2000 m). Birds from southern Peru and Chile averaged larger than those from central Peru (not significantly), and this gives rise to a north to south cline

of increased size. The only anomaly is that the females from the Ecuadorian lowlands have unusually long tarsi.

L. m. superciliaris males: 11 groups, 142 specimens.

The birds with longest wings are those in east central and eastern Brazil. Wing length decreased westward (to Matto Grosso) and southward (to the pampas). Even high altitude specimens from Bolivia had wings intermediate in length. Thus it seems that there is no cline in wing or tail length (nor in other characters examined) for this species, although it ranges from tropical Brazil to temperate Argentina (38° S. lat.) and montane Bolivia (4000 m.).

L. m. superciliaris females: 4 groups, 29 specimens.

There is no clinal variation from Brazil southward to Argentina. As with males, females from east-central Brazil are larger than birds from southern Brazil or Argentina. An anomaly, perhaps due to small sample size, is that Bolivian specimens averaged smaller than those from Brazil, albeit the latter were from much lower altitude.

L. m. militaris males: 10 groups, 176 specimens.

The smallest birds were those from Panama-Colombia and those from Trinidad. Birds from eastern Venezuela and the Guyanas were intermediate, while the largest

birds came from two locations on the Rio Tapajoz and Rio Andira in Amazonian Brazil. Birds from Ecuador, a small sample, were smaller than Amazonian birds and only slightly larger than those from Colombia.

L. m. militaris females: 3 groups, 46 specimens.

The only pattern evident is that birds from Panama and Colombia averaged smaller than those from the Guyanas, and the latter averaged smaller than birds from Brazil. However, the differences were not significant.

MULTIPLE DISCRIMINANT ANALYSIS

Rohwer (1972) used discriminant function analysis to identify possible hybrid specimens between magna and neglecta. He found relatively few individuals which could not be readily assigned to one or another of the species clusters, and he concluded (as did Lanyon 1957, 1966) that the species are nearly completely reproductively isolated.

The technique of multiple discriminant analysis will be described in the next chapter. I examined two relationships with this technique. I compared the two forms of Leistes which overlap in most of the measurements I obtained. I also compared defilippii with four groups of militaris. The technique has little advantage when groups can be distinguished adequately by a single

variable (for example the short tail of bellicosa distinguishes it from militaris).

DEFILIPPII VS MILITARIS

Figure 20 illustrates the individual birds in these groups plotted against the first two discriminant axes, and there is complete separation. This separation is accomplished entirely by the first axis and tail length (r=.740) and tarsus (r=.538) have the highest loadings on this axis.

Wing length and bill height have high loadings (r=.753 and r=.734) on the second axis which provides some separation of the militaris subgroups but not between species.

LEISTES

Ten geographical groupings of Leistes were compared with respect to the seven external measurements (figure 21). The five groups of L. m. militaris were from Panama and northwestern South America, Guyanas, western Amazonian Brazil, Rio Andira (Amazonian tributary), and eastern Amazonian Brazil. Five groups of superciliaris were from east-central Brazil, southern Brazil, Paraguay, western Argentina and the Argentine pampas. The two clusters of 69 militaris males and 106 superciliaris

males were well discriminated by the first two discriminant axes with only 7% of the total discriminant plane common to the two clusters. Within each species cluster the subgroups were poorly discriminated.

Bill length (r=.649) and bill height (r=.403) had the highest loadings on the first discriminant axis. The second axis, which contributed little to the discrimination, showed the highest correlations with wing and tail length (r=.813 and r=.736).

MEADOWLARK WEIGHTS

Weight has been a subject of controversy in avian systematics and ecology, mainly because of the extensive individual variation due to individual, behavioral and environmental factors. Baldwin and Kendeigh (1938) provided a major discussion of the sources of variation, and numerous studies have investigated one or another of these sources. Used judiciously, bird weights can be a useful indication of geographical variation.

Unfortunately few data are available on bird weights, and the data are not a random sample.

I have assembled information on meadowlark weights (Table 49) without attempting at present to analyze them to any extent. The only interpretation I have made concerns the male:female ratios in mean weight for

TABLE 49

MEADOWLARK WEIGHTS

	N	mean ± S.D.	Range	Source
LEISTES M. MILITARIS				
COLOMBIA				
male	1	45g		Cali
female	1	42g		Cali
SURINAM				
male	?		47-51g	Haverschmidt (1968)
female	?		38-43g	Haverschmidt (1968)
female	1	33g		Yale
TRINIDAD				
male	3	**45.0 ± 2.60**	**43.5-48g**	ffrench (1974)
LEISTES M. SUPERCILIARIS				
ARGENTINA				
male	1	52g		Fiora (1934)
male	4	55.25 ± 7.18	51-66	M.G.
female	3	40.90 ± 1.68	39-42	M.G., Yale
PEZITES DEFILIPPII				
ARGENTINA				
male	31	72.08 ± 4.33	61-81	M.G.
female	11	59.75 ± 3.01	52-66	M.G.
PEZITES BELLICOSA				
PERU, LIMA (Bujama)				
male	13	86.33 ± 4.63	74-92	M.G., L.L.S.
female	8	62.67 ± 3.98	58-68	M.G.

PEZITES MILITARIS MILITARIS (Table 49 con't)

SOUTHERN PAMPAS				
male	26	91.43 ± 3.41	84-98	M.G., L.L.S.
female	19	79.77 ± 7.82	64-90	M.G.
TIERRA DEL FUEGO, SANTA CRUZ, CHUBUT				
male	5	123.10 ± 8.52	111-131	P.H.
female	9	103.92 ±14.04	86-131	P.H.
NEUQUEN, SAN JUAN, LA RIOJA, S. CATAMARCA				
male	11	100.91 ± 9.53	82-111	M.G.
female	1	82.		M.G.
CATAMARCA (intermediate population)				
male	5	110.61 ± 8.59	102-122	M.G.

PEZITES MILITARIS CATAMARCANUS

CATAMARCA				
male	5	108.40 ± 3.36	103-112	M.G.
female	5	103.00 ± 8.51	93-112	M.G.
male	2	113.5	110-117	Fiora (1934).

SOURCES
M.G. = M.Gochfeld
L.L.S= Lester L. Short
P.H. = Philip Humphrey
Cali = Museum of Natural History, Cali
Yale = Peabody Museum, Yale, University.

	WEIGHT RATIOS BETWEEN SEXES	
	RAW WEIGHTS	CUBE ROOTS
L.m.militaris	1.17	1.05
L.m.superciliaris	1.35	1.10
P.defilippii	1.20	1.06
P. bellicosa	1.37	1.11
P.militaris		
pampas	1.14	1.05
Tierra d.Fuego	1.18	1.06
W.Argentina	1.23	1.07
Catamarcanus	1.05	1.02

different localities. Weights have been obtained from specimens collected by L. Short, by P. Humphrey, and by me.

The weight ratios of males to females vary from 1.05 for a small sample of catamarcanus to 1.35 and 1.37 for small samples of superciliaris and bellicosa. Ratios of defilippii and of militaris populations are close to 1.2, which is similar to the linear measurements obtained, even though the weights used were raw weights rather than cube roots. Ratios of the cube roots all lay between 1.02 and 1.11.

Although the data for most groups are scant, the weight changes generally parallel the clines in wing-length. A very interesting anomaly is that catamarcanus and adjacent birds are longer-winged than birds from Tierra del Fuego, yet the latter birds are substantially haevier (Mann-Whitney $U = 1$, $p = .03$). In view of the oft-stated, though unproven notion that birds of more migratory populations have longer wings, I would have predicted that per equivalent weight, birds from southern Argentina (known to be migratory, e.g., Humphrey et al. 1970) would have had longer wings than those from northern Argentina. It is possible that catamarcanus is migratory, but more likely weight and wing-length are subject to different selective pressures in the two areas.

DISCUSSION OF ECOGEOGRAPHICAL VARIATION

The subject of ecogeographical variation has engendered much debate with respect to such "rules" as Bergmann's and Allen's. Some debate has arisen because of the difficulties in employing such variable attributes as weight or such adaptive attributes as wing length, as sole measurements of size. Some confusion has arisen in treating certain characters (e.g., Bowers 1960), such as the avian bill which is probably much more susceptable to selective pressures of feeding than of thermoregulation.

The main problem is probably that of trying to resolve conflicting pressures imposed by several environmental variables (e.g., temperature and moisture) which do not vary together. For example, Hamilton (1958) found that in several species of Vireo the pattern of geographic variation was contrary to that predicted by Bergmann's rule, and he attributed this to variability in aridity. Rand (1961) found limited application of Bergmann's rule and noted that clines from arid to humid areas had longer-winged forms in the arid, regardless of temperature. James (1970) examined 12 species of eastern and central United States, and found support for Bergmann's rule in most cases. However, she also demonstrated substantial subtle microgeographic patterns and

that combining temperature and humidity provided a better predictor of wing-length, than temperature alone. Her study is the most complete to date.

As a partial indication of ecogeographic variation I did a linear regression of wing length on latitude for several populations.

I examined the following groups:

1. militaris males from western Argentina through Patagonia to Tierra del Fuego (n=67). The linear regression coefficient of .493 was significantly different from zero ($p < .001$).

2. militaris males from Chile (n=57). The regression coefficient was not significant, until I removed the two southernmost birds, whereupon the coefficient became -.229 (significantly different from zero, $p < .05$). Thus in northern Chile there is a reverse cline, which suddenly changes to a more predictable north-south cline as one gets south of 42° S. lat. Since there were only two specimens from the extreme south, the significance of the second aspect of the cline could not be shown. However, when all the birds were used, 3rd, 4th and 5th degree polynomials provided good fit to the data.

3. militaris females from Chile (n=16). The regression coefficient of -.188 did not differ from zero, and no cline could be demonstrated to the north of 41° S. lat.

4. militaris females from Catamarca to Mendoza, (n=21). Again the birds were larger to the north (associated in part with higher altitude), the regression coefficient of -.231 being significant ($p<.05$).

5. bellicosa males of all populations, (n=109). No apparent clinal variation within the latitudinal range of 0-22° S. lat.

It is likely that altitude plays an important role in many of the clines, and this has been considered for the bellicosa populations. Future investigation of ecogeographic variation should deal with two or more independent variables, such as altitude, and latitude, and perhaps moisture as well.

The factors underlying the observed patterns of variation are not simple. Although thermoregulation has been the preferred explanation for Bergmann's rule, McNab (1971) found that relatively few species of North American mammals provide a good fit, and that food availability and competition are more important determinants of size. Scholander (1955) and Irving (1957) questioned the role of thermoregulation because of the small magnitude of the energy conservation gained, but Kendeigh (1969) pointed out that ultimately size is a compromise among many selective factors, and that large size may increase thermoregulatory efficiency but would

also increase food requirements, and it might also diminish (or increase) risk of predation. The wide-ranging meadowlarks, a series of closely related taxa occuring in many different South American habitats, would provide a good opportunity to explore ecogeographic variation and the underlying physiological ecology in South America.

The data obtained in this study, both basic statistics by populations, and regression coefficients, demonstrate that in some groups clear north-south (or tropical-temperate) clines in size can be recognized. At present it is not fruitful to pursue these in greater detail, until more adequate samples can be obtained throughout the range of the species (e.g., southern Chile and Santa Cruz Province Argentina for militaris, northern Chile for bellicosa, and western Brazil for Leistes. Although it would be desirable to plot variation against some complex climatic variable (e.g., annual wet bulb temperatures as suggested by James 1970), these data are currently lacking for most of South America, particularly from the Andean region where the most complex variation patterns occur.

TABLE 50. Comparisons of meadowlark taxa and sexes by shape indices.

TAXON AND SEX	Tail / Wing	Bill / Wing	Tarsus / Wing	Width[a] / Height	Height[a] / Bill
militaris ♂♂	.75	.19	.28	.76	.38
militaris ♀♀	.74	.19	.29	.76	.41
defilippii ♂♂	.61	.17	.26	.77	.40
defilippii ♀♀	.62	.16	.27	.76	.48
bellicosa ♂♂	.61	.16	.31	.74	.50
bellicosa ♀♀	.60	.16	.33	.72	.52
magna ♂♂	.64		.35		
magna ♀♀	.62		.36		
neglecta ♂♂	.60		.32		
neglecta ♀♀	.60		.33		
L.m.militaris ♂♂	.63	.15	.31	.73	.54
L.m.militaris ♀♀	.63	.15	.33	.74	.57
superciliaris ♂♂	.61	.13	.30	.73	.65
superciliaris ♀♀	.60	.13	.32	.74	.64

SHAPE INDICES

The primary variables were examined as ratios or shape indices, tail/wing, bill/wing, tarsus/wing, bill width/bill height and bill height/bill length. Figure 22 represents an ordination of the forms and sexes of red-breasted meadowlarks with respect to three of these indices. For all five species males and females are close together, with very similar bill height/length ratios. In all cases females had markedly shorter wings relative to tarsi, and appear to the right of males with respect to the tarsus/wing axis. These indices ignore size, and demonstrate a previously unsuspected similarity of *bellicosa* to *Leistes*.

SUMMARY

1. The morphometric study was aimed at clarifying relationships within the meadowlark group, but more importantly at delineating ecogeographic variation and providing data to test for character displacement (see next chapter).

2. Seven measurements were obtained from study skins, and sources of variation are described for each variable chosen.

3. After discarding unsatisfactory specimens, a total of 496 male Pezites, 204 female Pezites, 318 male Leistes, and 75 female Leistes (total 1093) skins from 11 North American, 1 British, and 5 South American Museums formed the basis of this study.

4. Distributions of variables for all populations rarely showed a bad fit to the normal curve, and descriptive statistics were obtained on untransformed data.

5. For P. militaris birds from the Falklands had the longest bills and those from northwestern Argentina the longest wings. There was a south to north cline of decreasing size (wing length) for males in eastern Argentina and to a lesser extent in Chile.

6. For defilippii no evidence of geographic variability was discovered for males, while females from southern Buenos Aires were smaller than birds further north---apparently a reversed cline.

7. P. bellicosa from the Andes were significantly larger than coastal birds, while the latter show a size increase both northward and southward from Lima, with an apparent decrease again in Ecuador.

8. For L. m. militaris birds from Panama-Colombia and from Trinidad were small and Amazonian birds were larger.

9. In superciliaris birds from eastern Brazil had longer wings than elsewhere, with a decrease in wing length both to the west and south. Even high altitude specimens from Bolivia had shorter wings than in eastern Brazil.

10. Two comparisons were made using multiple discriminant analysis. In one case male defilippii could be perfectly distinguished from male militaris of four populations by the first discriminant axis with tail length and tarsus contributing most to the separation. In the other case five populations of L. m. militaris were compared with 5 populations of L. m. superciliaris and the two forms were almost completely separated by the first axis (mainly bill length and bill height), while the second axis added nothing.

11. Weight data from the literature (almost lacking), museum specimens, and personal specimens are tabulated. For militaris and defilippii male/female weight ratios are close to 1.2 while ratios of the cube root of weight lay between 1.02 and 1.11 for all forms. Although catamarcanus birds have longer wings than militaris from Tierra del Fuego, the latter were much heavier. This may be a seasonal variation, however.

12. The nature and patterns of ecogeographic variation are briefly considered. Several groups of specimens were tested for the regression of wing length on latitude, and statistically significant regression coefficients were found for militaris males from Mendoza to Tierra del Fuego, militaris males and females from Chile, militaris males from Catamarca to Mendoza, and bellicosa males. The influence of altitude was not tested in this analysis.

13. Three shape ratios (tarsus/wing, bill/wing, and bill height/length) were used to ordinate males and females of five meadowlark forms. Females were similar to males but had significantly shorter wings. In shape bellicosa appeared closer to Leistes than to the other Pezites.

CHAPTER 20 A MULTIVARIATE SEARCH FOR CHARACTER DISPLACEMENT IN NEOTROPICAL MEADOWLARKS

The existence of sympatry among three species of meadowlarks (*P. militaris*, *P. defilippii*, and *L. m. superciliaris*) on the Argentine pampas, offers an opportunity to search for character displacement. Brown and Wilson (1956) called attention to character displacement, as a morphological shift which occurs between two species, rendering them more different in their zone of sympatry than in allopatry. The divergence could occur to minimize the possibility of confusion during pair formation---thus to enhance pre-mating isolation. Or it could arise to minimize competition, accounting for niche shift. Or it could reflect adaptive differences to which interaction is irrelevant. Selander (1971) considered that much evidence for character displacement was inadequate, since geographic variation is a widespread phenomenon. To accomodate theories such as Cody's (1969) notion that in sympatry birds might become more similar (rather than less) to enhance aggressiveness and minimize competition, Grant (1972) widened the definition of character displacement to include both convergence and divergence. The theoretical aspects of character displacement are not considered here. The practical problem is to have two species with both

allopatric and sympatric populations, and to be able to recognize clear morphological (or behavioral, physiological, or biochemical) divergence. If a cline occurs, then a reversal or at least a sharp step in the cline at the point of sympatry, would be convincing evidence of character displacement.

The evolutionary mechanism----either reduction in competition or in hybridization----can be inferred from the type of character showing divergence.

In working with Pezites and Leistes I encountered certain problems which make them less than optimal for a study of character displacement. For militaris and defilippii there are suitable populations, but field studies have suggested that character displacement might not be likely. Firstly, militaris has probably not been present on the pampas in any numbers for more than two or three centuries, since previously there were hardly any elevated perches for it. Thus although incipient character displacement might occur, it might still be too early for it to be recognizable. Secondly, examination of foods of the two species indicates that although both are omnivorous, defilippii is much more insectivorous than is militaris. If this difference between two closely related forms evolved in allopatry, there would be little need for character divergence, except perhaps to further minimize the overlap. Finally,

although the two species are very similar in color pattern, vocalizations are likely to be the main factors active in species isolation (cf Lanyon 1957) and these are as different in allopatry as in sympatry.

For superciliaris and defilippii I have inadequate evidence concerning possible food competition or factors involved in isolation. These two are more similar to each other in behavior than is either to militaris. However, a search for character displacement is limited by the lack of an allopatric population of defilippii whose range lies entirely within the range of superciliaris.

METHODS:

I used bill length, culmen length, bill width, bill height, tail, wing, and tarsus length as morphological variables. The first two are largely redundant, but not entirely. No color or behavioral attributes have been employed in this study. Only male individuals were used, since specimens of females were less numerous. Only those individuals for which all seven characters were measurable were employed in this study.

The first discussion concerns militaris and defilippii from the southern pampas (Buenos Aires and La Saudade) compared with defilippii from the northern

pampas and militaris from Patagonia. The second discussion concerns defilippii compared with all populations of superciliaris. The locations of the populations are shown on the map (figure 23).

For each population univariate statistics and one way analyses of variance were performed, and any statistically significant results were examined to see whether there was evidence of character displacement. All univariate differences seemed due mainly to clinal variation with latitude. Altitude also contributed somewhat to the cline (see Chapter 19).

Consequently a multivariate approach was used to see whether evidence of more subtle character displacement might be found. The technique of multiple discriminant function analysis (see below) was used to simultaneously compare four populations:

MIL-S
DEF-S — sympatric populations

MIL-A
DEF-A — allopatric populations

MULTIVARIATE TECHNIQUES

A brief account of the applicability of the multivariate statistics employed is given here. Such statistics utilize simultaneously the information in several variables, in examining similarities or differences between groups or in measuring the relationships among several factors. Sneath and Sokal (1972) summarize many attributes of such statistics useful in classifying organisms. Such schemes are particularly attractive to entomologists and bacteriologists whose organisms do not lend themselves at all to more traditional taxonomic approaches.

With one group of organisms, a principal component analysis searches for new axes or hypothetical variables that do a better job of explaining the total variance within a system, than any of the individual variables actually measured. Just as one might make a bivariate scatter diagram of an organism against variables, one can plot an organism against two or more principal components. By examining the "loadings" or correlation coefficients between the original variables and the principal components, one can infer the relative importance of the original variables. Rising (1968) provides an example of the simplest (probably oversimplified) application of this technique in a strictly classical sense.

Discriminant analysis (for two or more groups) searches for roots that explain a maximum amount of the between group variance while minimizing the within group variance. It is the best linear function of all variables for separating the groups. Like principal component analysis, it eliminates the effect of intercorrelation between characters.

The programs I used are based on those on Cooley and Lohnes (1971) as modified by L. F. Marcus and J. Gulledge. The map (figure 23) showing the zone of sympatry, indicates the limits beyond which a bird would be assigned to one or the other allopatric group.

The role of the new discriminant variables is best explained by analogy. In comparing two groups of birds, it often happens that single variables, e.g., wing and tail lengths, are inadequate for separating the forms because of overlap. However, a combination of the two, such as wing/tail ratio, sometimes proves adequate or at least improves ones ability to discriminate between the two forms. Unknown individuals, can then be assigned to one group or another based on this ratio. Ecologists interested in feeding behavior are likely to attempt to measure a functional complex such as bill shape, by using an index or some function of two or more variables that are measured directly. The ratio of bill height to bill length is sometimes used to indicate bill shape differ-

ences, in the hope that this provides evidence on how niches can be discriminated. Where a combined variable proves more useful than the original variables, attention is likely to focus on these new variables in future studies.

These shape variables ideally represent functional complexes which are of direct interest. By comparison, discriminant function analysis creates variables which are mathematical constructs and which aid in discrimination, while not necessarily being of direct interest themselves. The variables may be a function of wing size + tail + bill + tarsus + weight. Just as individual birds can be plotted with respect to original variables, they can be plotted with respect to their position or projection on the discriminant variables. The plots on many different variables at once form hypervolumes, and this applies to either original or discriminant variables. Although the number of discriminant variables (or axes) in a multiple-group discriminant analysis is equal to the number of groups minus one, usually only the first two or three axes prove useful in discrimination, which allows them to be graphed in two or three dimensions.

MILITARIS - DEFILIPPII

Four populations were used in looking for character displacement between these two species in the zone of sympatry:

1.	*defilippii*	(32°30'S to 34°50'S)	DEF-A	n = 21
2.	*defilippii*	(35°30'S to 38°50'S)	DEF-S	n = 28
3.	*militaris*	(39° northward)	MIL-S	n = 29
4.	*militaris*	(39° southward)	MIL-A	n = 19

Inspection of the means $\pm$ standard deviations, (Table 51) reveals that in none of the seven characters, are the two populations DEF-A and DEF-S different. The two *militaris* populations, also show no appreciable differences other than a north-south cline of increasing wing length. Inspection also reveals a very strong difference in tail lengths ($<$ 85 mm in all but two *defilippii* and $>$ 85 mm in all but 5 *militaris*), and this accounts for most of the between species differences, (r=.59 with 1st discriminant axis).

A principal component analysis reveals some overlap between DEF-S and MIL-S when individuals are plotted against the first two principal components. The discriminant function analysis provided a distance matrix (see Table 52a) and a plot (see figure 24) which reveals the difference between the two species with little difference between allopatric and sympatric populations

within species.

Table 52b shows the factor pattern or loadings of the variables against the three discriminant axes. The first axis is almost entirely a function of tail length, while wing and culmen contribute mainly to the second axis, and bill-height to the third.

In view of the strong contribution of tail length, the same data were reanalyzed, omitting tail length entirely. The distance between the two species was now markedly reduced, but was still substantially greater than the within species distance. Moreover, the distance between DEF-S and MIL-S was less than the distance between DEF-A and MIL-A in both analyses. The increased similarity between two species in the area of sympatry, if significant, is contrary to anticipated divergence, and is consistent with convergence. However, exactly this similarity is to be wxpected for two closely related species in the area where they are sympatric, because of like response to the environment.

TABLE 51. Descriptive statistics for four populations and seven variables used in character displacement analysis for *militaris* and *defilippii*.

VARIABLE	Allopatric *defilippii* (DEF-A)	Sympatric *defilippii* (DEF-S)	Sympatric *militaris* (MIL-S)	Allopatric *militaris* (MIL-A)
	mean ± s.d.	mean ± s.d.	mean ± s.d.	mean ± s.d.
Wing Length	123.1 ± 2.62	123.6 ± 3.12	120.9 ± 2.98	123.2 ± 5.04
Tail Length	75.4 ± 3.87	76.3 ± 4.28	89.7 ± 3.13	91.0 ± 5.53
Bill Length	20.3 ± .79	21.0 ± 1.16	22.4 ± 1.29	22.8 ± 1.89
Tarsus Length	32.2 ± 1.06	32.3 ± 1.23	34.3 ± 1.20	34.6 ± 1.48
Bill Height	9.1 ± .36	8.9 ± .47	8.9 ± .48	9.0 ± .63
Bill Width	6.9 ± .34	6.7 ± .53	6.9 ± .50	7.0 ± .94
Culmen Length	26.6 ± 1.36	26.8 ± 1.39	29.13± 1.62	29.8 ± 1.83
Sample Size	21	28	29	19
Latitude	35°northward	35°-39°	36° - 39°	39°southward

TABLE 52. Generalized distance matrix and factor loadings for discriminant analysis of character displacement in militaris and defilippii.

A. Distant matrices in 3-dimensional space. Upper right triangle includes distances for 7 variables; lower left triangle is for 6 variables.

	DEF-A	DEF-S	MIL-S	MIL-A
DEF-A	-----	.84	37.22	37.28
DEF-S	.79	-----	31.79	31.52
MIL-S	10.95 v	7.06	-----	.65
MIL-A	11.83	8.10	.64	-----

Code

DEF-A = allopatric defilippii group
DEF-S = sympatric defilippii group
MIL-S = sympatric militaris group
MIL-A = allopatric militaris group

B. Factor loadings (=correlation coefficients) of original variables on 3 axes.

Seven Variable Analysis FIRST axis	SECOND axis	THIRD axis	VARIABLE	Six Variable Analysis FIRST axis	SECOND axis	THIRD axis
-.074	.683#	.488	Wing Length	-.135	.857##	.209
.589#	.203	.406	Tail Length	----	----	----
.246	.558#	-.130	Bill Length	.482	.403	-.150
.297	.212	.345	Tarsus Length	.572#	.108	.498
-.014	-.027	.776##	Bill Height	-.032	.139	.799##
.037	-.145	.464	Bill Width	.065	-.079	.556
.353	.821##	-.158	Culmen Length	.691#	.609#	-.193

= r > .500

= r > .700

DEFILIPPII - SUPERCILIARIS MDFA

The entire group of male defilippii was compared with five latitudinal groups of superciliaris (Table 53), and it proved entirely separable from superciliaris on the first discriminant axis. Variables contributing strongly to this axis were bill length (r=.859), wing length (r=.683) and tail length (r=.431). The second discriminant axis, reflecting mainly bill height (r=.742) was of some value in separating latitudinal groups of superciliaris. The plot of these groups on the first two axes was analyzed for separation, and 49.7% of the area covered by the cluster was unique to one group or another. Thus approximately half of the points within the entire superciliaris cluster could be identified to latitudinal group. An additional 30.2% of points were ambiguous with respect to two groups, while 20.1% of points were ambiguous among three or more of the groups.

If character displacement is occurring in the group of superciliaris that is sympatric with defilippii (35° S. lat. and southward), one would anticipate a reversal in a south to north cline of increasing size. Reference to the group means shows that from 15° to 30° S. lat. there does appear to be a slight (non-significant) size increase for wing, tail and tarsus, which is then reversed in the group at 30-35° S, a point well

north of the contact area. None of the univariate analyses provide evidence that character displacement has occurred.

In the multivariate scheme, one might anticipate that the sympatric group of superciliaris would be more distinguishable from defilippii than the other groups. This group, however, is closer (see generalized distance matrix, Table 54a) than two other groups, and no evidence of divergence can be seen. In the present analysis, the main discrimination between the two species is based on size. The magnitude of the difference is so great and so adequate for discrimination, that it might obsecure shape differences. Consequently, the analysis was repeated, with the values of defilippii variables reduced by 10%. This procedure reduced the overall distance between defilippii and superciliaris clusters and provided better resolution within the latter cluster, but did not change the position of the latitudinal groups with respect to defilippii.

It appears, therefore, that at least the characters chosen for analysis provide no evidence of character divergence in sympatry for defilippii and superciliaris. In view of the 20% difference in wing and tail measures and the 35% difference in bill lengths between the two species, there may be relatively low competition for food between them, and character divergence in size would

not be expected. The occurrence of interspecific territoriality between them is therefore of particular interest. Unfortunately adequate data on feeding and on food habits of superciliaris were not obtained. The only evidence relating to competition for food is that both were observed feeding on wheat, a superabundant food source over which competition is unlikely to be significant.

The similarity in coloration and pattern is probably of greater importance than potential competition for food, in promoting interspecific territoriality among these meadowlarks. Evidence for character displacement will be sought with respect to coloration and pattern in future studies of these species using reflectance spectrophotometry.

DISCUSSION

Univariate and multivariate analyses of seven external mensural variables have shown no evidence of character divergence or convergence in two sets of sympatric meadowlark species in South America. Failure to demonstrate the phenomenon may only mean that the characters chosen were inappropriate. Use of bill, leg, wing, and tail characters should be an adequate indication of adaptive complexes related to foraging and food-

getting, so that displacement or convergence in this area should have been detectable. On the other hand, convergence or divergence with respect to species recognition signals would more likely involve color or vocal features which have not yet been investigated.

Thielcke (1969) examined reported cases of vocal character displacement in birds and found reasons for alternative interpretations. Selander (1971) suggested that the abundant reports of character displacement in birds are due more to the attractiveness of the phenomenon than to clear ecological analyses. Grant (1972 and M.S.) has reinterpreted the classical case of character displacement in Asian nuthatches, as clinal geographical variation. One wonders whether the convincing examples of ecological displacement in the Galapagos finches (Lack 1947) will stand up to future scrutiny. At present, perhaps the most convincing examples of acoustic character displacement involve the species-recognition signals among anurans (Blair 1974).

Although no divergence was found among the sympatric populations of similar species, it is perhaps significant, that no marked convergence was apparent either, despite the interspecific territoriality maintained between defilippii and superciliaris. The slight convergence (of questionable significance) noted for militaris-defilippii in the zone of sympatry would not be predicted

TABLE 53. Descriptive Statistics for Four Populations and Seven Variables used in superciliaris-defilippii discriminant analysis.

Variable	defilippii	superciliaris				
	all	35°southward	30-35° S.Lat	25-30° S.Lat	20-25° S.Lat	20°northward
Wing Length	123.26 ±3.05	99.64 ±2.76	98.00 ±4.65	100.38 ±3.08	100.00 ±4.02	97.78 ±3.67
Tail Length	75.91 ±3.94	60.29 ±1.49	58.95 ±4.12	61.80 ±3.02	61.17 ±3.69	58.89 ±2.71
Bill Length	20.58 ±1.09	13.20 ± .85	12.69 ± .75	13.01 ± .48	13.49 ±1.11	13.37 ± .89
Tarsus Length	32.25 ±1.18	30.14 ± .88	29.84 ± .98	30.27 ± .81	30.06 ±1.30	29.73 ± .93
Bill Height	8.98 ± .45	8.80 ± .38	8.41 ± .42	8.29 ± .433	8.36 ± .40	8.15 ±.52
Bill Width	6.82 ± .46	6.36 ± .47	5.99 ± .38	6.21 ± .39	6.03 ± .39	5.97 ± .49
Culmen Length	26.21 ±1.46	18.60 ±1.14	18.31 ±1.15	18.89 ± .61	19.68 ±1.29	18.34 ±1.06
Sample Size	54	14	21	50	12	9

TABLE 54

Multiple discriminant analysis of *defilippii* and *superciliaris*, showing generalized distance matrix (a) in three dimensional discriminant space, and factor loadings for seven variables on the three axes.

A. Distance Matrix

	defilippii	*superciliaris* >35°	*superciliaris* 30-35°	*superciliaris* 25-30°	*superciliaris* 20-25°	*superciliaris* 15-20°
defilippii	-----	104.4	115.9	100.1	94.0	124.2
sup >35°	104.4	-----	1.4	2.0	2.9	2.2
sup 30-35°S	115.9	1.4	-----	1.6	1.9	0.5
sup 25-30°S	100.1	2.0	1.6	-----	1.0	2.7
sup 20-25°S	94.0	2.9	1.9	1.0	-----	2.9
sup 15-20°S	124.2	2.2	0.5	2.7	2.9	-----

B Factor loadings (=correlation coefficients) of original variables on three discriminant axes

Variable	Discriminant Axis FIRST	SECOND	THIRD
Wing Length	.683#	-.072	.197
Tail Length	.431	-.342	.267
Bill Length	.859##	.261	-.123
Tarsus Length	.209	-.142	.277
Bill Height	.125	.742##	.292
Bill Width	.157	.036	.707###
Culmen Length	.636#	-.078	-.397

\# = r > .50

\## = r > .70

in view of their lack of interspecific territoriality. However, the characters examined are not suited for examination of convergence, and further discussion awaits future analysis of other characters.

CRITIQUE OF ROHWER

Rohwer (1973) made a series of predictions relating to character convergence between S. magna and neglecta in the zone of sympatry. The predictions related to morphologic features including size and color and to behavioral features including song and fighting behavior. Rohwer's predictions are of considerable interest in view of the interspecific territoriality maintained by these two species (Lanyon 1956). Unfortunately the presentation includes some statistical errors, and the interpretation includes some ambiguities, which invite a reconsideration of Rohwer's conclusions.

a. Convergence in underpart color and pattern.

Rohwer reasoned that if the yellow underparts and the black V played a role in dominance, selection would act on neglecta in the zone of sympatry to enhance its brightness and increase the area of the V, so as to improve its chances in conflicts with magna. Rohwer's table 1 provides data on the three color indices (brightness, purity, wavelength) and on V-area. He

predicted that since only males were involved in territorial conflicts, only the male neglecta should show color and V changes while females should not.

Rohwer apparently did not predict that magna should also be under selective pressure to enhance these same features in the zone of sympatry, although he later comments that in magna the reverse changes occur. The analysis of variance which Rohwer used was suject to some difficulties because of the great disparity in sample sizes. He reported that for male neglecta three of the four measurements shifted in the predicted direction with one-tailed probabilities less than .05. However, his interpolation of the critical values of the F distribution appear in error, since two of the probabilities he lists are wrong. Only two of the four measurements actually changed significantly. For females, none of the four F ratios proved significant, however two of these were based on denominator degrees of freedom of 2 and 0.1 (fractional degrees of freedom are valid in the ANOVA he used), and with such constraints demonstration of significant change becomes virtually impossible. Thus the failure of females to change parallel to the males is in part a matter of small sample size. Most importantly, all eight of the means (4 for males and 4 for females) shifted towards those of magna. On the other hand, comparison of the sympatric and non-

sympatric magna populations, indicated that all eight of the measurements shifted towards those of neglecta, with two of the male and two of the female shifts being significant.

The data are entirely compatable with a west to east cline of increasing area of the black V, increasing color purity and "orangeness", and increasing darkness or saturation of the carotene pigmentation. The parallel response of the two species from west to east is just what one would predict for two closely related species subjected to similar environments. Whereas the shift of all 16 means was consistent with this hypothesis, only 4 of the means shifted in a direction consistent with the "convergence" hypothesis.

b. Responses to heterospecific vocalizations.

The primary songs of magna and neglecta are distinctive, and there is no evidence of a consistent convergence or divergence in voice in sympatry. Using playback tests, Rohwer found that both in allopatric and sympatric populations, male meadowlarks responded more strongly to autospecific than to heterospecific songs. However, when responses to heterospecific songs were graded for the 16 sympatric and 18 non-sympatric males tested, the former birds proved much more likely to respond to heterospecific song. This is no surprise

since meadowlarks learn songs (Lanyon 1957), and a meadowlark exposed to heterospecific song may learn to respond to it even without learning to sing it. However, no additional evidence has been adduced to clarify the role of learning in this respect.

c. Fighting in the zone of sympatry.

Rohwer predicted that if a male is surrounded by heterospecific songs, he is likely not to understand the significance of the vocalizations as substitutes for territorial fighting. Therefore, he suggested that fighting should be more common in sympatry than in monospecies populations, and the less common species (with more heterospecific around) should do more fighting. He used the signs of scarring about the head in prepared study skins, as evidence of fighting, and found the predicted results (but probabilities are again incorrect since a X^2=3.843 has a probability of .05, not .025 as stated).

Assuming that the wound criteria used by Rohwer are suitable, his claim that the wounds are density independent needs to be reconsidered. He does not have information on the dominance status of his males and whether they were on territory or seeking territory at the time of collection. Tinbergen (1939) showed that as Snow Bunting territories shrank with increased settling of

newly arrived males, the amount of fighting and aggression increased. Thus, although the number of territorial neighbors one can have is subject to geometric constraints, the frequency of conflicts is density-dependent. Thus if the area of sympatry had a greater density of meadowlarks than non-sympatric areas, the increased fighting might in part be explained.

Nonetheless Rohwer's finding is quite intriguing, and in view of the doubt over whether the observed scars actually reflect territorial fighting, direct observations of encounters in the area of sympatry---with respect to intensity, duration, and dominance relationships among the species---would be illuminating.

d. Body size of meadowlarks.

Rohwer notes that in inter-male conflicts a large body size is probably always an advantage, and he predicts that in the zone of sympatry neglecta should be larger than outside the zone. The same change might occur, but less markedly, for the larger magna. The data presented are all consistent with this hypothesis, but Rohwer is notably careful in interpreting this particular data set. Only one of the changes (male neglecta) was reported as significant (but the probability is $>.05$, rather than $<.05$ as listed).

It is possible that in the zone of sympatry,

environmental conditions favor a large size in both species, apart from interspecific conflict. There is also a time factor which is of considerable concern in interpreting all of these conclusions. The zone of sympatry studied by Rohwer is probably less than 50 years old according to his investigation. This may be too little time for some potential differences or similarities to evolve. Some of the changes observed---with respect to size and color---may be ecotypic, for the role of climatic variables in influencing these directly (ecotypic variation) rather than via selection, has not been adequately studied.

At present it appears that future considerations of the Sturnella interactions using adequate sample sizes would be valuable. Rohwer's suggestions, although interesting, cannot currently stand as evidence of character convergence.

SUMMARY

1. Character displacement is defined and the problems of studying it are considered. Multivariate discriminant analyses were performed to enhance the possibility of recognizing displacement.

2. Allopatric and sympatric populations of militaris and defilippii were examined and the sympatric popula-

tions showed somewhat lower discriminant-space distance than did allopatric. This finding is interpreted as showing no evidence for character displacement (with respect to the seven morphological variates chosen), and although consistent with convergence, is believed to represent similar responses of phylogenetically closely related species, to a common environment.

3. Five populations of superciliaris, one of them sympatric with defilippii also showed no evidence of character displacement.

4. Rohwer's purposed demonstration of character displacement in Sturnella is examined and an alternative explanation offered.

CHAPTER 21 INTERSPECIFIC TERRITORIALITY

Avian territorial behavior is mainly an intraspecific phenomenon, but attention has increasingly focused on interspecific aggressive behavior and territoriality. By such behavior, males of one species would exclude from their territory males of another species as well as males of their own species. Simmons (1951a) although not the first to describe such behavior, was the first to point out that it was of more than casual interest. He first suggested the ecological significance of interspecific territoriality as a possible alternative to competitive exclusion. Some recent authors (e.g., Ashmole 1968, Moynihan 1968, Cody 1969, 1973), have elaborated on interspecific territoriality as an alternative to character divergence in allowing two species to coexist in violation of the competitive exclusion principle (C.E.P.) without either excluding one another or shifting their niches so as to minimize competition.

Cody (1973) discusses how character convergence (Grant 1972) might occur to facilitate interspecific aggression and habitat partitioning, but many of the examples he invokes more likely reflect similarity by relationship rather than convergence (e.g., the Asian woodpeckers according to L. L. Short, pers. comm.)

Orians and Willson (1964) provided a detailed review of the question of interspecific territoriality and discuss its possible ecological importance as a particular adaptation for sympatric existence. Murray (1971) examined the phenomenon in terms of its evolution, emphasizing that, by its consequences, it is often transient, and that it can promote differential habitat selection and niche utilization.

I view interspecific territoriality as a spectrum of events from complete mutual exclusion where males of two species treat each other as they would conspecifics and participate equally in maintaining interspecific territoriality (e.g., S. magna and S. neglecta, Lanyon 1956a) to cases where one species completely dominates another which is likely to be forced out of its preferred habitat. Simmons (1951a) recognized that mutualistic cases might occur, but he believed they would be unusual and that in most cases only one species would be responsible for the interspecific exclusion, the other being a passive "partner". Murray (1971) predicts that such unequal relationships will be the usual form of interspecific territoriality. Although the available literature seems to support this prediction, it appears that there is much variability in the roles that two species may play, and there has been little attempt to quantify interspecific aggression so that different cases

can be meaningfully compared.

RECOGNITION OF INTERSPECIFIC TERRITORIALITY

Two criteria must be met in describing interspecific territoriality.

1. Where they occur in local sympatry, two species must occupy non-overlapping territories, and such non-overlap must not be related to a habitat mosaic.

2. The non-overlap must be maintained by interspecific aggression.

Although the latter can be readily observed, the former criterion may be difficult to test. There is, of course, no reason why both interspecific aggression and some degree of differential habitat selection, could not operate together to produce non-overlap, as, for example, in Lanyon's example of the meadowlarks (Lanyon 1956a, 1957), but this makes it more difficult to interpret the ecological significance of the interspecific territoriality. Murray's model (1971) relates these dynamically, the interspecific aggression functioning to promote differential habitat utilization and perhaps ultimately differential habitat preferences. Cody (1973) discusses "partial interspecific territoriality" in which two species avoid each other, showing non-overlap without aggressive behavior as well as differential habitat

selection. Since territoriality is usually defined by the defense of a resource, I do not consider mutual avoidance as territoriality. I confine attention to breeding territories. In view of the documented interspecific territoriality for North American Sturnella (Lanyon 1956a, 1957) I was interested in studying the territorial interactions of South American meadowlarks.

The data on interspecific territoriality were obtained during observations on habitat preferences and distribution in southeastern Buenos Aires Province, and during studies of territorial behavior at La Saudade.

The observations along roads involved stops from 10 minutes to almost three hours in areas occupied by meadowlarks. In all cases I attempted to census the number of territorial males of each species, and I recorded the number of "territorial encounters". Criteria for a territorial encounter are detailed below. In the present report I include data only from stops lasting 20 minutes or more and with more than a single encounter. Territorial activity fluctuates during a season, and where two species are concerned, the changes in territorial activity may be asynchronous. Consequently data have been grouped by weeks and analyzed on a weekly basis.

On the Saudade study area and near Bahia Blanca (BB7E) I mapped territories of the three meadowlark

species to assess the extent of territorial non-overlap, and also recorded the number of aggressive encounters related to the maintenance of territory.

CATEGORIES OF TERRITORIAL ENCOUNTERS

The following types of interaction were considered territorial (cf Lanyon 1957):

1. Physical attack: Although Rohwer (1973) implied that physical attacks were a frequent feature of territorial encounters among Sturnella males, Lanyon (1957 and pers. comm.) did not find this. I saw only two cases the first involving two defilippii, the other two militaris. Attacks on unyielding decoys were very frequent.

2. Face-offs and jump flights: Threats stopping short of physical contact usually took the form of "face-offs". Two males would posture in the bill-up position, holding it for many seconds. The birds would sometimes stand only inches apart. One bird would make a short jump-flight, usually about 2 meters, along the presumed territory border, and the other bird would follow. They remained silent during the face-offs.

3. Facing-away: Two birds at a territorial boundary, might display to each other, and then face-away, usually

without exaggerated posture. The appearance of "studied indifference" was sufficiently frequent to indicate that it is a display.

4. Primary song duetting: Two males sat near each other and alternated primary songs, across the presumed territorial border.

5. Flight song duets: One bird would give a flight song oriented toward or along a territorial boundary. The adjacent male would often follow suit, sometimes within seconds. A response within one minute was scored as positive. A later response was scored as positive if the second male flew toward the first one.

6. Chases: Any chase between two males, however brief, was scored as positive. Some chases were directed at neighboring birds or intruders, while others were aimed at over-flying males. This category would include a flight song or even a silent flight display, oriented towards a male.

These categories of behavior are not directly comparable, and probably are expressions of a continuum of aggressive behavior. Nonetheless, to provide adequate sample size I have combined them all into a single category. Accumulation of further data might reveal that certain of these behavioral events are more or less

likely to occur in an interspecific context than others. No such trend is apparent in the present data.

Moreover, I do not distinguish here between displays against a neighboring male (very often duets) and against strange intruders (usually chases), although the distinction may be important.

MAPPING METHODS

Utilized space refers to the area occupied by a bird in a given time period while territory (in this paper) refers to an area defended by a bird.

I made composite maps of territories (see Chapter 15) by mapping those points at which territorial encounters occurred. If two males were counter-singing, the point midway between them was considered a boundary point unless there was evidence to the contrary. When two birds oriented song-flights parallel to each other, this was taken to indicate a boundary.

ANALYTIC METHODS

In each territorial encounter a donor and recipient were noted. A trespassing bird that elicited an aggressive response from a territorial male and then yielded was considered the recipient, while the territorial victor was considered the donor. The number of donors equals the number of recipients. In a two-species system, I arranged the data into four cells.

These tables could be analyzed as 2 x 2 contingency tables, where the two species were compared for the independence of roles (donor and recipient) in displays. The contingency tables were analyzed directly using the Sokal and Rohlf (1969) FORTRAN program for calculating the Fisher Exact Probability of 2 x 2 tables. Alternatively one can examine the data as terms of a binomial expansion, where the marginal values for each row and column are expressed as probabilities ($p + q = 1$), and the expected values for each cell are based on the product of the marginal values for its row and column (analagous to the use of a Punnett Square in genetics). The 3 x 3 tables were treated in this fashion, and the observed values were compared for goodness of fit to expected values by the G-statistic (Sokal and Rohlf 1969). This has the advantage over the Chi Square of being more easily partitioned and of being less sensitive

to small expected values. The end result is the same, however, as G-statistics closely approximate Chi Square values.

Finally, in any species system, where one is interested in a measure of the relative frequency of intra- vs. interspecific displays it is reasonable to combine the diagonal cells and to compare only autospecific and heterospecific interactions, unless evidence indicates that the species differ strongly with respect to participation in heterospecific displays. The results of this analysis are shown in Table 59. In tables and text that follow the following abbreviations are used:

M = MIL = MILITARIS

S = SUP = SUPERCILIARIS

D = DEF = DEFILIPPII

DEF-SUP = a display with defilippii (as donor) chasing superciliaris (recipient).

METHODS FOR BOUNDARY AND LENGTH CORRECTIONS

Application of the binomial expansion produces expected values which do not take into account the relative availability of conspecific and heterospecific males. Thus if both species are highly clumped, then only those males at the boundary of the two clusters would have the opportunity to take part in hetero-

specific encounters.

Correction for availability could utilize either the relative number of auto- and heterospecific boundaries for the two species or the lengths of these boundaries. Both types of correction were employed separately in this study.

Relative lengths of boundaries were measured on the maps using a map measure to determine lengths of defilippii-defilippii, defilippii-superciliaris, and superciliaris-superciliaris boundaries. Then the number of borders in each category was counted.

In the case of superciliaris and defilippii which showed interspecific territoriality, counting auto-specific and heterospecific borders proved no problem, but for defilippii and militaris where territories overlapped, it was necessary to treat each intersection of a border of one species with a territory of the other as a shared border.

Table 55 gives an example of correcting the expected values for the number of auto vs. hetero-specific boundaries. For each species the percentage of boundaries that are auto- and hetereospecific is determined, and these percentages are multiplied times the original expected values. The new expected values are totalled, and the original total is divided by the new total, yielding a coefficient. This coefficient is used to

multiply the provisional expected values to provide new expected values, as in the following equations.

EX=original expected values (EX_a=expected value for autospecifics)

PEX=Provisional expected values (EX_h=expected value for heterospecifics)

CEX=Corrected expected values

HB=Heterospecific boundaries

AB=Autospecific boundaries

C=Coefficient of correction

1. $$PEX_a = \frac{AB}{AB+HB} \times EX_a$$

2. $$PEX_h = \frac{HB}{AB+HB} \times EX_h$$

3. $$C = \frac{(EX_a+EX_h)}{(PEX_a+PEX_h)}$$

4. $$CEX_a = C \times PEX_a$$ and

5. $$CEX_h = C \times PEX_h$$

TABLE 55 An example showing application of correction factor for number of boundaries (autospecific vs. heterospecific).

	INTERACTIONS		BOUNDARIES		EXPECTED VALUES	
SPECIES	OBS	EX	Number	%	PROVISIONAL (PEX)	CORRECTED (CEX)
D - D	29	21.8	35	74	16.23	27.6
D - M	3	10.2	12	26	2.61	4.4
Total	32	32.0	47	100	18.84	32.0
C_d = (32/18.84) = 1.70						
M - D	1	8.2	12	67	5.49	8.8
M - M	11	3.8	6	33	2.00	3.2
Total	12	12.0	18	100	7.49	12.0
C_m = (12/7.49) = 1.60						

D = defilippii M = militaris

RESULTS

General Observations: P. militaris males were found in small numbers at many different localities and were considered to be solitary. Their territories were linear and they frequently used utility poles or fences for song perches, and are believed to require such elevated perches (Short 1968, see Chapter 15). Because

of the sparse population and the fact that usually only ends of territories are defended, encounters between male P. militaris are relatively infrequent.

P. defilippii and superciliaris, tend to occur in clusters or grouped territories. The territories are relatively small (<1.0 hectares), and at least for defilippii, this is related to the fact that they gather much food for young off the territory. These species do not require elevated perches, but utilize frequent flight songs in territorial maintenance and probably in mate attraction as well.

Territories of P. militaris frequently overlap those of the other two species, and mutual tolerance is usual with only occasional interspecific clashes observed. In some cases these were noted after an intraspecific clash, where one individual -- usually the loser -- seemed to redirect an attack at a heterospecific male.

I found that militaris frequently trespassed on areas defended by defilippii, usually without eliciting a response. Confirmation of lack of interspecific territoriality appeared when I trapped a male militaris and a male defilippii at the same place on the same morning, each responding only to a conspecific song. Playback experiments (Chapter 14) showed that males of either species had a low tendency to respond to heterospecific song, compared to their responses to conspecific

song.

Males of defilippii and superciliaris generally maintained non-overlapping territories, and defilippii, frequently chased or displayed against superciliaris males along shared territorial borders. Prolonged countersinging or other territorial displays were infrequent at heterospecific boundaries compared with autospecific boundaries, but both species attacked overflying males regardless of species. Two sets of observations were analyzed.

SAMPLE A. militaris vs. defilippii (1970)

Data were obtained between Nov. 8 and Dec. 14, 1970 as follows, (divided into weekly samples):

First Week: Nov. 8-13, north and east of Bahia Blanca. Eight localities had both species displaying. Second Week: Nov. 14-20, Estancia La Saudade, two samples totalling about 360 minutes, in late morning and mid-afternoon, when territorial activity was low. Third Week: Nov. 21-22 at Bahia Blanca, a.m. and p.m., totalling 390 minutes. Fourth Week: Dec. 11-14, at La Saudade.

The data are presented in Table 56 as 2 x 2 contingency tables for the four week samples and the pooled sample. Each was analyzed for independence by Fisher Exact Probability (2-tailed; designated FEP2),

and then expected values for each class of interaction were computed from a binomial expansion and tested with G-statistic. Finally, for each sample and the total, the significance of the preponderance of autospecific displays was tested by a G-statistic. In all samples, there was a significant lack of interspecific aggressive displays.

SAMPLE B. P. militaris vs. defilippii (1971)

At Bahia Blanca, part of two days (Oct. 18 and Nov. 9, 1971) were devoted to observing interspecific aggression among 2 or 3 militaris and about 10 defilippii, on territories that were approximately mapped (fig. 14). Table 57a gives the observed and expected results for the two days and the total sample, and both show significant departures from independence, with a significant lack of interspecific (heterospecific) displays.

The territories mapped near Bahia Blanca showed extensive overlap between the three male militaris and the 11 male defilippii studied. Comparing the observations of 18 October with those of 9 November, there were fewer males (2 militaris and 9 defilippii) and fewer interactions (.095/minute compared with .25/minute) on the latter date. These observations were made both later in the day and later in the season, which may account in part for the reduced rate of interaction.

TABLE 56. Territorial interactions of *militaris* and *defilippii* (group A data) at various localities in Buen. Aires Province. Donor listed across top, recipient listed down the side. Fisher Exact Probability (cumulative, 2-tailed) designated as FEP 2=.

	WEEK 1		WEEK 2		WEEK 3		WEEK 4		POOLED SAMPLE	
	DONOR									
	DEF	MIL	DEF	MIL	DEF	MIL	DEF	MIL	DEF	MIL
DEF	212	7	53	1	133	0	118	4	516	12
MIL	4	32	1	6	2	8	8	17	15	63
TOTAL	216	39	54	7	135	8	126	21	531	75
	FEP2<.000001		FEP2=.000002		FEP2<.000001		FEP 2<.00000001		FEP2<.00000001	

Same data presented by species-interaction, with expected values based on the product of the marginal probabilities, multiplied by the total interactions for the sample. G-statistic has a chi-square distribution with three or one degrees of freedom.

	WEEK 1		WEEK 2		WEEK 3		WEEK 4		POOLED	SAMPLE
	EXP	OB	EXP	OB	EXP	OB	EXP	OB	EXPECTED	OBSERVED
DEF-DEF	185.5	212	47.8	53	125.6	133	104.6	118	462.7	516
DEF-MIL	30.5	4	6.2	1	9.4	2	21.4	8	68.3	15
MIL-DEF	33.5	7	6.2	1	7.4	0	17.4	4	65.3	12
MIL-MIL	5.5	32	0.8	6	0.6	8	3.6	17	9.7	63
G-statistic (df=3)	131.1		25.1		42.3		47.4		262.9	
AUTOSPECIFIC	191.0	244	48.6	59	126.2	141	108.2	135	472.4	579
HETEROSPECIFIC	64.0	11	12.4	2	14.8	2	38.8	12	133.6	27
G-statistic (df=1)	80.8		15.6		19.7		31.6		149.3	
Probability	<.000001		<.0005		<.00001		<.00001		<.0000001	

TABLE 57. Analysis of two day sample of territorial interactions between P. militaris and P. defillippii near Bahia Blanca (10/18/71 and 11/9/71): Goodness of fit of observed data to uncorrected and corrected values. (1 degree of freedom unless otherwise indicated). (D=DEF=P. defillippii and M=MIL=P. militaris)

		OCTOBER 18 (9:15–10:25 A.M.)			NOVEMBER 9 (4:05–5:30 P.M.)			COMBINED		
a.	INTERACTION	OBS	EXP		OBS	EXP		OBS	EXP	
	D – D	29	21.8		15	12.0		44	33.8	29.33
	D – M	3	10.2		1	4.0		4	14.2	G=42.4
	M – D	1	8.2	G=28.4 df=3 p<.0001	0	3.0	G=15.0 df=3 p<.005	1	11.2	df=3 p<.00001
	M – M	11	3.8		4	1.0		15	4.8	
		FEP=.000002			FEP 2=.002			FEP 2 .000001		
	CONDENSED INTERACTIONS	(Uncorrected)								
	Autospecific	40	25.6	G=23.5	19	13.0	G=10.5	59	38.6	G=38.8
	Heterospecific	4	18.4	p<.0001	1	7.0	p<.005	5	15.4	p<.00001
b.	CORRECTIONS FOR NUMBER OF AUTO vs. HETERO SPECIFIC BOUNDARIES									
	Autospecific	40	29.7	G=13.6	19	15.8	G=4.01	59	45.4	G=17.8
	Heterospecific	4	14.3	p <.001	1	4.2	p<.05	5	18.6	p<.0001
	CORRECTIONS FOR LENGTHS OF AUTO vs. HETERO SPECIFIC BOUNDARIES									
	Autospecific	40	29.3	G=15.1	19	16.1	G=3.57	59	49.6	G=9.9
	Heterospecific	4	13.7	p<.001	1	3.9	p>.05	5	14.4	p<.005

	DEF	MIL	DEF	MIL	DEF	MIL
Number present	30+	5	20+	4	—	—
Number observed	11	3	9	2	—	—
# Displays as "donor"[c]	32	12	16	4	48	16
# Autospecific borders	35	6	31	4	(34)	(5)
# Heterospecific borders	12	12	6	6	(10)	(10)
Length autosp. borders	.73	.32	.74	.29	(.73)	(.21)
Length heterosp. borders	.27	.68	.26	.71	(.27)	(.79)

[c]= this value used to weight daily values in calculation of numbers and lengths of borders in combined daily sample (numbers in parenthesis).

TABLE **58.** Territorial interactions of *Pezites defilippii* =(DEF) and *Leistes m. superciliaris* = (SUP) at Estancia La Saudade (G statistic for goodness of fit, df=3).

INTERACTION	OBSERVED	EXPECTED	No. of BOUNDARIES	RELATIVE LENGTH	CORRECTED by number	EXPECTED VALUES by length
		AREA Z		NOVEMBER 1970		
DEF - DEF	22	18.6				
DEF - SUP	9	12.4				
SUP - DEF	2	5.4	N O T M A P P E D			
SUP - SUP	7	3.6				
	G = 6.90					
		AREA A		OCTOBER 1971		
DEF - DEF	68	55.8	14	25	57.4	54.5
DEF - SUP	33	45.7	13	26	43.6	46.5
SUP - DEF	9	21.7	13	26	13.5	15.1
SUP - SUP	31	18.0	8	19	26.5	24.9
	G = 23.3					
		AREA B		NOVEMBER 1971		
DEF - DEF	51	44.3	26	48	45.5	48.3
DEF - SUP	15	21.7	24	36	20.5	17.7
SUP - DEF	2	8.7	24	36	11.6	11.4
SUP - SUP	11	4.3	6	10	1.4	1.6
	G = 18.1					

TABLE 59. Auto vs. heterospecific displays and single species goodness of fit tests to uncorrected and corrected expected values for encounters between P. defilippii = (DEF) and L. m. superciliaris = (SUP). 'Uses G statistic with df=1).

INTERACTION	AREA Z OBS	AREA Z EXP	AREA A OBS	AREA A EXP	AREA B OBS	AREA B EXP	TOTAL OBS	TOTAL EXP
Autospecific	29	22.2	99	73.8	62	48.3		
Heterospecific	11	17.8	42	67.4	17	30.4		
G Statistic	4.9		18.4		11.2			

INTERACTION	OBS	EXPECTED VALUES Unc.	Unc. No. Length		INTERACTION	OBS	EXPECTED VALUES Unc.	No. Length	
					AREA Z				
DEF - DEF	22	18.6			SUP - SUP	7	3.6		
DEF - SUP	9	12.4			SUP - DEF	2	5.4		
G STATISTIC	1.6				G STATISTIC		5.3		
					AREA A				
DEF - DEF	68	55.8	57.4	54.5	SUP - SUP	31	18.0	13.5	15.1
DEP - SUP	33	45.7	43.6	46.5	SUP - DEF	9	21.7	26.5	24.9
G STATISTIC		5.4 *	4.7 *	7.4 *	G STATISTIC		17.3 ***	32.0 ***	26.3 ***
					AREA B				
DEF - DEF	51	44.3	45.5	48.3	SUP - SUP	11	4.3	1.4	1.6
DEF - SUP	15	21.7	20.5	17.7	SUP - DEF	2	8.7	11.6	11.5
G STATISTIC *		3.3	2.3	0.6	G STATISTIC		14.8 ***	37.9 ***	35.9 ***

Probability levels: * p<.05 ** p<.01 *** p<.001

					POOLED RESULTS (A & B)				
DEF - DEF	119	102.9	102.8	100.1	SUP - SUP	42	25.0	26.6	26.7
DEF - SUP	48	64.1	64.2	67.4	SUP - DEF	11	28.0	26.4	26.0
G STATISTIC		6.82 *	6.91 *	8.57 **			23.0 ***	19.1 ***	19.1 ***

TABLE 60, Alternative non-random models for observed (uncorrected) frequencies of auto and heterospecific displays between Pezites defilippii = (DEF) and L. m. superciliaris = (SUP)

INTERACTION	OBSERVED #	OBSERVED % for sp.	EXPECTED Random	FREQUENCIES ACCORDING TO NEW MODELS DEF 33% SUP 20%	DEF 20% SUP 20%	DEF 20% SUP 10%	DEF 33% SUP 10%
				AREA Z			
DEF - DEF	22	71%	18.6	20.8	24.8	24.8	20.8
DEF - SUP	9	29%	12.6	10.8	6.2	6.2	10.8
SUP - DEF	2	22%	5.4	2.2	2.2	1.1	1.1
SUP - SUP	7	78%	3.6	6.8	6.8	9.9	9.9
G STATISTIC			6.9	.79	1.46	1.02	3.27
				AREA A			
DEF - DEF	68	67%	55.8	67.3	80.8	80.8	67.3
DEF - SUP	33	33%	45.7	33.7	20.2	20.2	33.7
SUP - DEF	9	23%	18.0	8.0	8.0	4.0	4.0
SUP - SUP	31	77%	21.7	32.0	32.0	36.0	36.0
G STATISTIC			23.3	.17	9.1	14.3	5.3
				AREA B			
DEF - DEF	51	77%	44.3	44.0	52.8	52.8	44.3
DEF - SUP	15	23%	21.7	22.0	13.2	13.2	21.7
SUP - DEF	2	15%	8.7	2.6	2.6	1.3	1.3
SUP - SUP	11	85%	4.3	10.4	10.4	11.7	11.7
G STATISTIC			18.1	3.75	0.48	0.66	3.65

TOTAL OBSERVED PROPORTIONS

	Observed	% for species	% for All
DEF - DEF	141	71%	54%
DEF - SUP	57	29%	22%
SUP - DEF	13	21%	5%
SUP - SUP	49	79%	19%
AUTOSPECIFIC	190	——	73%
HETEROSPECIFIC	70	——	27%

TABLE 61. An alternative non-random model for observed (uncorrected) frequencies of displays involving militaris and defilippii data.

Group B Data 1971

INTERACTION	OBSERVED	EXPECTED RANDOM	EXPECTED DEF 20% MIL 10%	EXPECTED DEF 10% MIL 10%	EXPECTED DEF 5% MIL 10%
DEF - DEF	44	33.8	38.4	43.2	45.6
DEF - MIL	4	14.2	9.6	4.8	2.4
MIL - DEF	1	11.2	1.6	1.6	1.6
MIL - MIL	15	4.8	14.4	14.4	14.4
G STATISTIC (df=3)		42.4	5.26	0.44	1.22

Group A Pooled Data 1970

INTERACTION	OBSERVED	EXPECTED RANDOM	EXPECTED DEF 20% MIL 10%	EXPECTED DEF 10% MIL 10%	EXPECTED DEF 5% MIL 10%
DEF - DEF	516	426.6	424.8	477.9	504.5
DEF - MIL	15	68.3	106.2	53.1	26.5
MIL - DEF	12	65.3	7.5	7.5	7.5
MIL - MIL	63	9.7	67.5	67.5	67.5
G STATISTIC (df=3)		262.9	144.6	43.8	8.8

In this sample, corrections for the number of shared boundaries and for their relative lengths, both reduced the G-statistic, indicating that the corrected expected values were more closely fit by the observed data. However, the deviations from expected were still highly significant ($p<.05$) and the effect of both corrections was similar.

Figures 12 and 13 show two additional mapped plots and reveal extensive territorial overlap between the two species.

INTERSPECIFIC TERRITORIALITY BETWEEN DEFILIPPII AND SUPERCILIARIS

On one day in 1970 and two days in 1971 I examined the territorial interactions of P. defilippii and L. m. superciliaris on three study plots. These observations were made after I had discovered the strong similarities in territorial displays between the two species and the apparent lack of territorial overlap. Both species tended to nest in grouped territories, and at the time I was under the impression that they tended to nest together with more than chance probability (not substantiated statistically, see Chapter 16). My impression of the similarities between these two birds agrees with Wetmore's (1926).

RESULTS:

AREA Z, Saudade, 1970

Area Z was mixed pasture with various grasses, including clumps of Stipa sp. On 14 November 1970, I worked along 300 meters of fence, observing about 4 pair of militaris, 5 superciliaris, and 39 defilippii, although only about a third of the latter were close enough to examine in detail. Since the militaris figured in only 4 of the 44 displays, I reexamined the data without it (see Table 58).

The three species contingency table yields a Chi square =27 ($df=4$, $p<.001$), and shows that defilippii is the most outgoing of the three, accounting for almost none of the deviation and acting as if it failed to distinguish between conspecific males and superciliaris. Considering only these two species, there is still a preponderance of intraspecific displays, due to the fact that superciliaris infrequently attacked defilippii, but the deviation from expected is barely significant ($X^2=4.67$; $.025<p<.05$). On this study area the territories were not mapped in sufficient detail to permit corrections for boundaries.

AREA A, Saudade, 1971

This study plot in a wheat field was mapped in detail the last week of October, 1971. Attention was focused on 10 males of defilippii, 10 of superciliaris and 2 P. militaris. On 28 October 1971, I noted 153 encounters (see Table 59) among the three species. Observed and expected values were compared with a G-statistic and the encounters were found to deviate significantly from those predicted by chance ($G=65.1$, $df=4$, $p<.0001$). There were only 46 heterospecific encounters (33 of these were DEF-SUP) compared with an expected of 82.6, and the deficit in these encounters was again very significant ($G=35.7$, $df=1$, $p<.0001$) with a marked deficit in heterospecific displays ($G=19.2$, $df=1$, $p<.0001$). It is of interest that defilippii realized 33 DEF-SUP displays which is 72% of the expected value of 45.8, while superciliaris realized only 9 SUP-DEF displays, or 41% of the 21.8 expected.

From the territorial maps, the number and boundary lengths of autospecific and heterospecific boundaries for each species were computed and these were used to obtain corrected expected values. The results were compared against these (Table 59).

AREA B, Saudade, 1971

Area B was also in a Saudade wheat field, and was mapped in early November, 1971. Aggressive encounters among 7 superciliaris males and 12 defilippii males were tabulated on 13 November (see Table 58). The observed encounters differ significantly from those expected at random ($G=18.1$; $p<.00001$ with a deficit in heterospecific encounters (observed 17, expected 30.4, $G=11.2$, $p<.0001$).

The results from all three areas are in general agreement. Each species is more likely to indulge in autospecific than in heterospecific displays, but defilippii chases superciliaris almost as often as would be predicted by chance. Further modifications of the analysis are considered below.

EFFECT OF CORRECTIONS FOR BOUNDARIES

The expected values for areas A and B were corrected for the relative availability of conspecific and heterospecific males by considering the relative number and relative lengths of the two types of borders separately (see Table 58). In some cases the G-statistic was increased when the observed values were compared with the newly derived expected values, whereas in other cases the goodness of fit test was improved by

correction. Since a male surrounded only by conspecific males has little opportunity to attack heterospecific males (strangers only), it is important to utilize one or the other type of correction. These will yield different results only if there is a large discrepancy in the length of autospecific and heterospecific borders.

SPECIES COMPARISONS

To detect differences between *defilippii* and *superciliaris* the data for each as donor were analyzed separately (Table 59). Uncorrected and corrected expected values were the basis for goodness of fit tests, and in all cases the G-statistics for *defilippii* were lower (usually insignificant) than those for *superciliaris* (usually significant). Thus most of the badness of fit to the random model is due to the failure of *superciliaris* to chase *defilippii*. The overall G-statistic for uncorrected values was 10.2 for *defilippii* ($p<.001$) and 24.2 for *superciliaris* ($p<.000001$).

ALTERNATIVE MODELS

Thus far I have assumed that in perfect interspecific territoriality, encounters could occur at random, depending only on the relative number and activities of the two species. It would be as reasonable to postulate that these birds discriminate perfectly and never attack heterospecific males, or to postulate that a fixed percentage of the attacks of one species would be on males of another species. The perfect discrimination model is difficult to test, only because the standard goodness of fit tests are unable to handle expected values of zero (L. Marcus, E. Scheinberg, R. Calhoun per. comm.). I test several of these alternative models which seem reasonable based on the currently available data. I test models where either 20% or 33% of the defilippii displays are directed against superciliaris, and where 10% and 20% of superciliaris displays are directed against defilippii. These models are suggested by data where defilippii actually had 29% heterospecific displays and superciliaris 21%. Obviously new, independently derived data would be needed to test these models. A model predicting 33% and 20% heterospecific displays for defilippii and superciliaris is well fit by the observed data. For militaris-defilippii data a model of 10% heterospecific displays for each

species is well fit, by the 1971 data, while a model of 5% heterospecific for defilippii and 10% for militaris is well fit by the 1970 data (Table 61).

DISCUSSION

Interspecific territoriality is of interest because it appears to represent an aberrant form of interaction, that tempts functional explanation. Brown (1969) pointed out that a functional approach to the study of avian territories was inappropriate, since it failed to consider the full diversity of territorial systems. The same applies in part to the study of interspecific territoriality. Attempts to understand its evolution or ecological function are of intellectual interest, but are presently premature since the diversity of interspecific territoriality and its prevalence are not adequately known. I consider here discussions by Orians and Willson (1964), Willson (1967), Moynihan (1968), Cody (1969, 1973), and Murray (1971).

Orians and Willson (1964) found that most reported cases of interspecific territoriality occurred among birds in structurally simple habitats. Willson (1967) described various aggressive encounters but in several cases it is likely that ecological segregation was the result of historical interspecific aggression, unstable

interspecific territoriality, and subsequent habitat shift as predicted by Murray (1971). Moreover, it is possible that differential habitat selection was primary and allowed species to coexist in the relatively simple but non-homogeneous habitats Willson studied, with minimal interspecific aggression.

Cody (1969) invokes a role for interspecific territoriality in facilitating coexistence among ecologically similar species. This would be important in simple habitats, where the opportunity for other forms of displacement are minimized.

Although theoretically interspecific territoriality is a way of partitioning usable habitat and could thereby stand as an alternative to competitive exclusion or character displacement it is not documented whether it actually functions to allow stable coexistence of ecologically similar forms. All of Cody's examples are open to question. Murray's model (1971) of interspecific territoriality involves misdirected aggression which rather than allowing stable coexistence, would force the submissive species into less suitable habitat, perhaps eventually resulting in changes in habitat preference, stable spatial separation, and decline in opportunity for interspecific aggression. One can argue that a behavior pattern which has the effect of reducing competition between two species (as with <u>defilippii</u> and

superciliaris) can not be considered "misdirected". Simmons (1951a) discussed the adaptiveness of such behavior in minimizing competition, and Lanyon (1956a) applied this same idea to the North American meadowlarks which show apparently perfect interspecific territoriality, where their preferred habitats meet.

Another aspect of Murray's hypothesis is that interspecific territoriality is maladaptive because of the implied "waste" of time and energy in attacking heterospecific individuals. However, taking Grant's idea of hexagonal territories (1968) as the end result of packing many birds into one habitat, a territorial male will have six neighbors regardless of how many conspecific and heterospecific. To the extent that the two species are similar in their overall demands, their population in sympatry would equal the population that either species could maintain in the absence of the other. Thus it is possible that there will be no increased time-energy expenditure in sympatry (unless the combined total of the two species is greater). This would need to be quantified and the time-energy budget calculated in such a way, that aggression against conspecific and heterospecific birds could be compared. Because of the risk of stolen matings, it is preferable to have ones territory surrounded by heterospecific males who presumably cannot fertilize the female. This advantage to

interspecific territoriality probably cannot lead to its evolution, however.

Moynihan (1968) and Cody (1973) have proposed that selection for convergence in appearance (particularly color pattern and voice) can occur to promote certain species interactions. Moynihan (1968) was concerned mainly with species interactions in mixed flocks, while Cody (1969, 1973) has stated that convergence to promote interspecific aggression, has arisen among ecologically similar species, to allow them to coexist. Cody (1973) analyzes several avian groups which he believes demonstrate character convergence, but field studies and detailed studies of geographic variation have yet to be performed. Since most cases of interspecific territoriality thus far reported (see Cody 1973) remain to be adequately studied and also involve species more closely related than Cody acknowledged.

It is reasonable to believe -- although there is little evidence available -- that close similarity is essential for interspecific aggression, since for any species there would be a fairly discrete range of signals that would elicit (or release) aggressive behavior. This belief is the basis for Cody's hypothesis that competing species, where they become sympatric, could show morphological convergence with respect to just such releasers.

However, it is also true that closely related

species are often very similar in appearance, and the occurence of interspecific territoriality could be interpreted as confirmation of close relationship rather than of convergence. The ultimate test depends on delineating the relationships between the forms in question based on characters other than those signals that might function in interspecific aggression. Thus far the documented cases of interspecific territoriality appear to involve closely related species, and a demonstration of convergence is wanting.

An unexpected result of the field work was the observation of interspecific territoriality between defilippii and superciliaris, but not between defilippii and militaris. Since the latter pair, but not the former, had been considered congeneric, and since most interspecific territoriality involves congeners (in the present use of the term) (see for example Cody 1973), the reverse interaction would have been predicted.

These results are, however, of only limited value in clarifying the hypotheses put forth by Murray (1971) and Cody (1973). To test Murray's hypothesis one would want species A and B to have similar habitat requirements, to engage in aggression when they become sympatric, and to secondarily acquire new habitat preferences. To test Cody's hypothesis, one would want to see two species that are not very closely related, demonstrate morphologic

or behavioral convergence related to agonistic signalling, where the two become sympatric. The meadowlarks only partially fulfill these criteria.

My observations on militaris outside the pampas indicate that its habitat utilization differs from that of defilippii. If it is, as seems likely, a recent invader of the pampas, the different habitat utilization and territorial arrangements may have existed prior to and may have facilitated sympatry. Thus far there is no evidence of character divergence (see Chapter 18) between the two species on the pampas, and it is uncertain to what extent their differences may have been enhanced in sympatry. Such enhancement is plausible, because data on food utilization (see Chapter 16) reveal similarities. Yet direct observation reveals that aggression between the two species, is infrequent.

Morphological examination of the forms of Leistes compared with defilippii give no evidence of either character convergence or divergence.

The fact that L. m. militaris in northern South America engages in flight displays and has similar vocalizations (see Chapter 11) although far removed from other red-breasted meadowlarks, suggests that behavioral similarities between superciliaris and defilippii should not be considered convergent, but reflect the close relationship emphasized by Short (1968).

Quantifying the relative contribution of two species to interspecific territoriality can provide a single index value of equivalence. One can look at all heterospecific encounters and determine how many of these have species A or B as a donor. The percentage contributions of the species can be multiplied together, and the highest product occurs when each species makes equal contribution. (If $p + q = 1$, the maximum value of pq is achieved when $p = .5$).

The product ranges from zero (only one species is the donor in interspecific displays) to 0.25 (both species participate equally). The application of such an index to different meadowlark localities will require more data, but such an index could be compared across many species systems, against other similarity measurements, such as percent difference on size, or some similarity coefficient (e.g., Mahalanobis D^2 statistic from multiple discriminant function analysis). If Cody's suggestion (1969, 1973) that increased similarity enhances interspecific aggression, is important, one would expect to see a correlation between increasing index of equality and increasing index of similarity.

The main result of this study is to indicate the complexity of the situation, and the inadequacy of the usually published data (including some of the data in this study) in testing the main hypotheses related to

interspecific territoriality. It reaffirms Brown's (1969) point, that the diversity of interactions must be studied in detail.

The rapid habitat changes occurring in many parts of the world, for example the forested areas of northern South America, may result in many new cases of sympatry, and may afford many new opportunities to examine the effects of sympatry and potential competition on morphology and behavior.

SUMMARY

1. Interspecific territoriality is the defense of a resource, usually the breeding area, against members of another species. It may be mutual, with members of both species treating heterospecifics and conspecifics in a similar fashion, or it may be one-sided.

2. Lanyon documented nearly mutual interspecific territoriality for the Eastern and Western Meadowlark, and in the present study a more one-sided relationship has been demonstrated for defilippii and superciliaris on the the Argentine pampas, where they occur in the same habitats. This phenomenon could be documented clearly in wheat fields which offer a nearly uniform environment, and it is not known whether interspecific aggression or differential habitat selection will operate in areas of

non-uniform vegetation. Examination of their interaction in non-uniform areas would allow a test of Murray's model.

The general similarity in color pattern, vocalizations, and flight display between the two species probably play important roles in the interspecific territoriality, while the size difference probably accounts for the unilateral aggression.

3. P. militaris and defilippii populations on the pampas differ in social structure, behavior and habitat utilization and have broadly overlapping territories. Interspecific aggression is infrequent relative to the opportunity for interaction and to the frequency of such interactions between defilippii and superciliaris.

4. Even between superciliaris and defilippii there is a substantially lower frequency of interspecific aggressive encounters than is predicted by a random model, and this difference is mainly, but not entirely, due to the failure of superciliaris to chase defilippii.

5. The relative frequencies of auto- and heterospecific encounters can be compared with random models or models of fixed probabilities by goodness of fit tests in a manner which allows the comparison of one species system with another or of the role of the two species

within the system.

6. Since the probability of an interspecific display is a function not only of the individual and species but of the relative availability of males of different species, correction factors can be employed. In the present study, such corrections usually, but not always improved the goodness of fit.

7. Quantitative study of the frequency of interspecific aggression and of the equivalence of participation by both species, will allow one to determine whether morphological differences, particularly the size differences suggested in this study, are importatn factors in a system of this sort. Such data could also be compared with similarity measures of morphology to provide a test of the hypothesis of adaptive convergence.

8. The data from the present study are in part consistent with Murray's model, although within the area studied there was no evidence that the submissive species was being forced into suboptimal habitat by interspecific aggression. An adequate test of Murray's hypothesis would require productivity studies in different habitats to determine whether for the species in question, habitats could be ranked by suitability.

SECTION VI. EVOLUTION AND CONCLUSIONS

Chapters 22 - 24

22. Geographic Variation and Meadowlark Taxa
23. Speciation and Relationships
24. General Summary and Conclusions

In this section I review the taxa of red-breasted meadowlarks and consider some of the patterns of geographic variation in morphology. Chapter 23 deals with relationships and phylogeny within the meadowlark assemblage, and several hypothetical phylogenies are presented (figure 25) to account for similarities among taxa. Clarification of phylogeny requires a detailed study based on many characters within the assemblage and also among close relatives outside the assemblage. Chapter 24 summarizes the major findings in this study.

CHAPTER 22 GEOGRAPHIC VARIATION AND MEADOWLARK TAXA

TAXA OF RED-BREASTED MEADOWLARKS

In this chapter I review certain aspects of the similarities and differences in the taxa of Red-breasted Meadowlarks. I will consider the nature of geographic variation and the subspecies of meadowlarks, as well as the differences between species. Although as a formal taxonomic category the subspecies has come under attack, I will continue to utilize it in this report. Wilson and Brown (1953) demonstrated the difficulties in applying the subspecies concept. However, I think that once a population is recognized as distinctive, giving it a subspecific name may be of value in calling attention to its existence and encouraging further study. It will be no surprise to me, if in most cases the named subspecies eventually prove inadequate to describe geographic variation, but until refined studies are undertaken, subspecies designations are useful. As used here, a subspecies is a geographically continuous assemblage of populations which form a recognizably distinct subdivision of a species. Mayr (1963) defines it as an aggregate of local populations of a species inhabiting a geographic subdivision of the species range, and <u>differing taxonomically</u> from other populations. The

latter phrase presumably refers to significant difference based on morphologic or other characters.

Appendix IV contains data on the morphometric analyses of various meadowlark taxa. Table 50 indicates the shape ratios of the different taxa, (see figure 22). Finally, Table 62 summarizes miscellaneous aspects of meadowlark biology, to clarify similarities and differences.

MILITARIS

The clinal variation in Chile and Argentina has already been described. The northern ends of the clines are quite similar to each other, and although isolated by the highest part of the Andean chain, there is as yet no means of distinguishing them. The race falklandicus is large, long-tailed and long-billed and is characterized by a somewhat spatulate tip to the bill. It is similar in many respects to birds from Tierra del Fuego, and if a greater number of specimens in comparable plumages was available, it might turn out that this form is not consistently distinguishable from mainland birds.

Zotta (1937) described catamarcanus from Corral Quemado, southwestern Catamarca as "bien distinto" characterized mainly by its paler coloration above and below. This form occurs in river valleys on the very arid

TABLE 62. Summary of meadowlark characteristics: comparisons of major taxa.

CHARACTER	STURNELLA		PEZITES			LEISTES (MILITARIS)	
	NEGLECTA	MAGNA	MILITARIS	BELLICOSA	DEFILIPPII	SUPERCILIARIS	MILITARIS
RANGE							
North America	yes	yes					
n. South America		yes					yes
Tropical S. America		marginal				yes	yes
Pacific Coast			yes	yes		once	
South Temperate			yes		yes	yes	
SYMPATRY WITH	magna	neglecta L.m.militaris	superciliaris defilippii	none	superciliaris P.militaris	defilippii militaris	magna
SEXUAL DIMORPHISM (P=plumage, S=size)			P S=1.2	P S=1.2	P S=1.2	P S=1.1	P S=1.1
Underpart Color	yellow	yellow	red	red	red	red	red
Underwing Color	white	white	white	white	black	black	black
Regular flight display	yes	no	no	yes	yes	yes	yes
Usual 1° Song perch	<2m	<2m	>2m	<2m	<1m	<2m	<2m
Role of Warbled song	flight song	rare flight	rare flight	flight song	sex chase	sex chase	unknown
Rectangular terminal buzz to 1° song				yes	yes	yes	yes
Repertoire Size for 1° song	c7	>15	5-12	1-4	1	unknown	unknown

eastern slope of the Andes, in areas drier than those occurring near Bariloche. One would predict the paler coloration from Gloger's rule, although birds of eastern Patagonia also inhabit very dry climates but are darker than catamarcanus. In central Catamarca I found a population of birds with both pale and intermediate forms, suggesting intergradation between nominate militaris and catamarcanus. This location in the valley of the Rio Santa Maria is isolated by a high dry plateau from the Rio Belem, although the distance is only 30 km. On this plateau I collected typical dark militaris with small gonads on 5 January 1971. These birds may have been migrants. It is interesting that Corral Quemado, the type of locality of catamarcanus is in the drainage basin of the Rio Belem, and a bird collected at this locality appeared to be typical of militaris, as were birds collected 100 km southwest at Tinogasta.

DEFILIPPII

Hudson (Sclater and Hudson 1888) and Wetmore (1926) gave clear indication of why this species differed from militaris and the latter author found the two together during the breeding season at Carhue (about 40 km northwest of Saudade). Blake (1968) treated them as conspecific, but Short (1968) found the two forms breeding

sympatrically near Bahia Blanca and northward. He recognized most of the differences between defilippii and militaris during his brief study of them, and the differences he mentioned are consistent. The differences in plumage and behavior are greater between these species then between magna and neglecta. The range is small and the birds quite homogeneous so that no geographical variation is evident at present.

BELLICOSA

This species has long been aligned with militaris primarily on the basis of the white wing linings. Surprisingly Zimmer (1930) mentions no difference between them (except for the shorter bill of bellicosa), although that form has a much shorter tail as well. Short (1968) pointed out several plumage features which differ from militaris, and treated bellicosa as a separate species. On plumage and shape, bellicosa is at least as distinct as defilippii. Its vocal behavior also suggests that it is distinct, although it approaches catamarcanus with respect to flight song behavior. Its primary song, however, is unlike militaris and is more similar to defilippii (Chapter 10). Interestingly, Zimmer (1930: 435) remarked on the similarity of primary songs of bellicosa from Huanuco, to S. magna. The flight song

is very similar to that of S. neglecta in my experience.

This species is characterized by white feathering on thighs and lower abdomen. Philippi and Landbeck (1861) described the form albipes from Arica in extreme northern Chile (present day map). This form was described as even whiter than typical Peruvian and Ecuadorian birds. Bond (1953) noted that specimens from southern Peru were more pink (less scarlet) below and that females had hardly any pink on their underparts, and he referred these to albipes. His specimens were mainly in fresh plumage, and having compared worn specimens from southern Peru with worn specimens from central Peru, I am unable to recognize any differences. If the subtle differences are consistent, then application of spectrophotometric techniques may confirm the distinctiveness of albipes.

Zimmer (1930) commented on possible distinctiveness of birds from the mountains of central Peru, and actually prepared a description of P. b. rufigula from Huanuco (M.S. in A.M.N.H.). He apparently changed his mind, however, and the description was never published. The chief difference is in the pink throats of the females (a consistent character, but one approached in occasional females from other parts of Peru). Close examination indicates that males from Huanuco, Cajamarca, and other montane localities may have a slightly more orange tone

to the underparts than do coastal birds, but the difference is very subtle. This will be examined in the future with reflectance spectrophotometry. In my statistical analyses I found that montane birds averaged significantly larger than coastal birds, and since they are isolated in montane valleys, it may prove desirable to recognize this form by name.

For completion it is worth mentioning that Cabanis (1851) described the form brevirostris which he attributed to southeastern Brazil. Zimmer (1930) notes that the characters coincide with those of bellicosa.

LEISTES M. MILITARIS AND L. M. SUPERCILIARIS

The northern form (militaris) and the southern form (superciliaris) differ in shape of bill which is stouter in the latter (see Appendix IV), in the eyeline (which is almost always absent in the former), and in the red bend of wing of militaris. The northern form extends to about 5°S latitude, occurring south of the Amazon, and reaching Maroins in northern Matto Grosso (Naumberg 1930). It is separated by about 5-10° of latitude from the range of superciliaris. In eastern Brazil it extends southward to the Maranhao coast, (Hellmayr 1929); in western Brazil it occurs on the Rio Purus (Gyldenstolpe 1951).

With the exception of birds from northwestern Venezuela, Colombia, Panama and Trinidad, militaris averages larger than superciliaris. The few specimens from eastern Ecuador are large, suggesting that it was colonized along the Amazon, rather than from Colombia.

Superciliaris occurs in central Brazil southward to the vicinity of Bahia Blanca. In mountains it ranges up to over 4000 m in Bolivia (e.g., Gyldenstolpe 1945). It is not known whether birds of this form occur in Maranhao, but it occurs in Ceara (Hellmayr 1929). Near Recife (8° S. lat.) Lamm (1948) reported that it was common. It occurs westward to the lowlands of eastern and highlands of central Bolivia, perhaps to Peru. Both forms of Leistes have been reported in eastern Peru; L. m. militaris was apparently present near Xeberos, Amazonas (Peru) in numbers at one time (see Sclater and Salvin 1873:267), and Hellmayr (1919) reports on three specimens of superciliaris from Yahuarmayo (13°18' S x 70°18' W), Puno. Near Pucallpa, Loreto, where I judged that perhaps 500 sq. mi. of forest have been cleared, and where several species from the open country of Bolivia have recently been found (D. Pearson pers. comm.) I spent five days in a vain search for Leistes.

There is currently no evidence that the two forms are anywhere in contact, although it seems reasonable that they might meet in the vicinity of the Rio Santa

Maria (western Amazonas) or in Maranhao. The likelihood of their meeting in the present century seems guaranteed by extensive destruction of Amazonian forests. Haffer (1959) and F. C. Lehmann (pers. comm.) noted the advance of Leistes in western Colombia follwoing forest destruction, and I found it common at several localities in the Cauca Valley in 1973, although it had been unknown there 25 years earlier. L. Kiff (pers. comm.) indicates that L. m. militaris has recently appeared in southwestern Costa Rica, along with several other open-country species.

Goodall et al. (1957) mention that there is a Chilean specimen of superciliaris taken at 3000 m in Coquimbo. There are no other records for Leistes west of the Andes, and the provenance of this specimen would be very interesting since no Leistes has been encountered there subsequently.

Short (1968) compared bill shape differences between the two forms, and suggested that superciliaris was sufficiently different to be considered a separate species. Results of statistical analyses are consistent with either interpretation. On multiple discriminant analysis, the five populations of militaris and five populations of superciliaris, showed only about 10% overlap when plotted against the first two discriminant axes (figure 21). I did not find any apparent differences

in behavior between the two forms. However, there are differences in voice, consistent with the existence of two species. In view of the considerable intraspecific variation in primary song for both forms, I cannot presently evaluate the songs as species characters. Moreover, my attempts to test *Leistes* with playback experiments have not yet been successful. At present it seems a moot point whether the two are best treated as one or two species. Throughout this paper I have considered them conspecific, but any additional comment should be deferred pending more extensive examination of their biology or, if possible, their interaction when they come into contact.

It is worth mentioning that a form *erythrothorax* (Pelzeln, 1870) was described from the Rio Madeira. Hellmayr (1910) treated it as *L. m. militaris*, while Gyldenstolpe (1951) suggested that it might be distinct. Morphometric examination reveals that Amazonian birds do average larger than other *L. m. militaris* specimens, but the nature of the variation is unknown at present and it seems pointless to recognize the Amazonian birds as distinct.

Another form, *petilus* (Bangs 1911) was named from Entre Rios, but Wetmore (1926) did not consider it distinct. The morphometric analysis emphasizes the uniformity of *superciliaris* and I could distinguish no

color variants.

SUMMARY

This chapter has briefly considered rationales for taxonomic treatment of the red-breasted meadowlarks at the species and subspecies level. Short's (1968) suggestion that *bellicosa* and *defilippii* are not conspecific with *militaris* was amply confirmed in this study. The evidence concerning *L. m. superciliaris* was less clear however. The validity of the forms *P. b. albipes* and *P. m. falklandicus* is questioned.

CHAPTER 23 SPECIATION AND RELATIONSHIPS

The geographic isolation model of speciation, wherein physically isolated populations gradually accumulate genetic differences to the point of becoming reproductively isolated (with or without concomitant morphologic distinctiveness) is now widely accepted, having been championed by Jordan (1896) among others, and Mayr (1942, 1963). Models of sympatric speciation have been proposed from time to time and cannot be entirely discarded (although see Mayr 1963 to the contrary). J. Maynard Smith (1966) has discussed the theoretical constraints for sympatric speciation models. Payne (1973) discussed the foster-specific brood parasitism of Indigobirds on Firefinches in Africa, a situation which tempts interpretation as sympatric speciation. He carefully relates the possible accumulation of certain differences in sympatry to the probable occurrence of geographic isolation, presenting the observed species distributions as an interaction of the two factors. The occurence of speciation in sympatry would require an intrinsic barrier to gene flow, and since in birds there are almost no studies relevant to gene flow and since birds are highly mobile, the geographic model can be accepted for the present as the common mechanism.

The degree of differentiation and the existence of

speciation can be measured after the extrinsic barrier has disappeared and secondary contact has occurred. The strongest degree of speciation would involve a pre-existent pre-mating isolating mechanism. The slightest degree would involve minor differences, with no disadvantage accruing to hybrids. A moderate degree would involve disadvantage of hybrids. In the first case speciation has occurred; in the second case it has not and the differences are likely to be swamped. In the third case, reinforcement of isolating mechanisms, an event proposed on theoretical grounds by Fisher (1930) is likely to occur, with selection favoring adults that do not interbreed (Sibley 1961). Many variants of the second case, with complete swamping, gradual clines, steep clines, narrow hybrid zones, etc. have received attention in studies of avian speciation.

The reliance of militaris on elevated perches and its distribution in low woodland areas through southern and western Argentina suggests that it is a recent arrival on the pampas and that it has only recently come into contact with defilippii. Although the immediate history of that contact is lost, the behavioral, ecological, and morphological differences indicate that speciation was well-advanced at the time contact was reestablished. I have mentioned (see above) only two transient instances of mixed pairing and the possible

occurrence of a hybrid between the two species. A male defilippii courted a female militaris after I trapped her mate in the defilippii territory. This mixed pair persisted at least a half day, but was not apparent a week later. At Saudade, a defilippii male courted a militaris female while her mate was occupied at a decoy. She did not fly away nor did she take an active part in the display which consisted of rapid alternations between crouched and head-up postures by the male. The proceedings were interupted by the arrival of the militaris male and the departure of the defilippii male.

On 1 November 1971, in the Buenos Aires panhandle, about 40 km southwest of Bahia Blanca (kmp 742 on Rte. 3), I observed a female meadowlark which could not be identified. The bird had dark underwing linings typical of defilippii but had the distinctive pale throat of female militaris. Only militaris were present in the area, the nearest defilippii having been seen about 10 km to the north. I did not encounter any more defilippii as I drove southward, so this bird occurred at the extreme of the defilippii range. It was very wary and could not be collected, despite the fact that I collected 9 other specimens at the same spot (these were all on territory, however). It is possible that this bird was a hybrid, and its occurrence at the limit of the range of one species would be a classic situation for hybridization

between otherwise isolated species (e.g., Lanyon 1966). I never found any stable interspecific pairing, and it is safe to say that reproductive isolation is nearly perfect between them.

Lanyon (1966) discusses hybridization between the more similar, but reproductively isolated, Sturnella magna and neglecta. Hybrids occur when one species, thus far neglecta, pioneers new locations beyond the range of the species, where the opportunity to find a conspecific mate is negligible.

Sympatry between defilippii and superciliaris involves two well-defferentiated forms. I found no evidence of even transient mixed pairings between these, but since the female superciliaris spend much time out of sight, there were few instances when both members of a pair of superciliaris could be seen.

BIOGEOGRAPHY -- Leistes

The two forms of Leistes are presently separated by a forest belt in central Brazil. In view of the evidence for dynamic changes in the grassland-forest or arid-mesic vegetation during the Pleistocene (Haffer 1974, van der Hammen 1974, Vuilleumier 1971) it seems most reasonable to invoke isolation of a northern and southern form at a time of heavy forest advance. B. S.

Vuilleumier (1971) shows a map of inferred geological features during Wurm glaciation, with a large marine transgression overlying much of the Amazon basin. At the same time a transgression overlay the Parana-Paraguay basin, and may have contributed to speciation in the southern meadowlark range.

The most extensive speculation on the evolutionary history of South American savannah birds is provided by Haffer (1967c) who suggests that the savannah region of Brazil can be treated as a nucleus from which, during arid periods of expansion, open-country birds extended northwestward. The current distribution of Leistes is consistent with this suggestion. A non-differentiated population in central Brazil undergoes expansion, is divided by a marine or forest transgression and undergoes speciation with two new populations north of the Amazon and in southern Brazil. Haffer (1967b,c) provides a map indicating how a savannah form might spread from the Orinoco into western Venezuela, then into northern Colombia. The continued extension of Leistes northward in Central America and southward in western Colombia (although due to habitat disturbance) continues the pattern of Haffer's reconstruction. This begs the question of what ancestral form a pro-Leistes might evolve from and where the development might have occurred.

Assuming that Pezites and Sturnella had a common

ancestor (whether or not it resembles Leistes is not relevant), the same mechanism can be invoked for splitting the ancestral population into two isolates which gave rise to a northern yellow-breasted and a southern red-breasted form.

BELLICOSA

In Chile, bellicosa and militaris are separated by the Atacama desert. Populations of bellicosa occur along the Peruvian coast into Ecuador, wherever suitable habitat occurs. To the east, the main Andean chain effectively isolates bellicosa for its entire length, yet the species also occurs in scattered pockets in many inter-Andean valleys from Huanuco north to Ecuador. Moutains extend at least to 4500 m (15,000'), and certainly meadowlarks do not currently cross them.

It seems unlikely that the contact across the Andes dates back to the Pliocene uplift, and even since the uplift it is not likely that mesic habitat would have bridged the montane and coastal regions (B. S. Vuilleumier 1971), while the present conditions are too dry to support grassland on the mountain slopes.

The evidence points to a former contact across mountain passes. Chapman (1917, 1926), Koepcke (1961), Vuilleumier (1969) have shown that birds could have

crossed the low Porculla Pass (2150 m) in northern Peru, the Maranon route. Haffer (1967B) has pointed out that the Andes probably reached their present height in the Pleistocene, and it is unclear whether the pass was actually lower at the time of contact.

The distribution of bellicosa near Huanacabamba, in the Maranon Valley (at Bagua, T. Parker pers. comm.), in Cajamarca, and in Huanuco suggests that trans-Andean movement was via the pass and river systems. The isolation of birds at Huanuco may not have existed during drier times when contact could have been established northward along the Huallaga River.

It is not clear what direction the trans-Andean movement followed. There is no reason to assume that Peruvian bellicosa derived from Chilean militaris, or vice versa. Rather, both must have derived from populations dwelling east of the Andes. It seems reasonable to suppose that during alternations of dry and wet periods, birds from the lowland could have colonized the river valleys on the eastern face of the Andes. I was impressed, for example, by the occurrence of L. m. militaris at 3000 m (9900') on Cerro Munchique, Cauca Valley, Colombia, where the species is a recent arrival. The montane population would have been the source of the Pacific birds, which would presumably have reached the coast in northern Peru and then spread

northwards and southwards. The complex current distributional pattern of this species would be very interesting to examine, particularly in view of morphologic divergence in southern Peru and in the central Andes.

RELATIONSHIPS AMONG THE MEADOWLARKS

A study of the evolutionary relationships of the meadowlarks both within the complex and between the complex and its nearest relative is beyond the scope of the present study. A more detailed anatomical examination of the meadowlarks and related forms would be required for such a study. However, certain general observations can be made. Sclater (1886) considered 5 subfamilies of the Icteridae, the most distinct being the Cassicinae (cacique and oropendola lineage) characterized by a frontal shield on the bill and naked nares. The remaining four groups included the Agelaeinae and Sturnellinae with a straight culmen and the Icterinae and Quiscalinae with curved culmen. He mentions the elongated outer secondaries of the Sturnellines as a means of separating them from the Agelaeinae (including Dolichonyx, Molothrus, Agelaeus, Leistes, Xanthocephalus Amblyramphus, Pseudoleistes, Nesopsar, and Curaeus).

Beecher (1951) apparently considered Sturnella to

be a lineage separate from Pezites and Leistes, and mentions that the loss of the boss on the central groove of the horny palate, rendered it unlikely that Pezites could have evolved from Leistes. However, both could have evolved from a common ancestor, with the boss being lost subsequent to divergence, as Beecher noted. He suspected that the two gaping genera, Pezites and Sturnella may have arisen independently in different parts of the range of Agelaius (p.430), but elsewhere (p.424) that these are only two genera with a free lacrymal bone, which he relates to the gaping habit. However, since other icterids gape, one wonders why it has not appeared in other lines if it was indeed evolved separately in Pezites and Sturnella.

In his discussion of meadowlark relationships, (Short 1968) suggested that Pezites and Sturnella could have arisen from an Agelaius-like blackbird, through a Leistes-like form. He noted, however, that it was difficult to judge the affinities of bellicosa with respect to militaris and defillippii. Wetmore (1926) noted that in some respects defilippii was more similar to superciliaris than to P. militaris. I find it difficult to determine whether militaris or bellicosa are closer to the ancestor of Sturnella, and in fact the only clear picture of relationships at present are that the two forms of Sturnella and the two forms of Leistes are

monophyletic groups, while the position of the forms of Pezites is unclear.

In Figure 25 I list alternative phylogenies which suggest directions for future studies of the relationships of meadowlarks. The alternatives chosen are not exhaustive, but emphasize the questions which I think are the most interesting.

A. This emphasizes the unity of Pezites, its relationship to Sturnella, and the uncertain relationship of bellicosa.

B. This emphasizes the closeness of militaris to Sturnella and the similarities between defilippii and bellicosa.

C. This emphasizes similarity of Leistes, bellicosa and defilippii.

D. This deemphasizes relationships, viewing Pezites species as "steps" on the way to a Sturnella form.

E. This is a somewhat fanciful representation of the similarities between bellicosa and neglecta and between militaris and magna. Although it is not a likely phylogeny, it emphasizes certain similarities with respect to voice.

Beecher (1951) made what seems like an alternative suggestion, that Sturnella and Pezites, arose independently from an Agelaius-like bird. At first glance this seems contrary to the suggestion that they are related monophyletically. However, if the ancestral form were itself recognizable as a meadowlark, this would be quite consistent with monophyly. The ancestral form might have been similar to Leistes, or Leistes might have arisen quite separately.

Choosing between the more plasuable of these hypotheses will require investigation of additional characters within the meadowlarks and their related taxa.

SUMMARY

1. The geographic speciation model, whether or not it is the exclusive mode of speciation, is believed to be the dominant mode in birds. Speciation is best measured when secondary contact has been reestablished following isolation.

2. There was no good evidence of stable interspecific pairing between militaris and defilippii, and the observed attempted stolen matings, transient pairing, and possible hybrid, to not contradict the statement that the two forms are reproductively isolated.

3. The geographic variation of bellicosa and its possible relationship to militaris and to other forms are considered. The biogeographical history is unclear. Existence of populations in inter-Andean valleys is best explained by contact through low passes.

4. The relationships of two forms of Leistes are considered uncertain, for they are not currently known to be in contact. They are here treated as conspecific.

5. The relationships within the meadowlark assemblage and to other groups of icterids are only briefly considered. The behavioral, ecologic, and morphologic characters thus far examined, provide no clear picture for phylogeny. Several alternative phylogenetic hypotheses are figured, and further characters both within and without the assemblage will have to be examined.

CHAPTER 24 GENERAL SUMMARY AND CONCLUSIONS

The red-breasted meadowlarks (Pezites and Leistes) are widespread and conspicuous in neotropical grasslands from Tierra del Fuego northwards to southwestern Costa Rica (see figure 1, and Kiff 1975). They are expanding their range in tropical South America as forests are being cut.

This study was undertaken to compare the ecology, behavior and morphology of these meadowlarks focusing on the comparative biology of three forms (P. militaris, P. defilippii, and L. militaris superciliaris) in their zone of sympatry on the southern pampas of Buenos Aires Province, Argentina. Current taxonomic treatments of species and subspecies are listed in Table 1.

In the field I studied the comparative behavior and ecology of the meadowlarks, and these studies were supplemented by examining geographic variation in several features of external morphology. During the course of this study I measured 1093 skins of male and female red-breasted meadowlarks, which allowed me to detect some of the patterns of geographic variation. However, material from several interesting areas (see chapter 19) is still unavailable.

FIELD WORK

I spent approximately five months in Argentina, two months in Peru, and briefer periods in Venezuela, Surinam and Columbia (Table 2). Part of the field work involved surveys to document the distribution, habitat preferences, and population structure of the different forms. In Argentina I concentrated field effort on the pampas of southern Buenos Aires Province working mainly at Estancia La Saudade near Saavedra, 92 km north of Bahia Blanca. There I found three forms, defilippii, militaris and superciliaris, breeding together. Field work included observations on behavior, recording of vocalizations, playback experiments designed to test responses to autospecific and heterospecific signals, and observations of brood parasitism and reproductive biology. In addition, I mapped and measured utilized space and territories and studied territorial interactions.

RELATIONSHIPS WITHIN THE MEADOWLARK ASSEMBLAGE

Morphologically the meadowlarks are rather uniform in shape (summarized in Appendix 4 and chapter 19) and plumage pattern. Several taxa (e.g., Sturnella magna and neglecta and P. bellicosa) are conspicuously short-tailed. Bill shape varies within the Sturnelline

assemblage from the relatively short conical bill of L. m. superciliaris to the long slender bills of Sturnella. Clarification of the phylogeny of meadowlarks awaits a detailed study of their close relatives among the Icteridae.

That Sturnella magna and neglecta are very close relatives is apparent from comparisons of their plumage, behavior and ecology (see Lanyon 1957). Although once considered conspecific, Lanyon (1957) found that in their zone of sympatry they maintain reproductive isolation and can be considered distinct species with associated distinctive vocalizations and behavior patterns. He believes that the interspecific territoriality they maintain is an outcome of their close similarity in plumage, and reflects their close relationship.

The two forms of Leistes remain to be studied in detail. Short (1968) emphasized the difference in bill shape and treated L. superciliaris as a separate species. Morphologically the two forms are almost perfectly distinguishable by the presence of the pale superciliary line in superciliaris and the bill shape characteristics. However, I find that the two forms are similar in behavior, and I cannot evaluate apparent differences in vocalizations until more data are obtained from other parts of the range. There seems little point in

attempting a definitive statement now, since extensive clearing of Amazonian forests (observed by me in 1975 and much publicized in popular literature) practically assures that the two forms will soon come in contact. At present, although they closely approach each other in Maranhão and in southwestern Amazonia, I have been unable to find any evidence of actual contact.

The genus Pezites, although treated as monotypic by some recent authors (e.g., Blake 1968) contains three species which are very distinctive in behavior and ecology, and show consistent morphological differences as well. In some respects defilippii resembles Leistes more closely than it does the other Pezites (a similarity mentioned also by Wetmore 1926). P. bellicosa is similar in vocal behavior to S. neglecta and its short tail is similar to that of Sturnella. P. militaris is much longer tailed than other meadowlarks and is distinctive in its utilization of elevated perches. At present it is difficult to assess the relationships of Pezites at the species level, and this difficulty and apparent mosaic of similarities, is a reason for considering the entire assemblage to be closely related. This supports Short's (1968) contention that all forms be treated congeneric.

HABITAT AND DISPERSION

The habitats selected by red-breasted meadowlarks are very variable with respect to floristic composition, though less variable with respect to physiognomy.

All meadowlarks are mainly grassland birds, and *P. militaris* is the most distinct in requiring elevated perches, and tolerating very sparse ground cover. It seems to require only a few clumps of grass or forbs in which to place its nest. It tolerates relatively dry habitat, but cannot breed without some moist areas. Thus its distribution through the arid Patagonian scrub is dependent on seeps, streams, or moist ravines. It has the widest habitat utilization of the group. *P. bellicosa* also seems more tolerant of habitat variation (probably similar to *Sturnella*) than either *defilippii* or *Leistes*. The latter two species apparently require very extensive ground cover (probably at least 80%) with vegetation at leat 40 cm high. Of the two, *superciliaris* may have a preference for or at least greater tolerance of taller vegetation. The two species were often found together in the same fields at Saudade, in which place they seemed to be choosing the same habitat. It is not known, however, to what extent the clustering reflected habitat preference or sociality.

Several lines of evidence indicate that *superciliaris*

and defilippii nest in loose colonies. I found clusters of territories in some fields whereas other fields, similar to my eye, were unoccupied. The observed clustering did not reflect a vegetation mosaic, and clustering was particularly conspicuous in wheat-growing areas which provide relatively uniform habitat. Observations on behavior indicate contagiousness of singing consistent with the prediction that more social stimulation occurs in larger aggregates of birds.

On the pampas, I found no evidence that militaris was clustered. Rather their distribution appeared more or less uniform along roads where elevated perches were available. In arid areas where territories were not linear, I found birds clustered around available water and the same is true for the distribution of bellicosa which on the arid Peruvian coast is restricted to river valleys.

TERRITORIALITY

All meadowlarks are territorial and resident males typically display aggressive behavior towards intruders. In some localities spontaneous territorial encounters are infrequently observed (i.e. for P. militaris) but are readily elicited by decoy and playback. This suggests that birds on neighboring territories may

establish an "understanding" which leads to a decreased frequency of territorial encounters, although the underlying tendency to defend territories is not diminished. In P. defilippii, bellicosa and L. m. superciliaris responses to decoys and playback are generally less strong than for P. militaris. This may in part reflect technical differences in the strength of the stimulus provided by decoy and playback, but may also reflect the fact that these species nest in loose colonies (see chapter 16) and are less aggressive to begin with. This matter needs to be explored in detail.

Territories of P. militaris are Nearly Type A, except that birds frequently make long forays beyond the limits of their defended area. They utilize elevated perches to defend territories, and therefore a large part of the boundary between two territories is apparently ignored with encounters occurring mainly along fences where two territories abut. Territories of the other species studied are Type B, and although much foraging is done on territory, most pairs make long foraging trips off territory on a very regular basis when feeding young. I did not see any evidence that on these off-territory flights the adults were able to forage in territories defended by other birds. There remained ample habitat that was not defended by any meadowlarks (that is, the study area was unsaturated). Moreover, when a pair was

itself feeding fledglings it no longer seemed to defend its former territory.

BREEDING BIOLOGY

All species of meadowlarks are probably polygynous although the evidence for *Leistes* is still only circumstantial. On study areas at Saudade and near Bahia Blanca, and in travels elsewhere it appeared that for *P. militaris* and *defilippii* polygyny occurred commonly. In the few pairs studied in detail there was some degree of serial polygyny, but at least one male had both females incubating simultaneously. The evolutionary implications of polygyny are discussed. It is probably always an advantage for a male to mate with two or more females and McLaren (1972) has suggested that the main purpose of territoriality is to facilitate polygyny. Discussion has usually focused on the advantage to the female, and whether she can raise more young mated to a polygamous vs. a monogamous male. In the latter case male contribution to nestling care is compromised (see Table 5). It is usually suggested (e.g., Orians 1969, Verner 1964) that where males stake out territories of differing quality, a female benefits by mating with a male on a better territory (who may incidentally be a genetically superior male) even if he is already mated to another and she must care for the young alone.

However, in this study I emphasize that in a species where the male normally contributes only a small amount of parental care, or where he may actually compromise nest success by carelessness (see chapter 7), there may be no disadvantage to dispensing with his care, and therefore no disadvantage or obstacle to polygyny.

I usually could not observe how pair formation occurred. In a few instances, unmated female defilippii were observed approaching an area where territorial males were established. Males apparently responded to her by giving flight songs and she would land in the territory of a male, elicit a flight chase, and either return with him or visit another territory. The phenomenon was not observed frequently enough to learn how females actually choose a mate or whether males actually increase their song frequency or change behavior when females approach. The responses of a single female successively to several males indicates that it is the female who chooses a mate. Whether there are certain species-specific vocalizations involved could not be answered in this study. However, no instances of stable interspecific pairing were observed during the field work.

COURTSHIP AND PAIR BONDS

This study revealed that sex chases are a prominent feature of pair bond maintenance. Sex chases were initiated by females giving special solicitation notes (distinct from pre-copulatory solicitation notes) as they flew up from a territory. The males followed the females in rapid low twisting flights often over several territories where they might be joined by resident males. Sex chases were particularly prominent in *defilippii* and *bellicosa*. They were observed less frequently in *P. militaris*, either because that species pairs earlier, or because unlike the other species the male and female of a *militaris* pair usually remain in close proximity often foraging only a meter or two apart. Since they spend much of their time in visual contact sex chases may be less important in that species.

NESTING

All meadowlark species nest on the ground and the nest is usually concealed under vegetation. Nests may have an intrinsic dome in some species, but frequently have an extrinsic dome so that the contents are not visible from above. Male meadowlarks are not known to participate in nest construction, although in *P. militaris*, the male often accompanies the female, and

may occasionally carry nest building. It is unlikely that the male's material is used in nest construction. Most nest material is apparently obtained on the ground, probably close to the nest site, and females are almost never seen carrying material (except P. militaris in a few instances, see chapter 8). This makes it difficult to find nests and is believed to be an anti-predator or anti-cowbird strategy.

I found no evidence that the male incubates or broods the young although Martin (1974) reported that in some instances male Bobolinks may brood young. Lanyon (1957) has discussed and dismissed anecdotal reports of incubation by male Sturnella. Incubation lasts approximately 14 days in P. militaris and there are no suitable data for the other species of red-breasted meadowlarks.

In the first few days after hatching the female is responsible for almost all the feeding (except at a few defilippii nests) as well as brooding of young. The amount of time spent brooding diminishes rapidly, and even nocturnal brooding may terminate by day 6 at which time the nestlings are well-feathered. Fledging occurs after the 8th day. Male care increases during the nestling period so that in the second week some males contribute a third or more of the care. I did not have adequate opportunity to compare visits to primary and secondary nests by polygynous males, although in one

case a defilippii male did make fewer visits to feed at his secondary nest (chapter 7).

On visits to the nest females of all three Pezites species show greater care and patience and less tolerance of observers than do males. If an intruder is visible, even 50 meters from the nest, a female with food will wait longer (even an hour or more in some cases) and may fly away rather than visit the nest. Females typically land in the grass some distance from the nest, walk to it on foot, and then walk away after feeding before taking flight. Males may do this to a small extent, but frequently land and take off directly at the nest site, thereby facilitating nest finding. This "carelessness" suggests that males may hinder as well as help at the nest.

I did not have the opportunity to study families of fledglings except for anecdotal observations on P. militaris. I found that males and females both care for fledglings, often separately, and that males participate at least equally in this aspect of parental care. This would afford the opportunity for a female to initiate a second brood, but I could not document this in the present study.

BROOD PARASITISM

An important finding in this study is the heavy parasitism by the Shiny Cowbird (Molothrus bonariensis) on militaris and the absence of parasitism of defilippii. This differential parasitism is believed to be due largely to the different nest placement and adult behavior, whereby cowbirds have an easier time finding militaris nests which are near elevated perches. It is likely that militaris is a recent arrival on the pampas and is historically naive in its confrontation with the cowbird (as Mayfield 1960 suggests for Kirtland's Warbler). Perhaps also since militaris young are larger than cowbird young and may easily coexist or even outcompete them in some nests, there is relatively less selective pressure operating on militaris than on smaller host species. However, since cowbirds do remove and destroy host eggs and since nestling cowbirds may attract predators to the nest, there is clearly a disadvantage in being parasitized. Cowbirds seem to spend more time watching militaris than defilippii, at least on the Saudade study area, and they apparently respond positively to militaris vocalizations. This suggests some degree of foster-specificity, yet I saw no cases of militaris feeding cowbird fledglings, which would be necessary to perpetuate a line of militaris-favoring cowbirds. Even without such a tradition of foster-

specificity, cowbirds could still respond favorably to militaris if an adult cowbird learns that it is easier to find militaris nests than nests of other hosts. Although no meadowlarks are known to have successfully raised cowbirds (Friedmann 1963 and pers. comm.) meadowlarks are the most conspicuous passerines over much of the pampas and may attract cowbirds just on strength of numbers and prominence.

INTERSPECIFIC INTERACTION

On the pampas study areas I found that territories of P. militaris extensively overlapped those of defilippii and superciliaris and that there was infrequent interspecific aggression manifested----less than I had anticipated on the basis of plumage similarity. However, I found much less territorial overlap between defilippii and superciliaris and over a short period their territories were essentially non-overlapping. Moreover there were no habitat features which would explain the non-overlap, and I was able to study the birds in two wheatfields which provided essentially uniform habitats. The interspecific territoriality appeared to be maintained by interspecific aggression, particularly by defilippii males against superciliaris. The latter species only occasionally attacked intruding defilippii. In some

cases defilippii males showed the same aggression towards the heterospecific as towards conspecific males.

The aggressive interactions were counted and compared to the frequency of encounters predicted on the basis of the number of available territorial males of either species. Although there was always an excess of autospecific encounters, this was due mainly to the deficit of heterospecific aggression by superciliaris. This interspecific territoriality is one-sided, compared to the nearly mutual interaction reported by Lanyon (1956a, 1957) for S. magna and S. neglecta. A means of quantifying and evaluating interspecific aggression is presented (chapter 21), and the ecologic and evolutionary significance of interspecific territoriality is briefly considered.

No evidence for convergence has been found, and Cody's suggestion (1969, 1973) that convergence occurs to promote interspecific territoriality and facilitate coexistence, is considered unsupported. Rather the apparent similarities and resulting interspecific territoriality are believed to reflect the close relationship of the superciliaris and defilippii.

VOCALIZATIONS

Territorial defense involves both primary and flight songs in bellicosa and defilippii and probably in superciliaris as well. Birds may give flight songs moving to or from a territorial encounter or may give flight songs parallel to a shared border. More common are countersinging bouts of primary songs, sometimes coupled with other displays such as jump flights along the border. Many of the territorial displays closely resemble those described for Sturnella (Lanyon 1957). P. militaris infrequently gives flight songs and these seem to reflect intense excitement rather than territorial aggression. However, Lanyon (pers. comm.) observed more frequent flight singing by the race P. m. catamarcanus, which may have a greater tendency to use flight singing in territorial interactions.

Primary songs of defilippii, bellicosa, and superciliaris are quite similar in having several introductory notes and a terminal buzz. The songs differ somewhat in duration and quality of introductory notes and in quality and shape of the buzz. Their flight songs are much less similar. The bellicosa flight song is a rich warble, in which it resembles S. neglecta. P. defilippii gives a series of whistled notes that are quite pure, and Leistes gives a song more similar to its primary song, but ending in a series of whistled "tu"

notes (chapter 11). The warbled song of bellicosa is very similar to the rare flight songs of militaris and of S. magna, and also resemble the unstereotyped "rehearsed" songs given by most of the species. In those species where I have heard vocalizations during sex chases, the sounds are usually warbled and are related to the "rehearsed" song. Thus bellicosa and neglecta appear to have modified this available vocalization for use as a regular flight display.

Primary songs of militaris were the most complex among the red-breasted meadowlarks, and two types, long and short, may occur. The repertoire size varies from 5 to 12 in the few males studied adequately. Some song patterns were shared between widely spaced geographic localities. Male defilippii apparently have only one primary song pattern in their repertoire. In the population of bellicosa at Bujama, Peru, there were two main song patterns which were always readily distinguishable. No male was known to sing both patterns so it is not proper to refer to these as song types until further recordings are obtained or other populations examined. Analysis of bellicosa primary songs revealed a bimodality in duration of the terminal buzz, many lasting less than 400 msec, and others lasting longer than 450 msec. Two of the marked males were documented singing both a short-buzz and long-buzz song, but it is

not yet known whether these are different song types or different patterns of a single song type. The repertoire size was found to be 1 - 4 based on five marked males. Primary songs of Leistes are higher pitched (mainly 4000 - 7500 hz) than Pezites (mainly 3500 - 6000 hz), and some energy was apparent at 10,000 hz. Between the two forms of Leistes, I found that superciliaris tended to have more complex introductory notes, and that the terminal buzz notes of the two forms differed in quality.

For all meadowlarks there is overall similarity in calls, particularly in the "chup" notes, although there are some consistent between-species differences in pitch and in emphasis. The "chup" note of militaris is lower pitched than defilippii, with energy mainly below 3 khz. The defilippii "chup" tended to be biphasic, whereas militaris notes were not. The "chup" of bellicosa tended to be a click type of note. Leistes gives a "tup" note which was longer in duration than any Pezites note and showed a greater resemblance to the "chup" of neglecta. These "chup" notes appeared in various contexts including mild alarm and territorial aggression. Both sexes gave the call, but it was given very often by males, and only occasionally by females. Males of bellicosa occasionally engaged in long periods of counter-calling across territorial boundaries. I found no difference in the note of catamarcanus compared with

militaris from the pampas and Patagonia.

I recorded a variety of "peet" notes given by defilippii males during moments of territorial or sexual excitement. These notes had no clear counterpart in militaris which may give "chup" notes in the same context. In bellicosa I noted a variety of steep-figure calls in these circumstances, and such calls were used by bellicosa and seldom by the other species.

Several call notes were heard only in flight (see chapter 12). Of particular interest is a "weet" note given by female defilippii (and perhaps also by males), which resembles notes given by both magna and neglecta during migration. The present study did not reveal whether females actually distinguish conspecific males on the basis of species-specific call notes, but there are enough inter-species differences to suggest that such discrimination can occur.

On only one occasion did I hear a chatter, typical of S. magna, this was given by a female militaris near Bariloche, Argentina. It is possible that such notes are given more frequently but have been overlooked. No counterpart of the roll was heard. Young meadowlarks may give high intensity alarm notes when handled. As in many species, adults may respond to such notes by mobbing the intruder. Such behavior was well-developed only in defilippii, males of which showed a high level

of aggression against me. In such situations bellicosa adults were variably and moderately aggressive and militaris hardly aggressive at all.

Although female song is infrequent among passerines, I noted it regularly in P. militaris, females of which frequently accompany their mates in territorial encounters. Females did duet with their mates, sometimes matching the male song and other times giving only some harsh notes. Such female song was sometimes heard spontaneously, but was readily elicited by attracting males to playback. None of the other meadowlark species have female song. A few individual females of defilippii and bellicosa occasionally gave male-type flight displays accompanied by harsh female-type notes. These songs were confined to a brief period and are believed to reflect high androgen levels occurring during the peak of hormone production during the reproductive cycle.

Playback experiments were conducted using a mounted bird or replica as a decoy, accompanied by either single or dual speaker playbacks (the latter confined to studies of bellicosa). Most males responded strongly to playback of conspecific primary song, with militaris responding more aggressively than the other species. Males were trapped for color marking in the same fashion. It was not possible to trap males with any but conspecific song, and even when birds approached a decoy with a hetero-

specific song, the duration of their visit was generally short. Since birds sometimes responded to silent decoys (no playback) it is apparent that these brief responses to heterospecific song may be attributable to the visual stimulus. Dual speaker tests with bellicosa revealed much stronger responses to conspecific primary song than to any other signal, but some bellicosa did respond initially to defilippii primary songs which are superficially similar. It may be advantageous to eliminate visual stimuli from playback tests as emphasized by Ewert (MS). In some tests it was found that departures from a decoy were more useful than attraction to the decoy in clarifying the roles of visual and acoustic stimuli. Birds attracted to a decoy with the wrong song were much more likely to leave than birds attracted to a conspecific song.

The results of this study emphasize the importance of male responses to primary songs. It is apparent that males respond mainly to conspecific song. Unfortunately with the equipment used it was not possible to make a fair test of Leistes songs.

FOOD AND FEEDING

Studies of food and feeding are fundamental to evaluating niches and competition, but are often much easier to envision in theory than to conduct. Although Cody (1968) provided an elaborate theory of feeding strategies involving species-specific differences in rate of progression (including data on meadowlarks), I was unable to observe foraging behavior in the field since the birds were virtually invisible in the grass. This casts doubt on the reliabitity of the meadowlark data reported by Cody since they must have been studied in very atypical habitat.

P. defilippii and Leistes usually foraged in dense grass and militaris and bellicosa usually also did so, although the latter often foraged in more clear areas or on the edge of patches of vegetation. Inter-sex feeding differences were noted casually, particularly at a time when nestlings were being fed and females made repeated trips to foraging areas while males often could not be found. In many instances male militaris closely accompanied their females to the nest even if they did not actually feed young themselves. Male defilippii, which usually did not associate closely with females, often did so when nestlings were being fed.

Stomach contents were examined from specimens, and

were evaluated for the volume of insect and plant material. All forms, particularly females, became insectivorous at a time when young were being fed, and more granivorous late in the season, particularly when wheat was ripening. In the zone of sympatry I found much overlap in food taken by militaris and defilippii (superciliaris material was inadequate). In each species there were some granivorous and some insectivorous individuals, although on the whole defilippii proved more insectivorous than militaris. The results are summarized in Table 48.

Although no food sampling was done, I judged that at Saudade, orthopterans were superabundant early in the breeding season, and it is unlikely that there was any real competition at this time. When young were being fed and adults travelled a considerable distance, returning with one large insect larva at a time, there may have been competition. Later when grain is ripening there is certainly no opportunity for competition. The fact that there is already a moderate degree of species difference in food selected, as well as a great abundance of food during most of the season, means that militaris and defilippii compete relatively little except perhaps at the time when young are being fed. It would be useful to identify the actual food items brought to nestlings, feeding rates, nestling growth, and inter-

action of birds on the feeding grounds----details that were beyond the scope of this study.

The coexistence of three apparently closely related meadowlark species on the pampas of Buenos Aires Province, raises the question of how they avoid competitive exclusion. I was not able to evaluate their realized niche in sympatry compared with niche breadth in allopatry to see whether compression had occurred. Using multiple discriminant analysis I found no evidence of morphologic character displacement. The observed interspecific territoriality between two of the three species probably has no effect on competition, in the sense proposed by Cody (1973) (minimizing space overlap among competitors). It may minimize intraspecific competition for an individual if it is surrounded by heterospecifics rather than by conspecifics, but this is a different matter and one which requires future investigation.

In view of the size differences among the meadowlarks and the differences in bill shape, it seems likely that they had differentiated to a sufficient degree such that they competed only minimally when they became sympatric. Moreover, since for much of the year there is probably a superabundance of food, it is likely that competition if it occurs is confined to a brief (but important) period when young are being fed. Study of

competition among pampas meadowlarks should focus on this period.

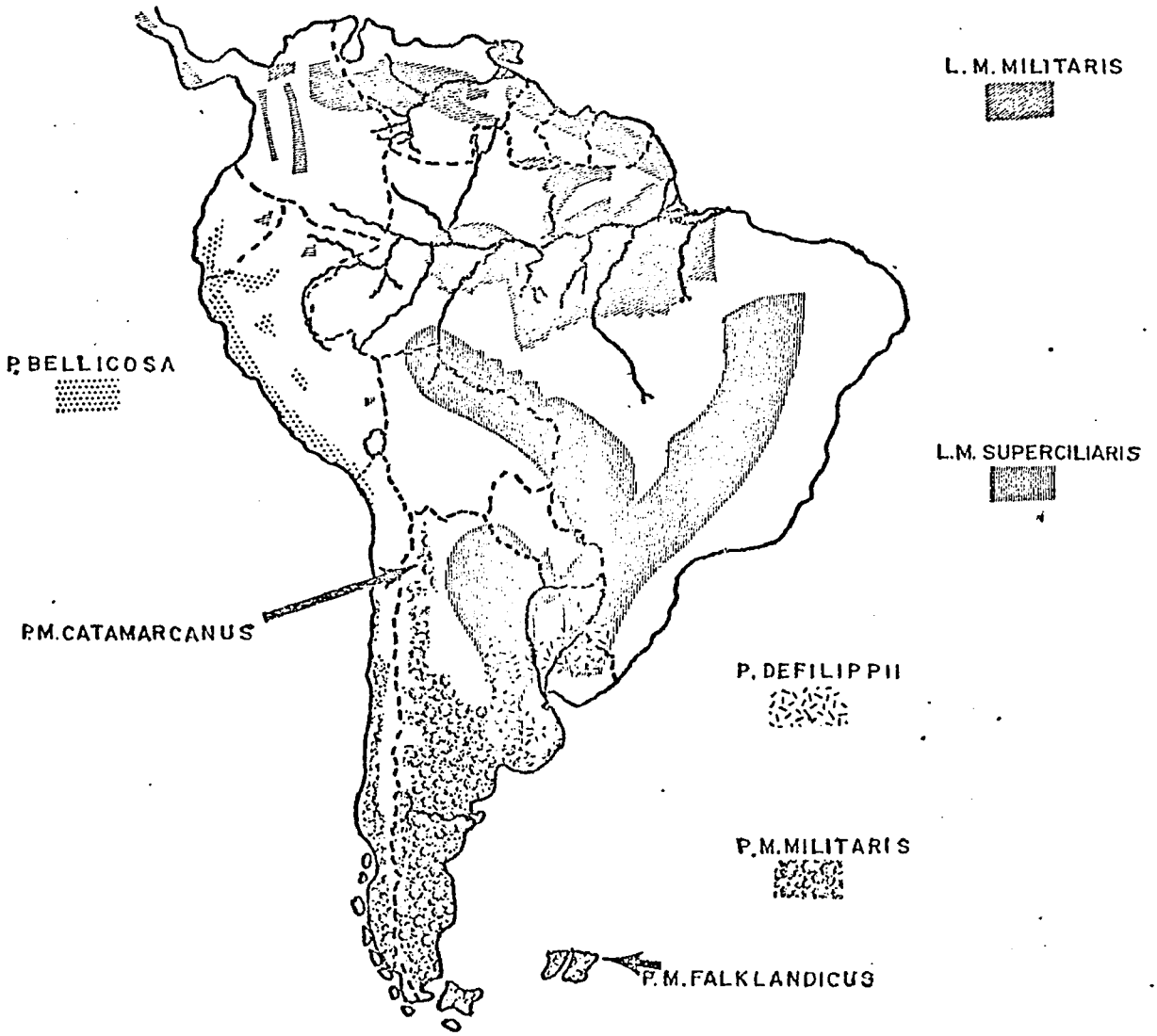


FIGURE 1. Distribution of Red-breasted Meadowlarks. Irregular areas delineated for L.m.militaris and L.m.superciliaris denote lack of documentation of distribution in central Brazil, and extensions of range with forest clearing in northern South America.

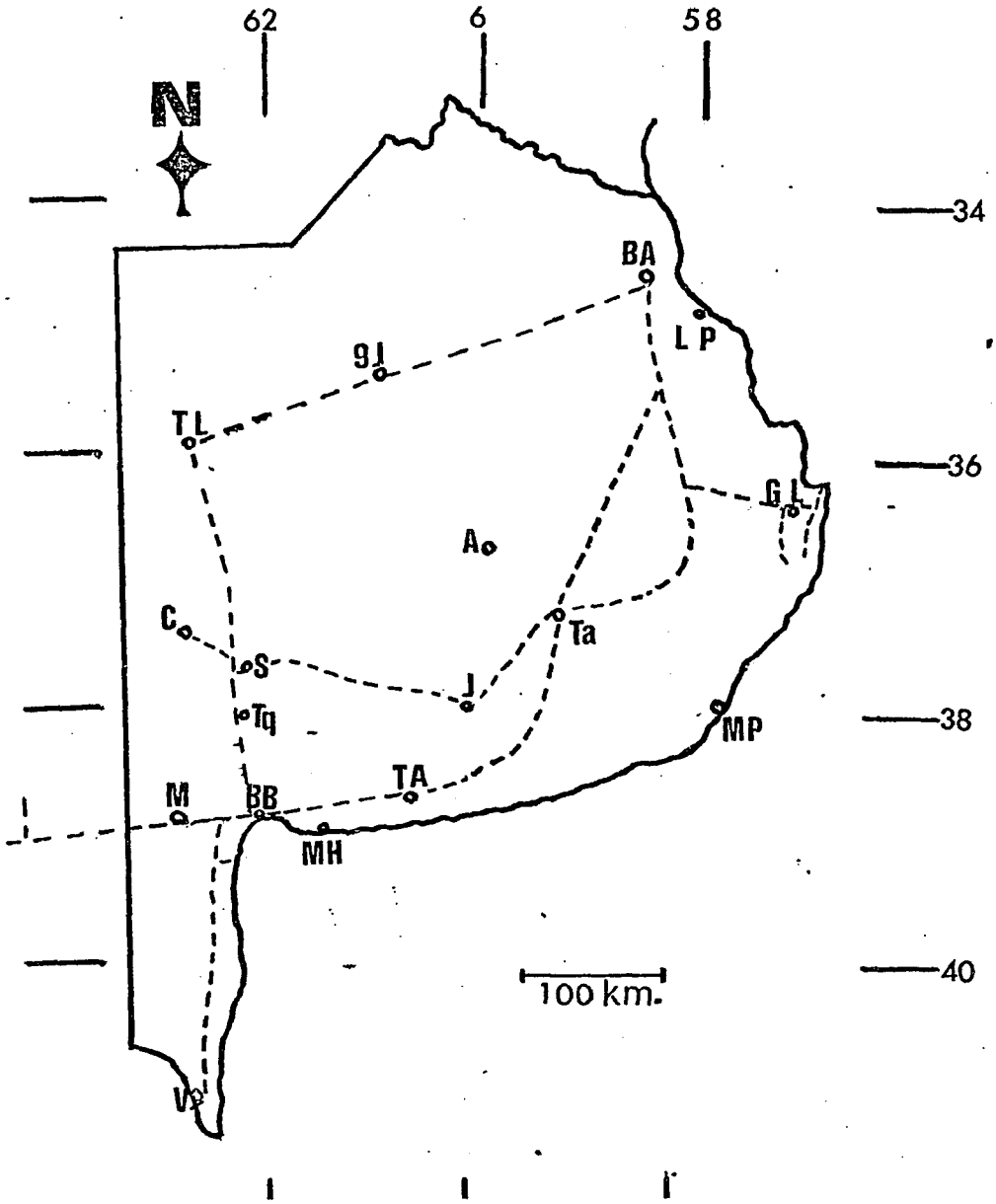


FIGURE **2.** Buenos Aires Province showing routes travelled.

A= Azul BA=Buenos Aires BB=Bahia Blanca C=Carhue
GL=G'ral Lavalle J=Juarez LP=La Plata M=Medanos
MH=Monte Hermosa MP=Mar del Plata S=Saavedra Ta=Tandil
TA=Tres Arroyos TL=Trenque Lauquen Tq=Tournquist V=Viedma
9J=Nueve de Julio D=Dolores SV=Sierra Ventana

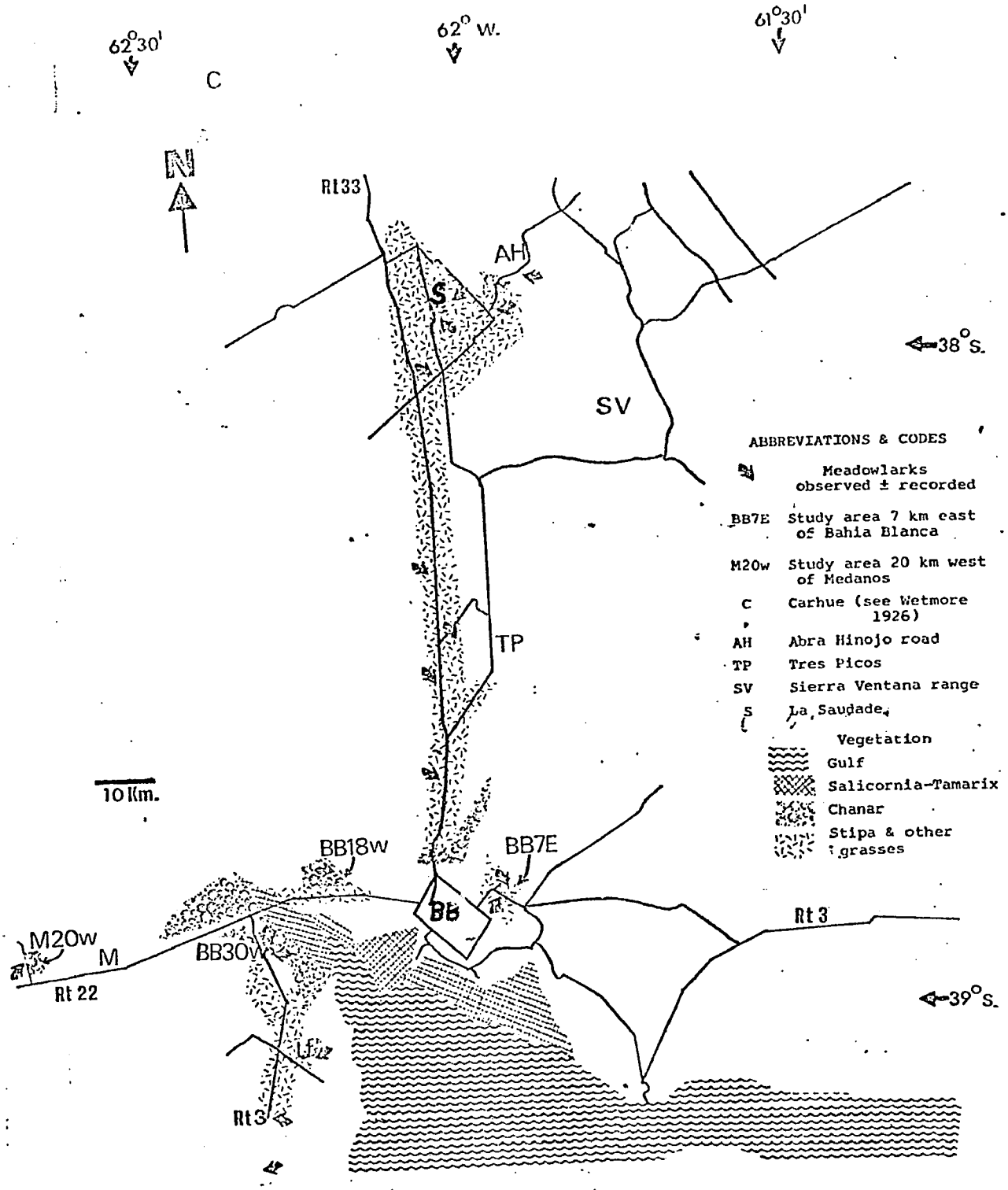


Figure 3. Map of southern pampas showing region from Saavedra (S) to Bahia Blanca (BB).

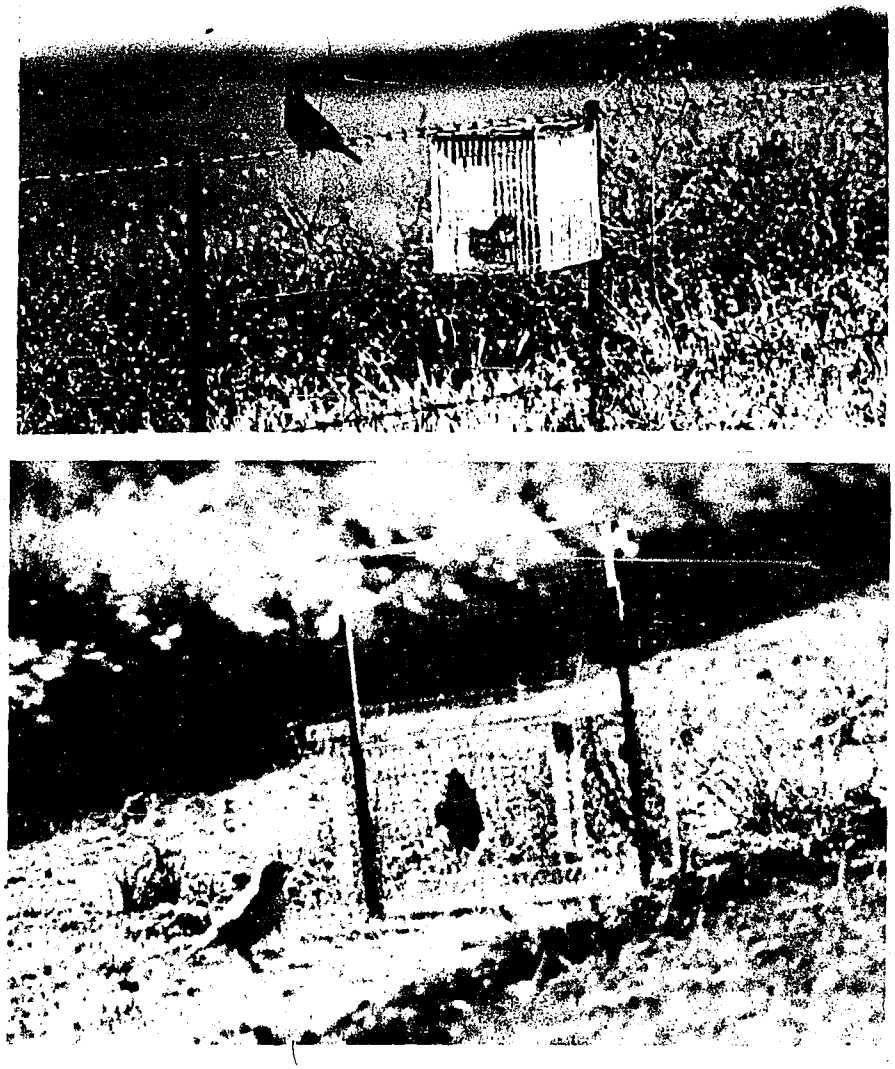


FIG 4. Two methods for capturing male Pezites with traps containing a stuffed bird as decoy and nearby tape recorder playing continuous loop.

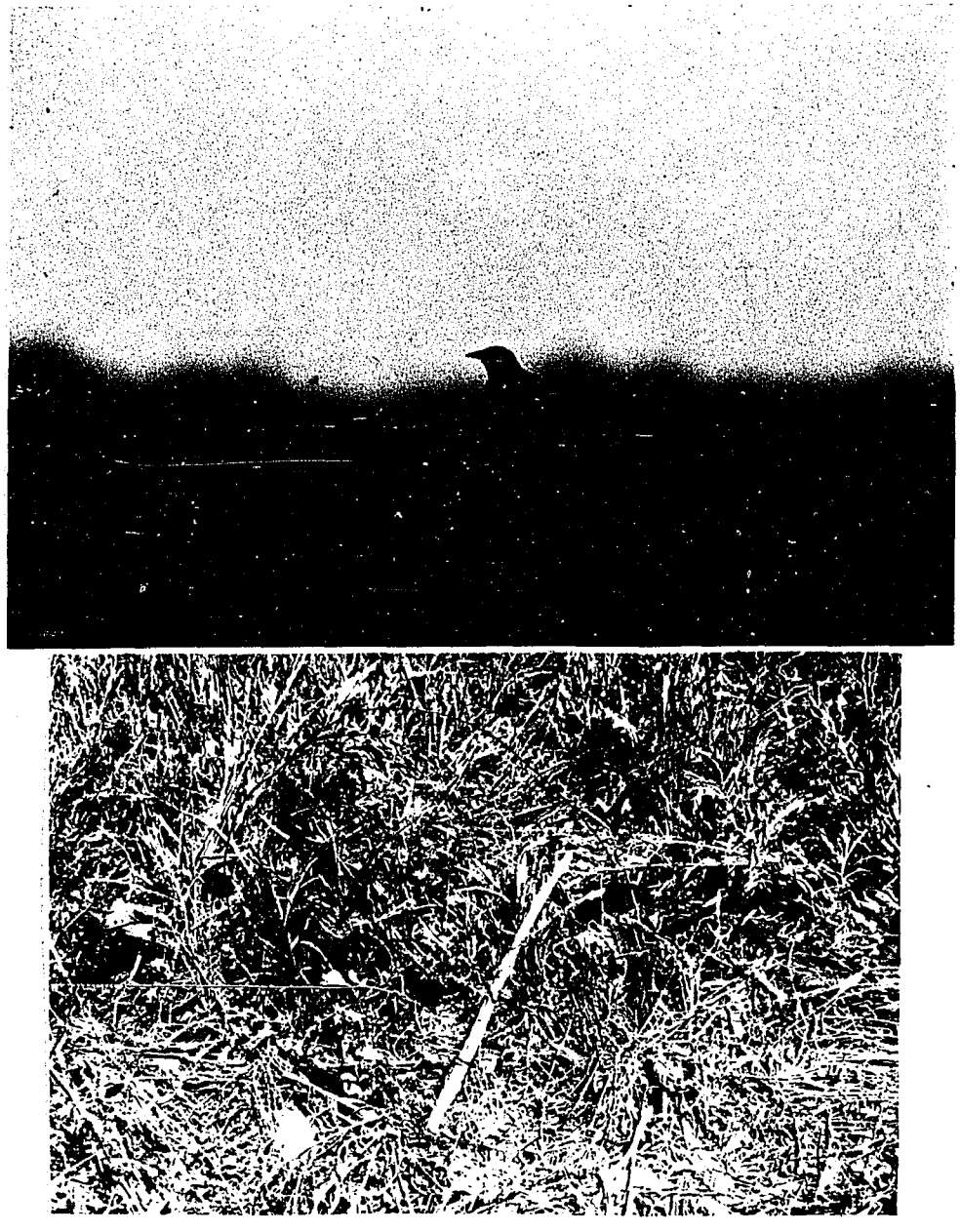


FIG 5 A. Color-marked male P. militaris YY/BB.

B. Drop trap over nest of P. militaris at Saudade. Trap consists of dome of green mist-netting erected over vegetation clump. Entrance consists of a weighted flap operated remotely from a blind.

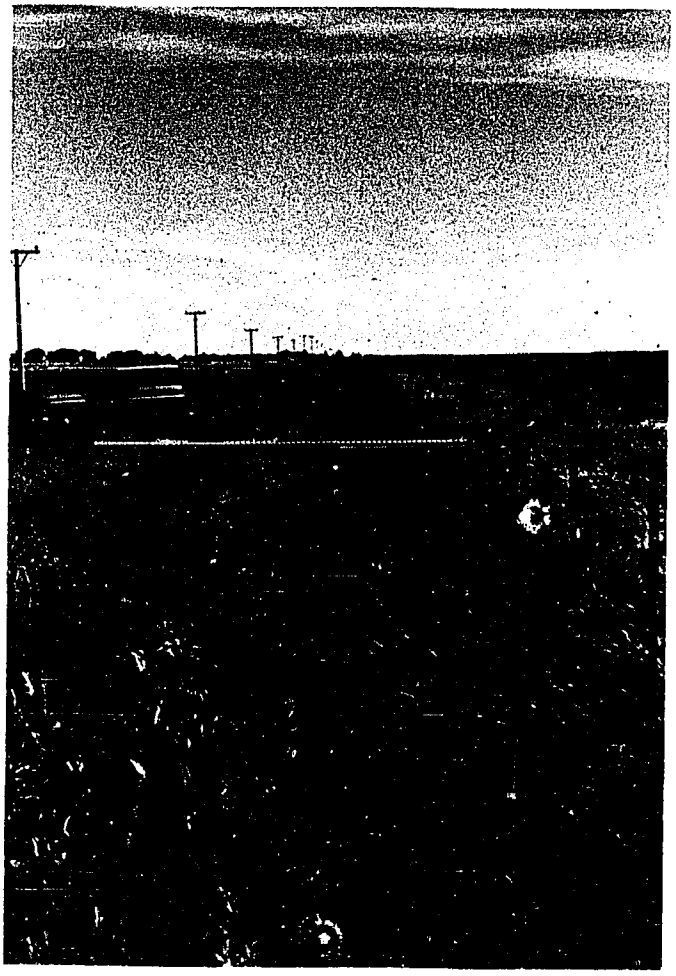


FIG 6. Saudade study area on pampas showing fence and fencerow vegetation. To right of fence is pasture with *Stipa* and *Bromus*, and uniform wheatfield is in right rear.



FIG 7. Monte chañar (Geoffroyia decorticans) typical of study area 30 km west of Bahia Blanca. Canopy height is about 2 - 3 meters.

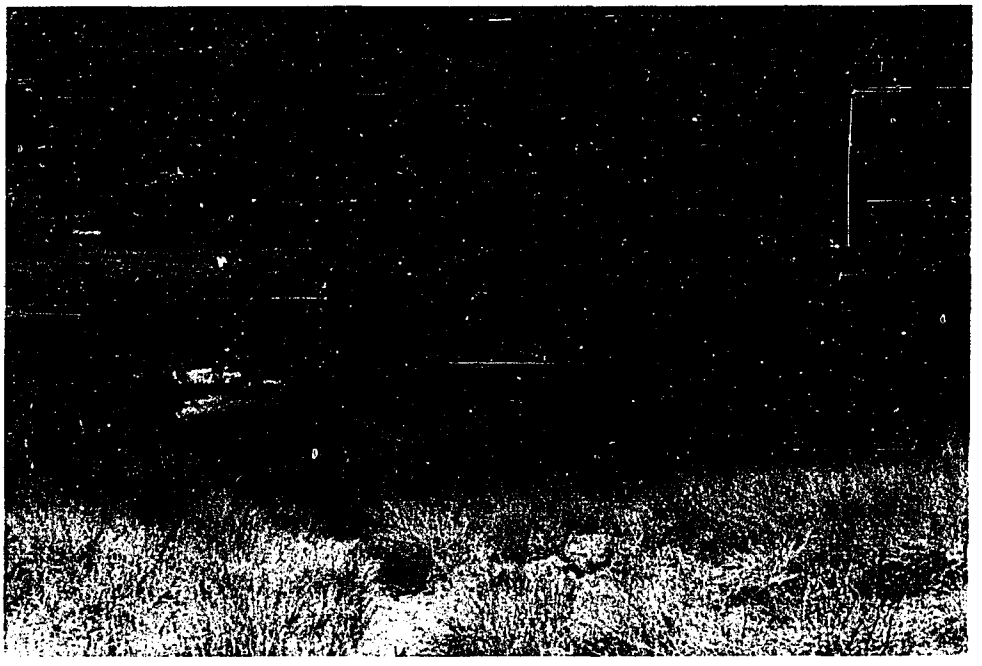
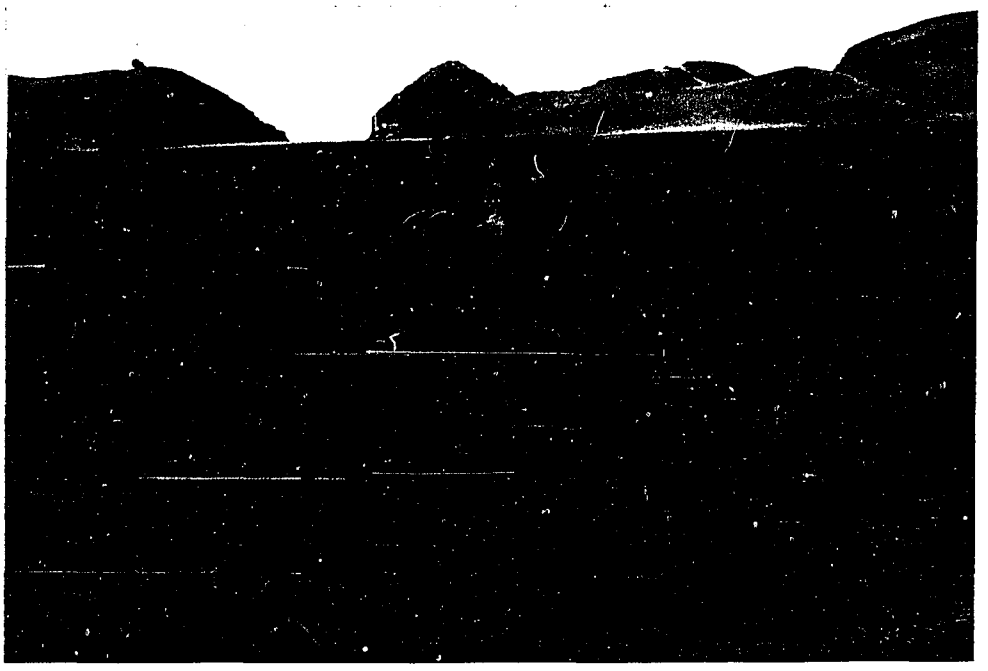


FIG 8. Riverine marsh with tall tussock grass at kmp 957 (route 40) along the Rio Santa Maria in north-eastern Catamarca.



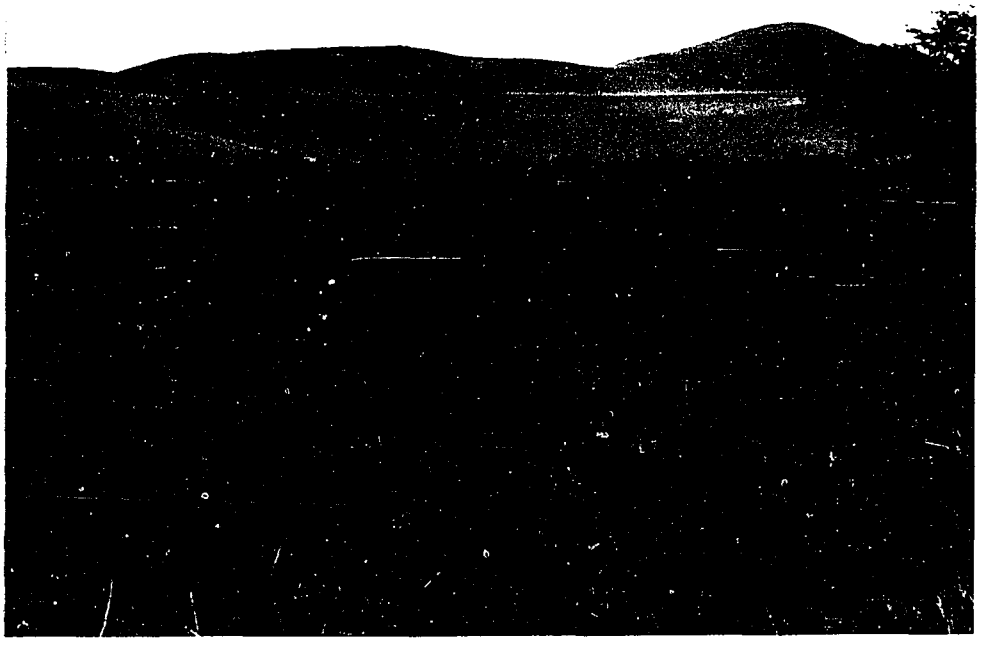


FIG 9. Bujama Study area.

A. Marshland, dark vegetation is Scirpus. Barren sand dunes and rocky sea-cliffs are in background. Other vegetation has been disturbed by pasturage or cultivation.

B. Pasture land, truck crops and corn fields. Tip of Huarango (Acacia macracantha) grove is at extreme right.

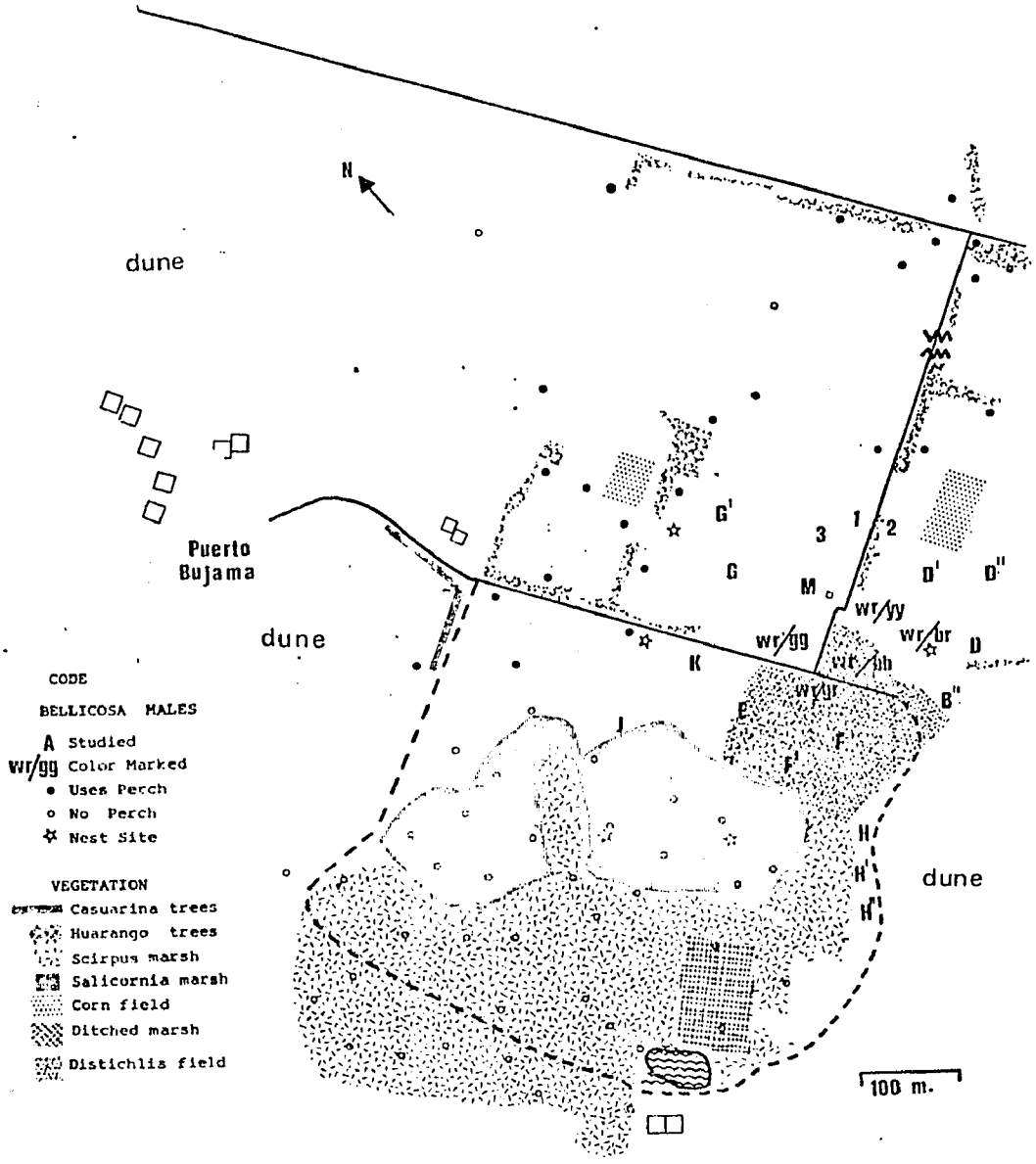


FIGURE 10. Study area at Bujama, Dept. of Lima, Peru.

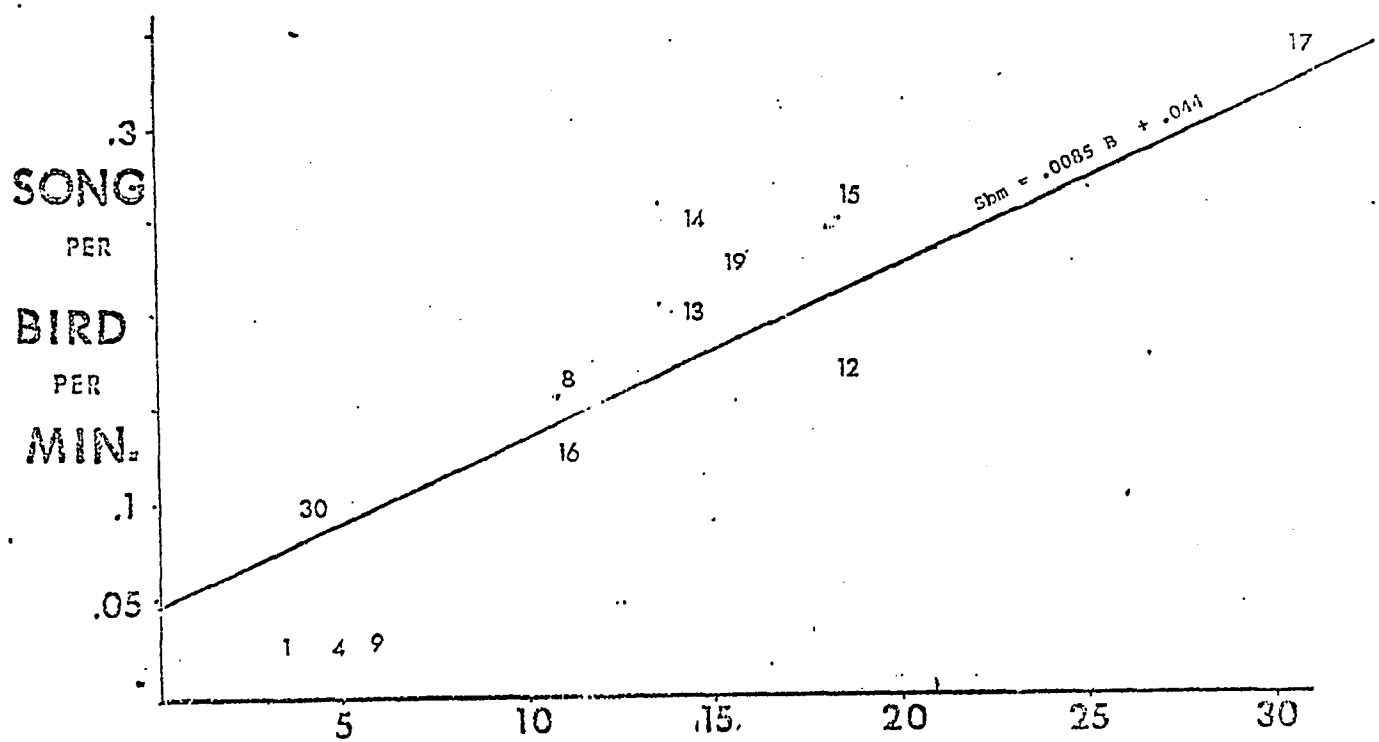


Figure 11. Linear regression of song frequency on group size for defilippii. Sbm = songs/bird/minute
(numbers refer to the roadside census points where data was taken)

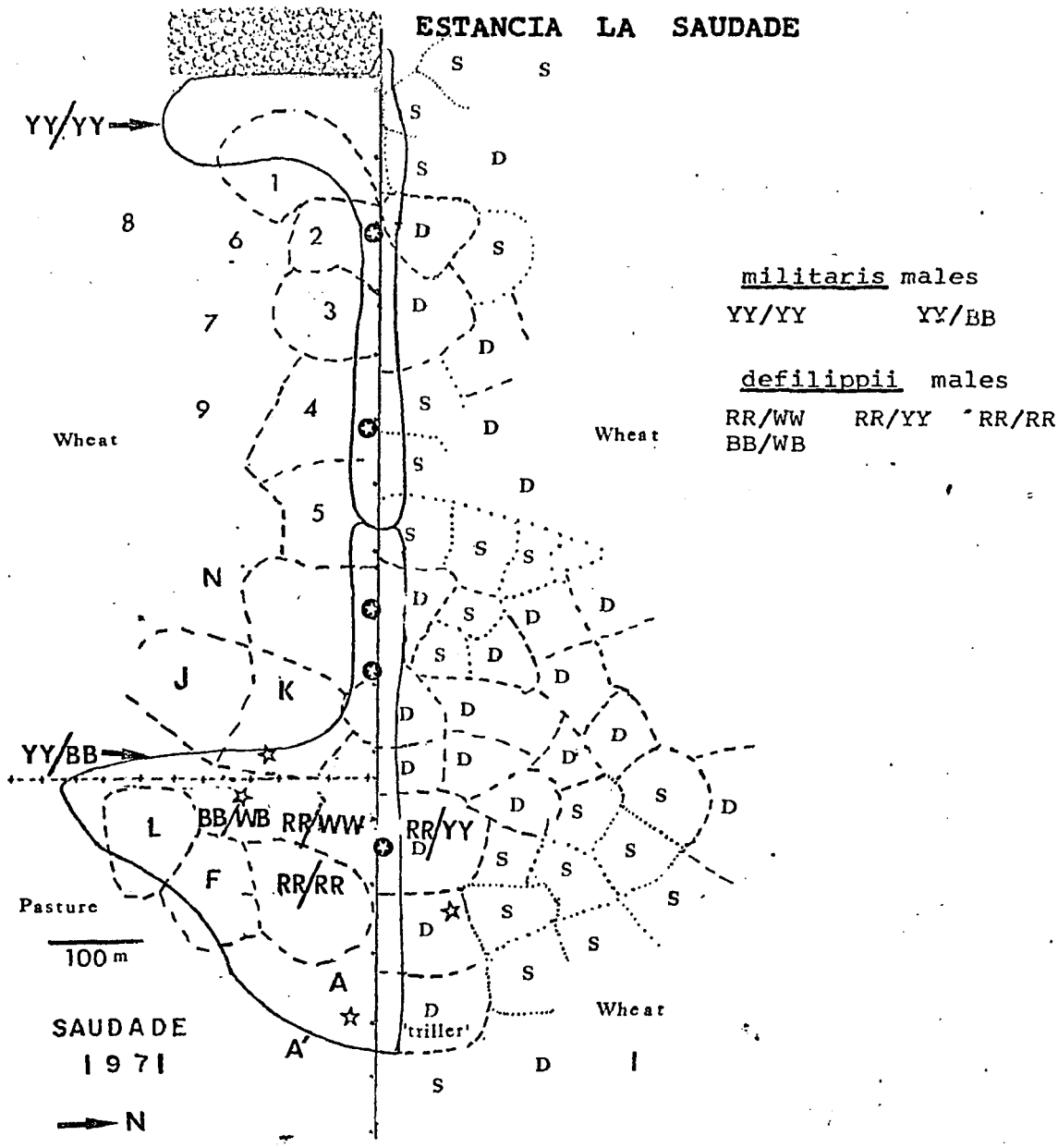


Figure 12. Composite map of meadowlark territories

1 or J = unmarked male defilippii

D=unmarked male defilippii
S=unmarked male superciliaris

Differences in territory size reflect in part different effort and time of mapping. Wooded portion is main estancia plantation.

-+--+--+-- = fence

..... = superciliaris territory

———— = militaris territory

------ = defilippii territory

militaris nest

defilippii nest

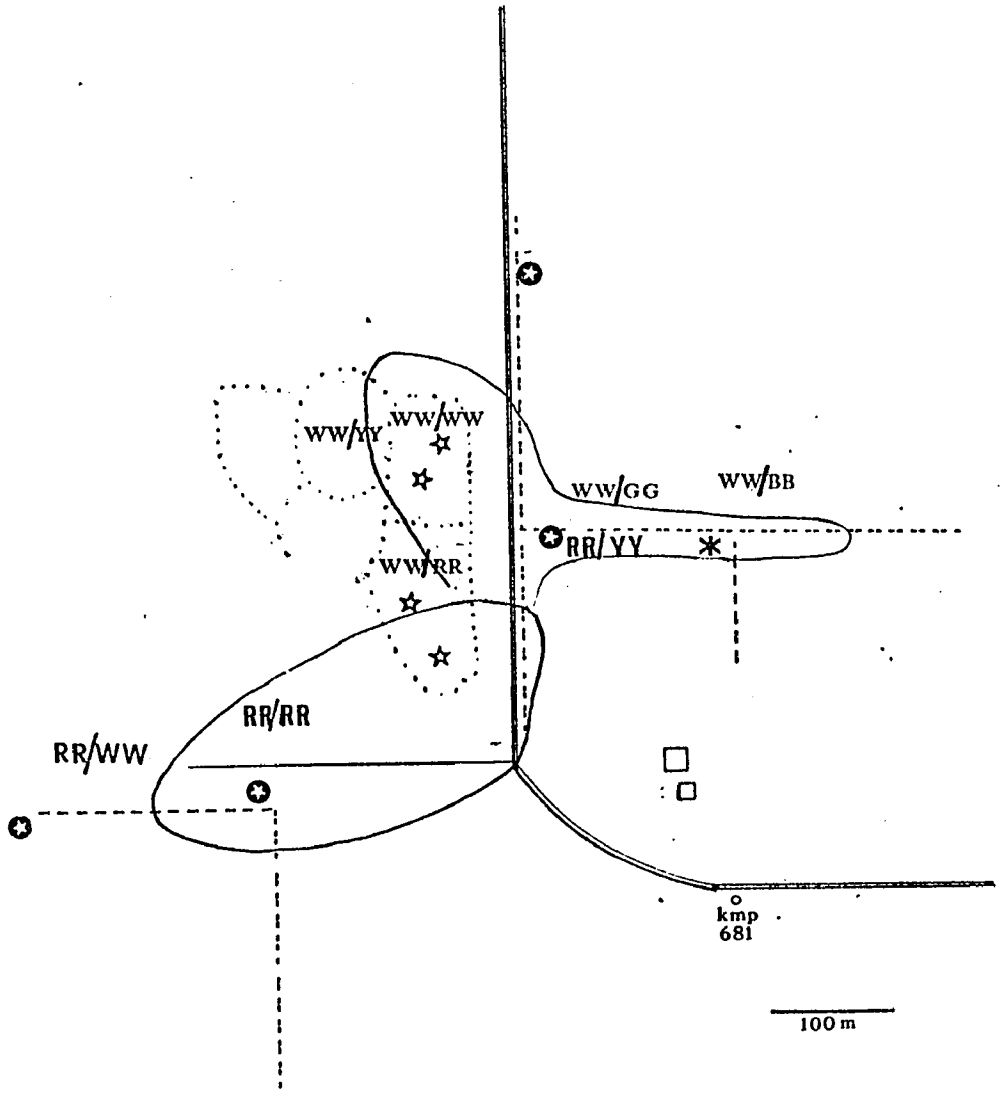
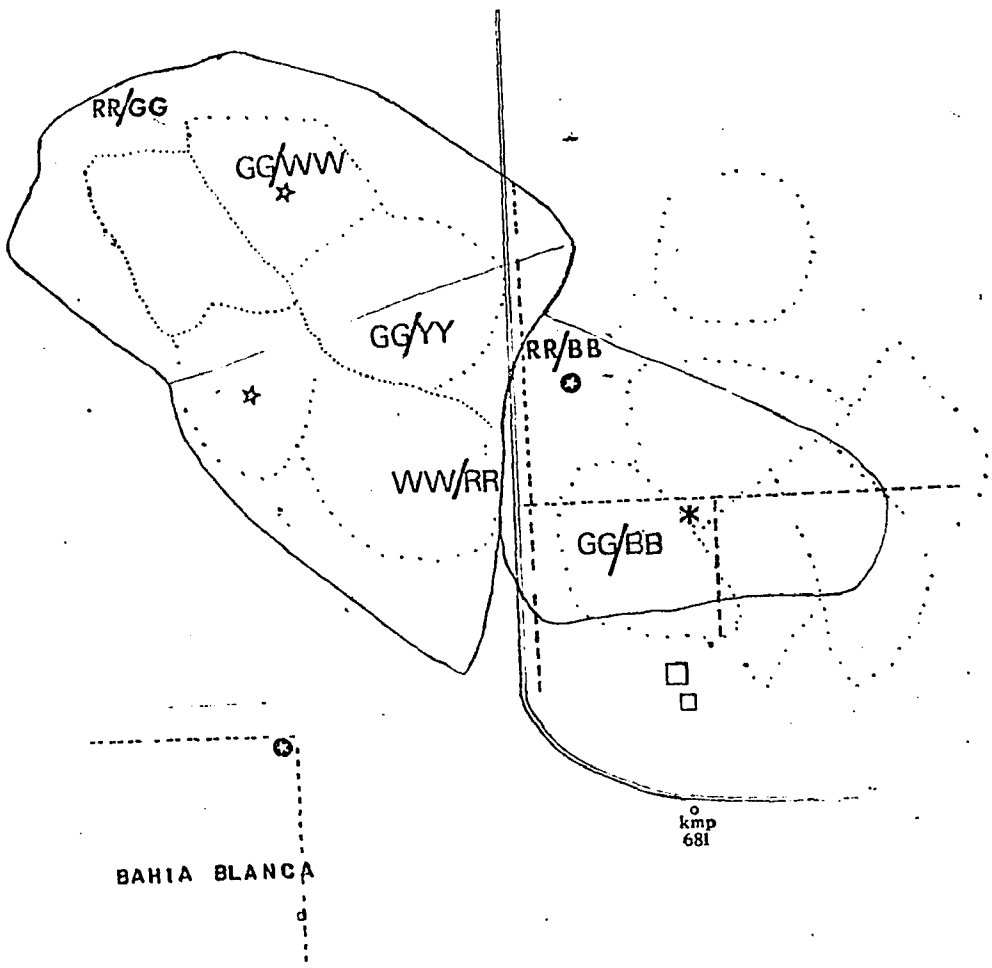


FIGURE 13 Bahia Blanca study area, December 1970.
Boldface RR/-- militaris males
Regular WW/-- defilippii males
militaris nest
defilippii nest
windmill
fence



Code same as figure 12.

militaris males are RR/GG and RR/BB
defilippii males are GG/BB, GG/WW, GG/YY, WW/RR

militaris boundary ····· defilippii boundary

Figure 14. Meadowlark territories on study area 7 km east of Bahia Blanca in 1971.

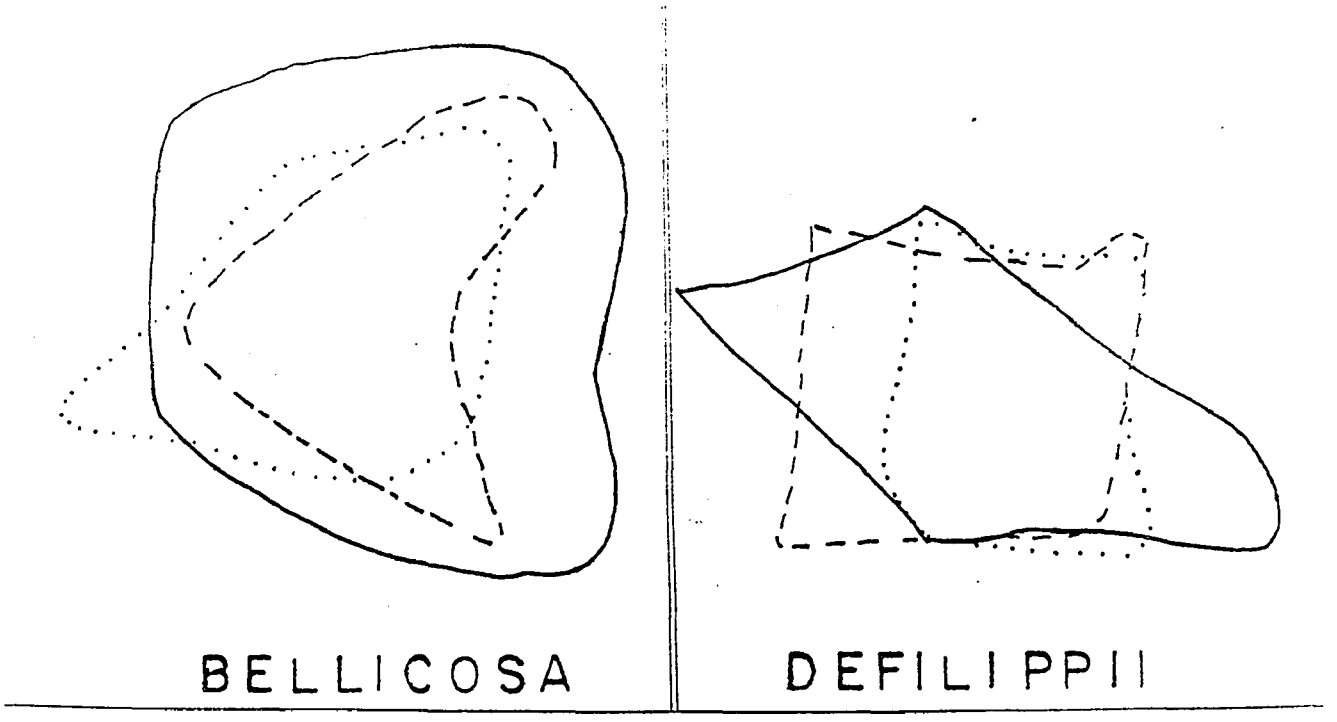


FIGURE 15. Changes in defended area for two meadowlark territories.
A. ♂ WR/BB bellicosa at Bujama (1972): --- 4 Sep. ... 5 Sep. ___ 6 Sep.
B. ♂ RR/BB defilippii at Saudade (1971):--24 Oct. ...27 Oct. ___12 Nov.

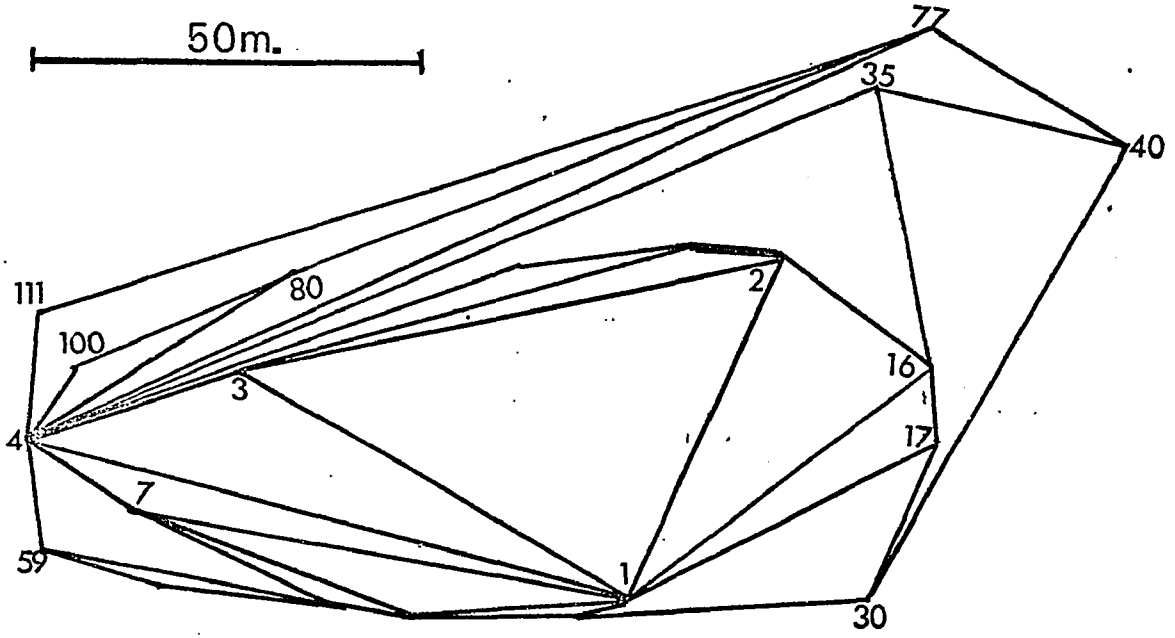


FIGURE 16. Increase in observed territory size for the "Triller" at Saudade. Numbers indicate the number of the observed position change.

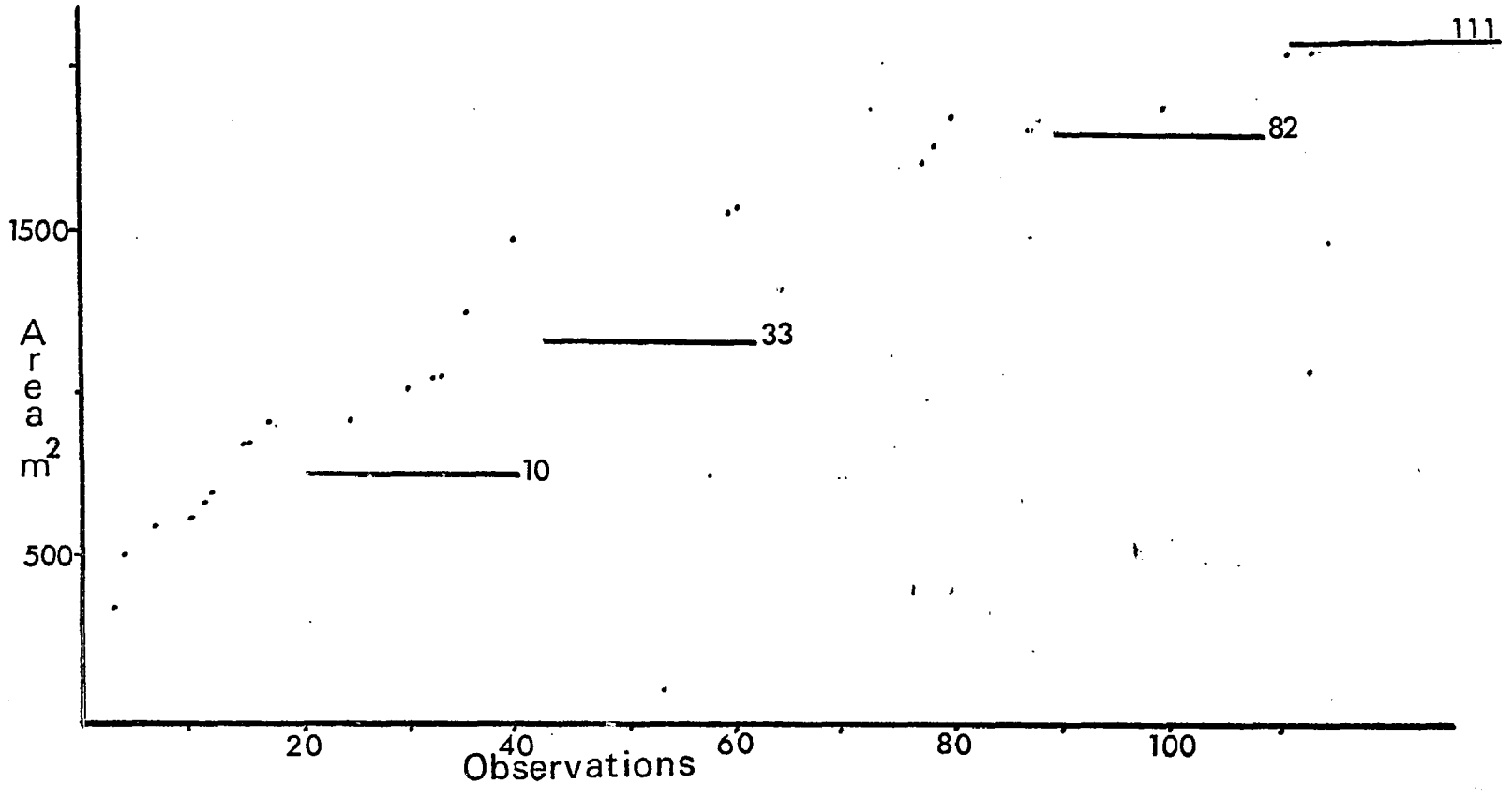


FIGURE 17 . Observation/Area Curve for Triller activity at Saudade. Four lines show apparent asymptotes reached after certain numbers of observations.

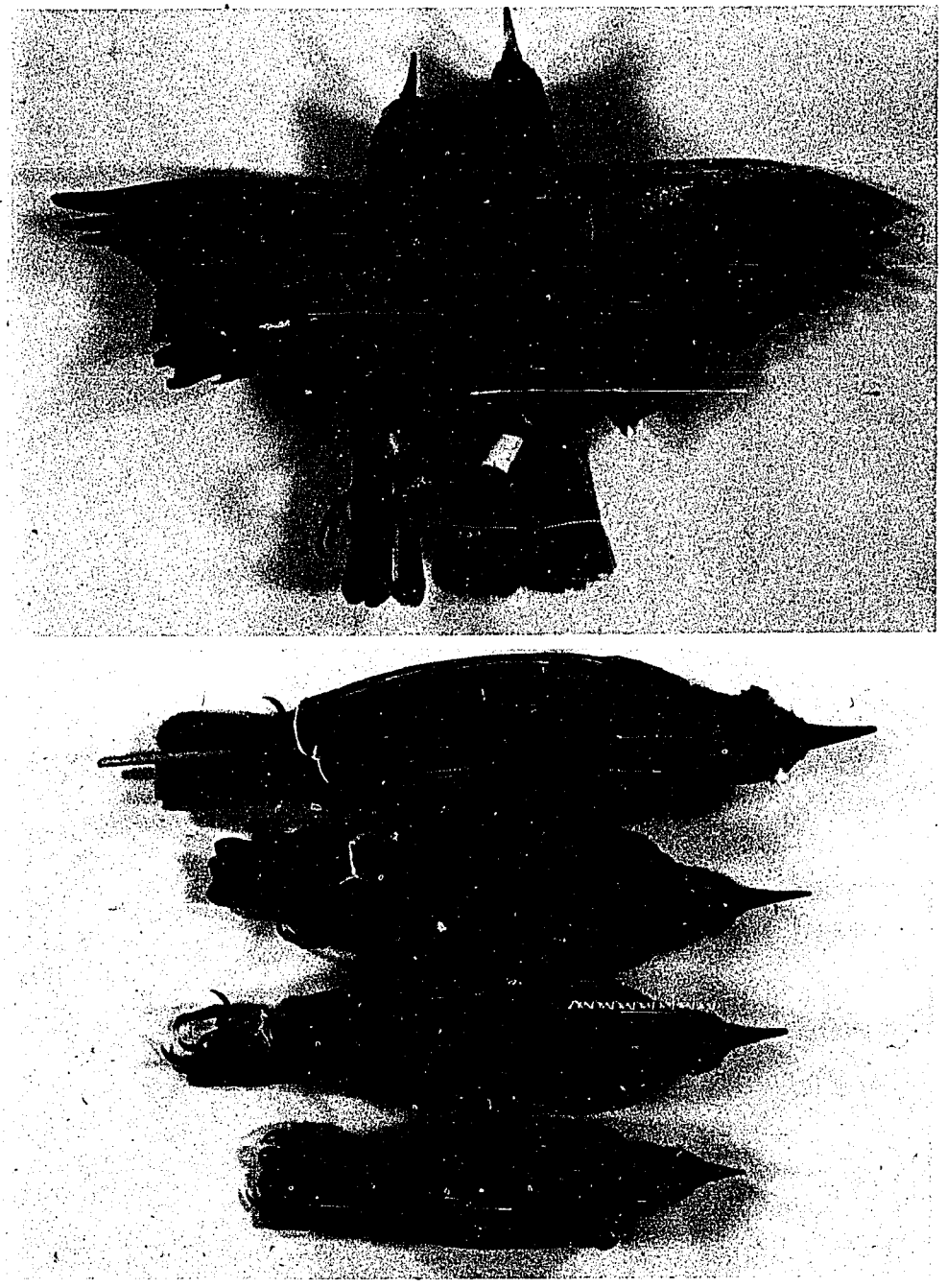


FIG 18. Male specimens of red-breasted meadowlarks.
A. Adult male defilippii (left) and militaris (right) showing different under wing linings.

B. (top to bottom) militaris, defilippii (worn plumage) defilippii (fresh plumage) and superciliaris.

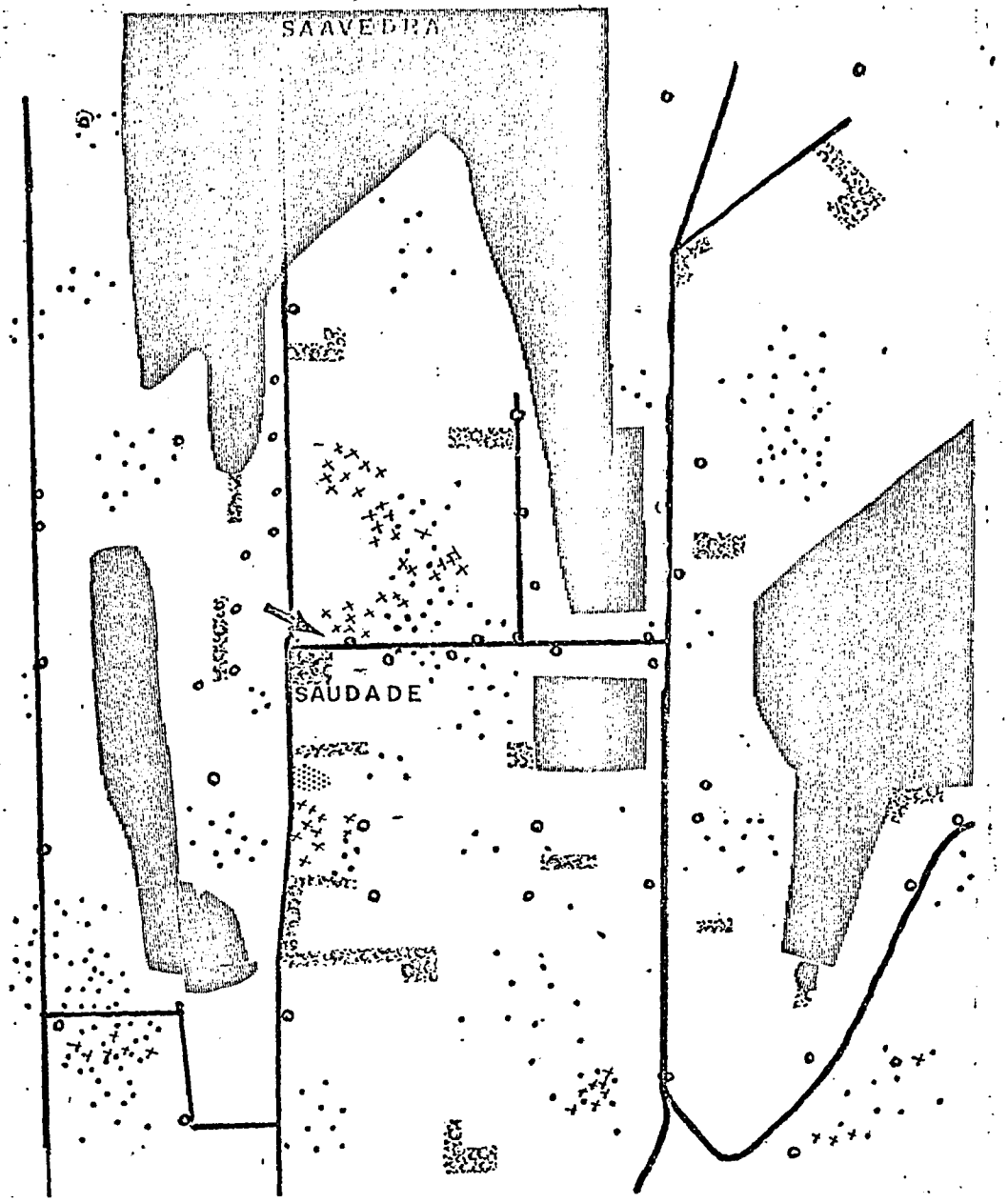


FIGURE 19 Estancia La Saudade and surrounding area. Arrow and asterisk mark main study area. Cross hatched areas were not censused.

• defilippii + superciliaris ○ militaris

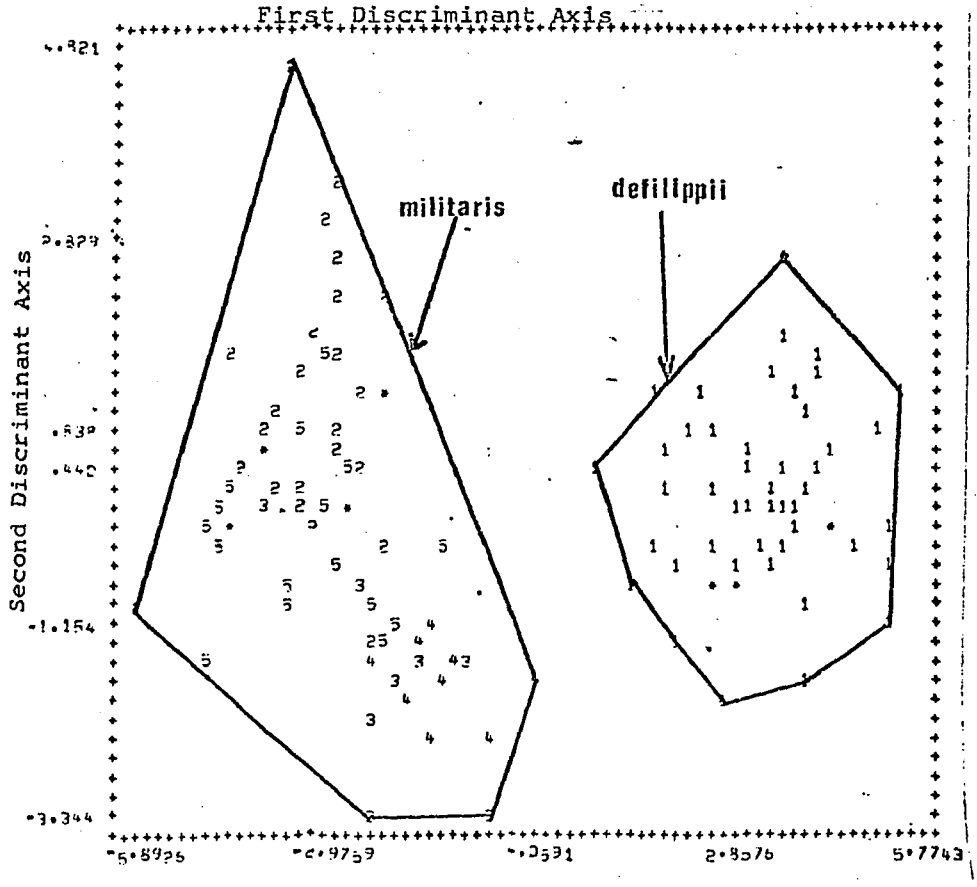
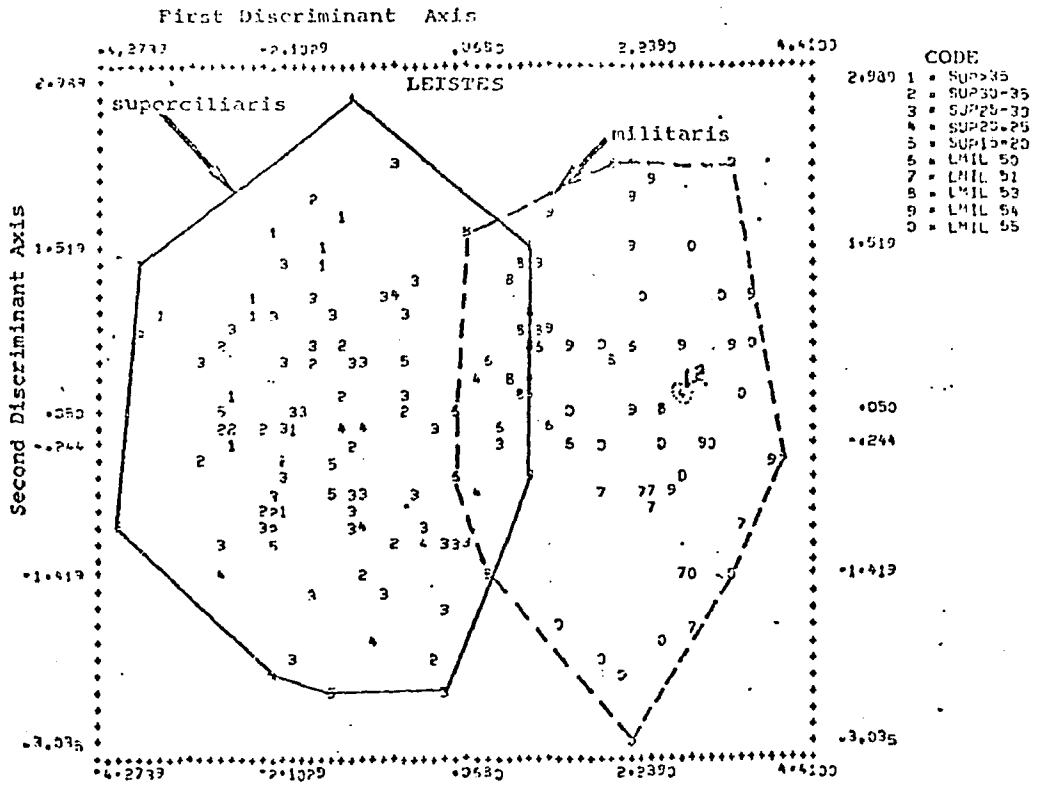


FIGURE 20 Clusters of male militaris and defilippii plotted against first two discriminant axes. First axis provides 100% discrimination of the two species. Second axis provides some separation of militaris cluster.

Code: 1. defilippii
2. militaris-Tierra del Fuego and Patagonia
3. militaris-northern pampas
4. militaris-southern pampas
5. militaris-Andes (La Rioja to San Juan)



Individual male Leistes plotted on first two discriminant axes. Area of overlap amounts to 11 % of superciliaris cluster, 15% of militaris cluster, and 7 % of total plane.
12 denotes a superciliaris specimen which would be identified as a militaris on the basis of measurements. It proved to be superciliaris on basis of plumage and derivation.

KEY. 1-5 superciliaris 6-0 militaris
(1--south of 35° S. lat. 2--30-35° S. lat. 3--25-30° S. lat.
4--20-25° S. lat. 5--15-20° S. lat.
6--N.W. South America 7--Guyanas & Trinidad 8--Amazonian Brazil
9--Boca Rio Andira,Brazil 0--east-central Brazil)

Figure 21. Multiple discriminant analysis of 10 geographic groups of male Leistes.

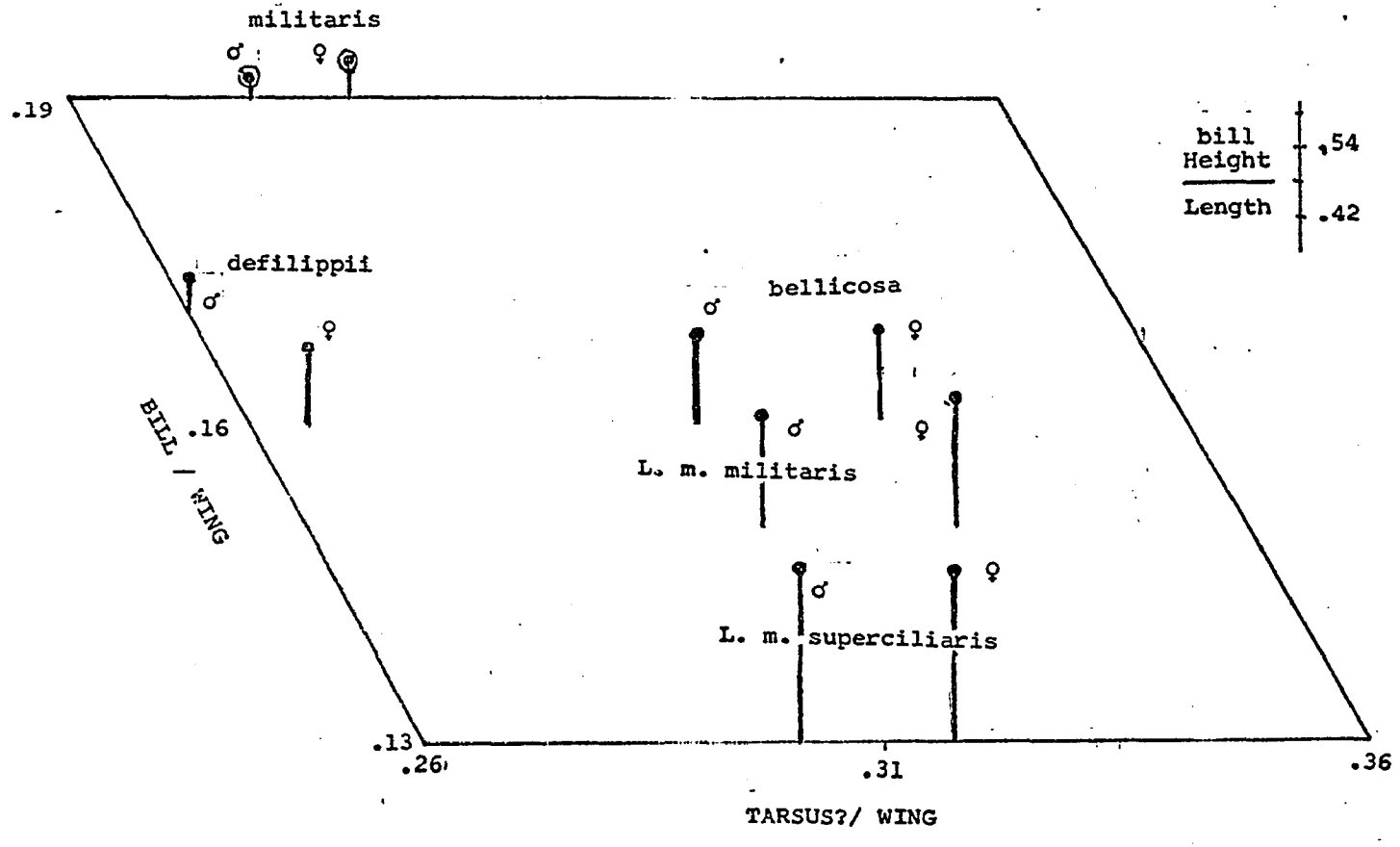


FIGURE 22. Ordination of meadowlark taxa with with respect to 3 shape indices. Circle around militaris emphasizes the long tail.

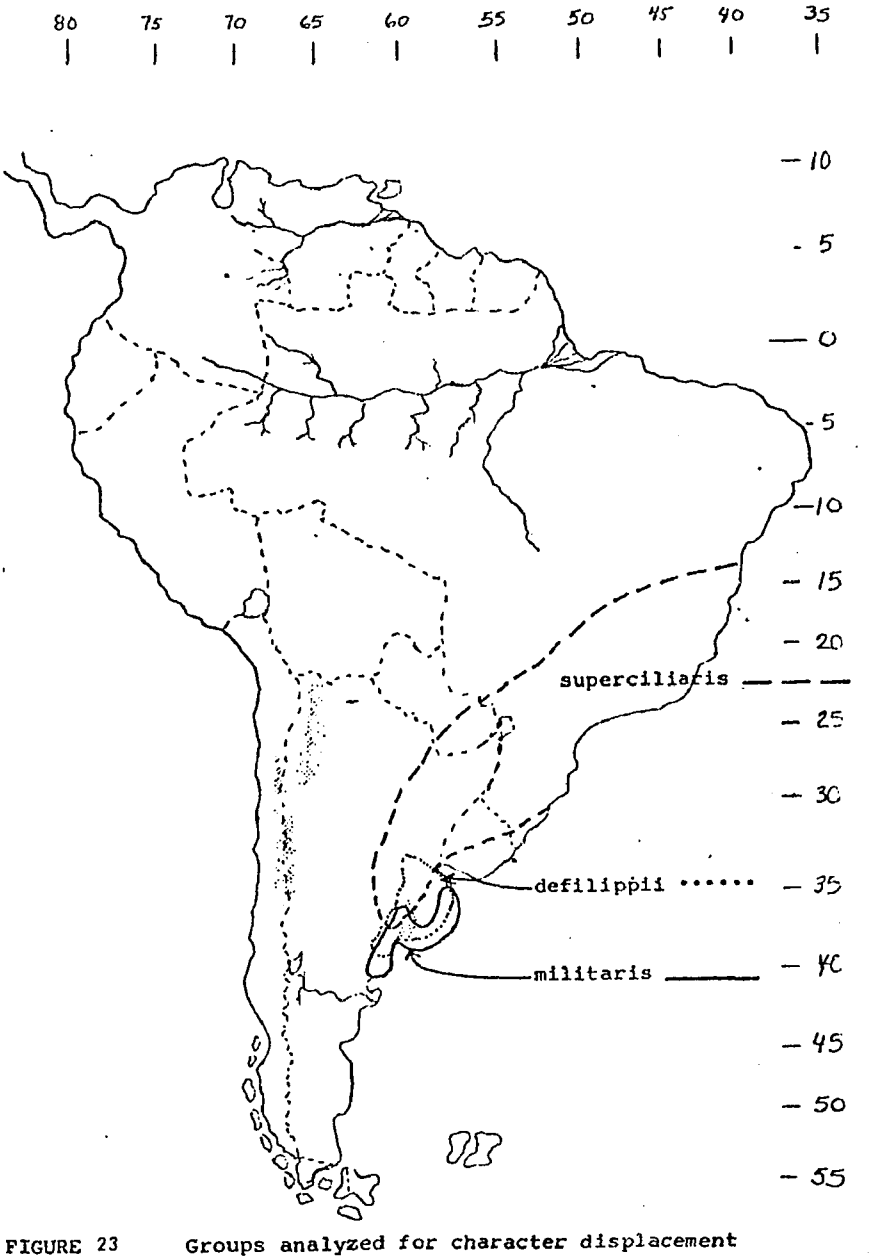


FIGURE 23 Groups analyzed for character displacement

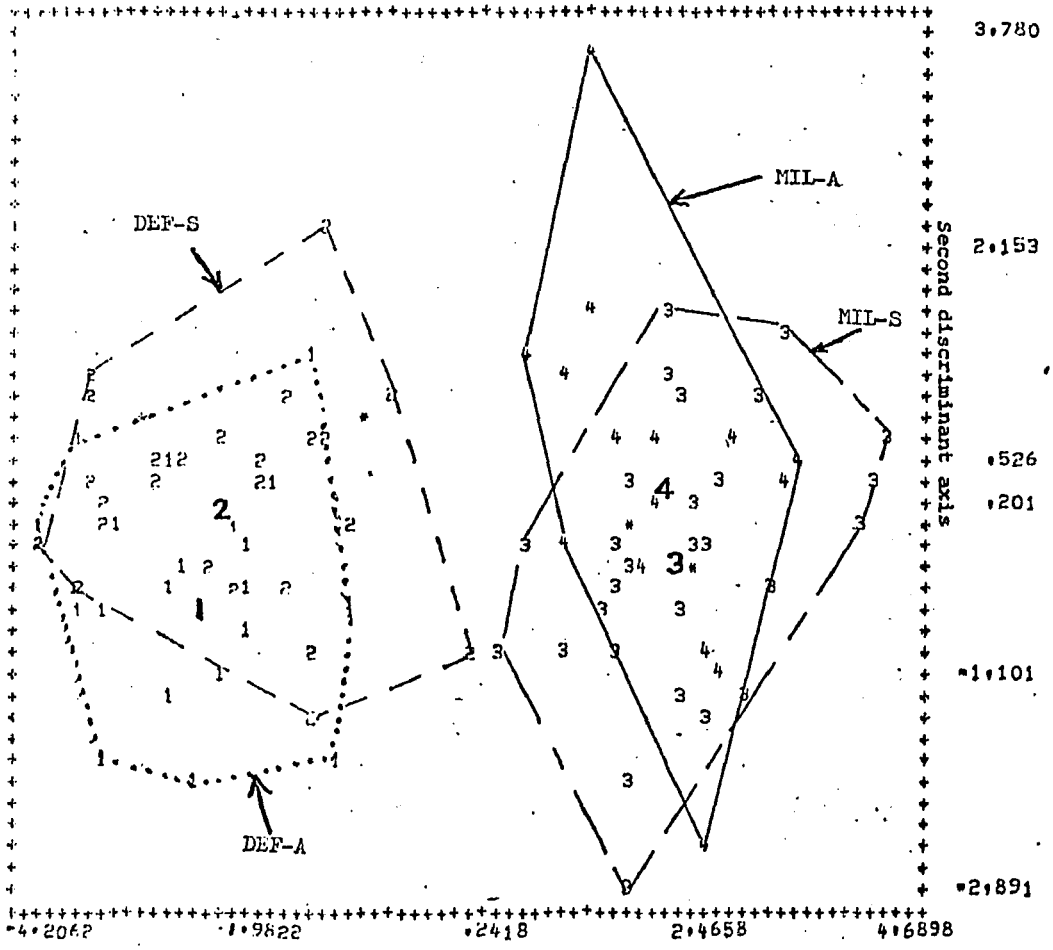


FIGURE 24. Multiple discriminant analysis of allopatric and sympatric populations of militaris and defilippii. Individuals in each population are plotted against first two discriminant axes.

Small numbers represent individuals
Large boldface numbers represent centroids
* two or more individuals coincide
Dotted, dashed and continuous lines enclose clusters

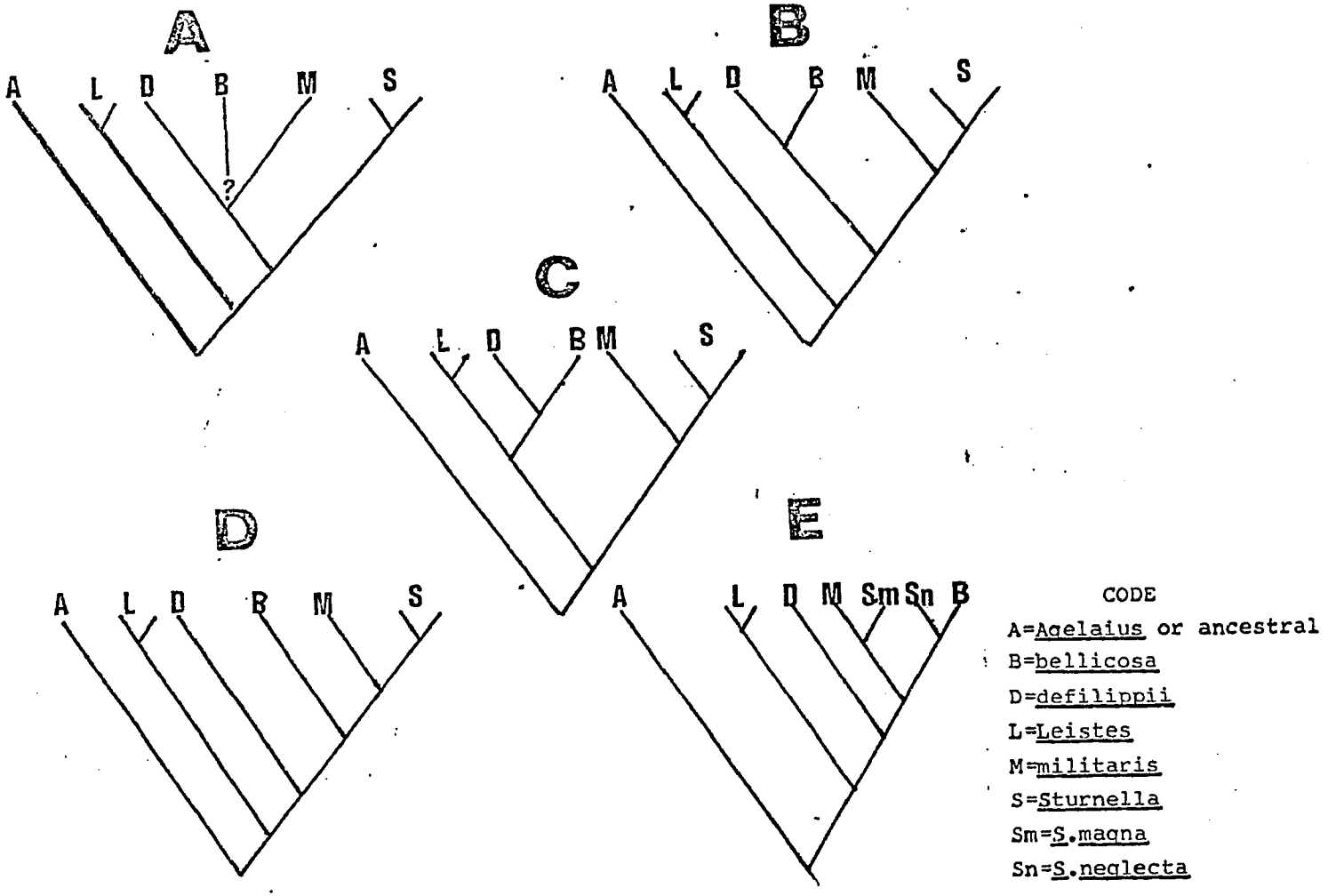
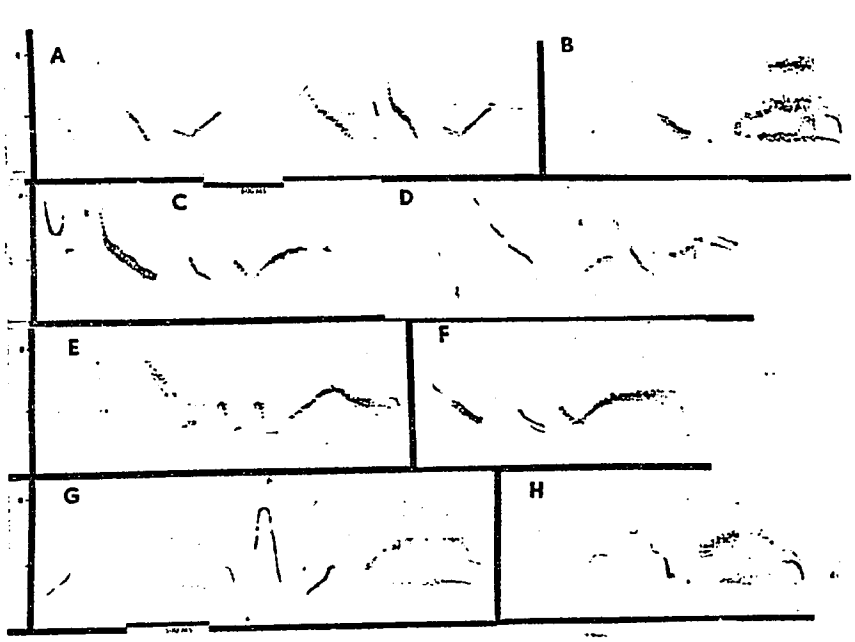


FIGURE 25 . Five alternative phylogenetic hypotheses for meadowlarks. (For discussion see text)

APPENDIX I SONOGRAMS

This appendix contains 53 plates of sonograms of vocalizations of red-breasted meadowlarks. All were made using a narrow band pass filter unless wide band or WB is indicated.

PRIMARY SONGS OF MILITARIS MALE YY/BB (Saudade 1971)



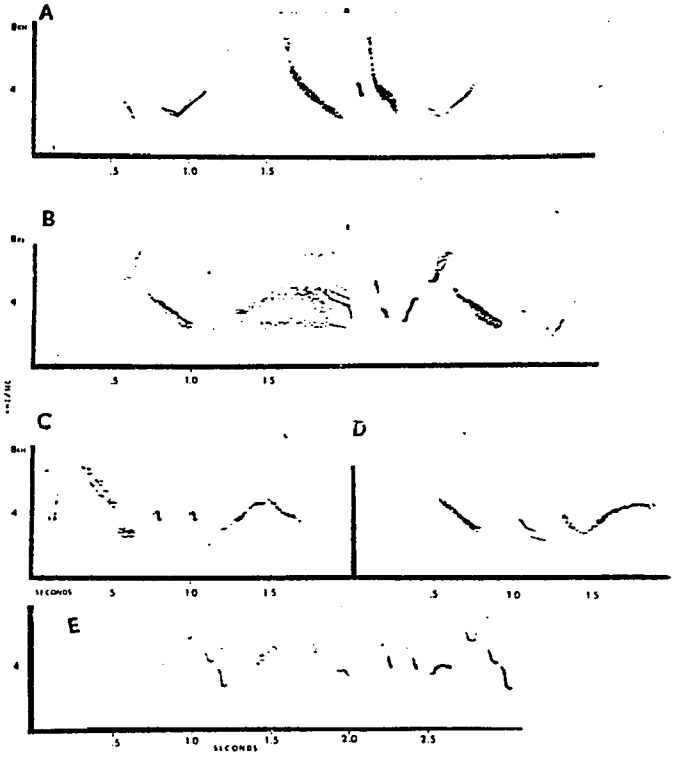


PLATE 1. A,E, And G represent double songs, the latter with two buzzes.
F. is a simple three element song. H. Has complex whistled introduction.

PLATE 2. A is a double song (identical to 1A. but with additional introductory note).
B. complex double song C&D. Simple primary songs.
D. (same as 1F, recorded 3 weeks later). E. Complex double song.

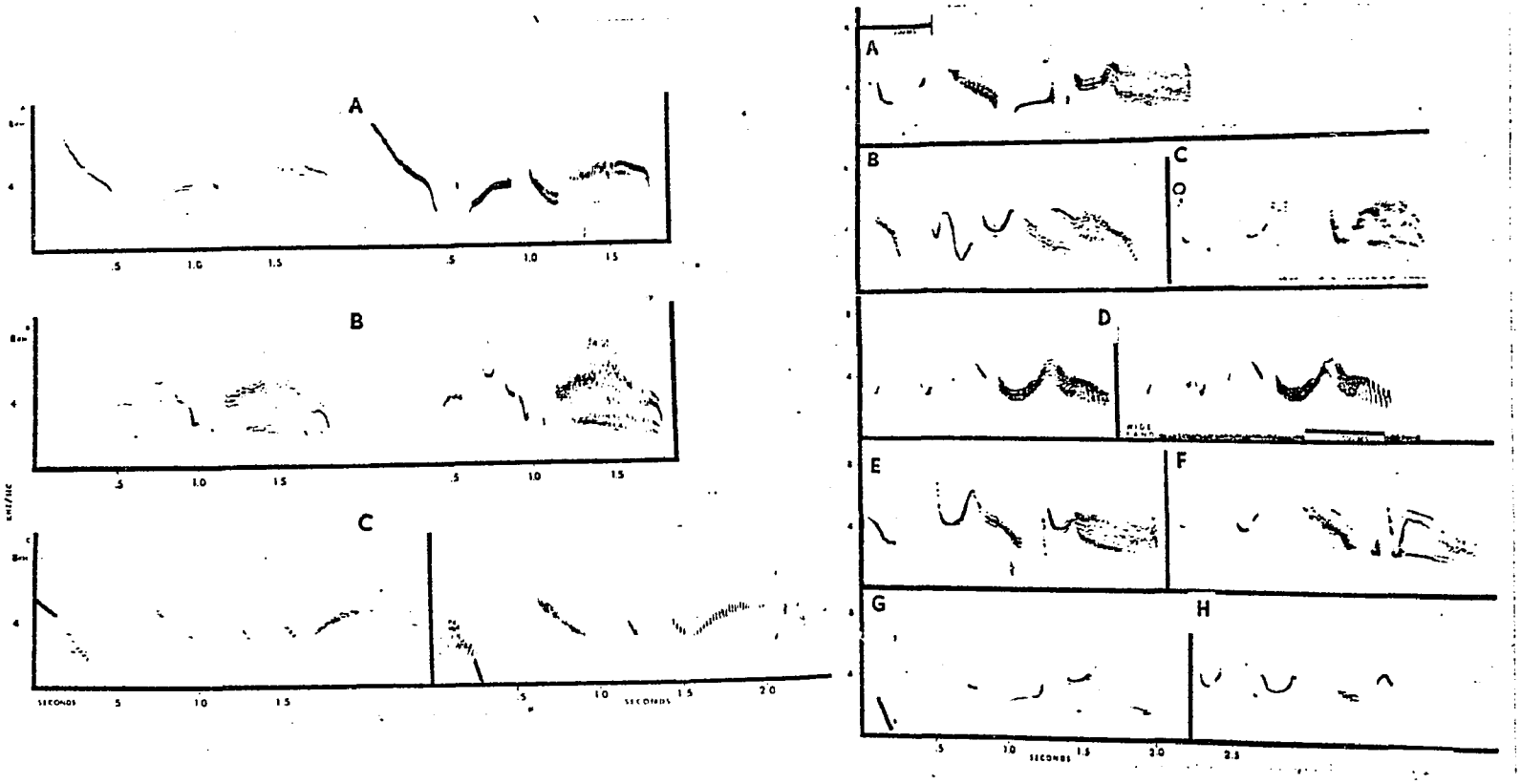


PLATE 3. Additional primary songs of militaris YY/BB (Saudade 1971).Wide band on right.
A. Primary with long introductory note. B. Same as 1H.
C. Same as 1 F. Descending note in A is modulated at 200 hz, buzz modulated at 50 hz.

PLATE 4. Primary songs of militaris 30 km west of Bahia Blanca (BB30W).
A. BB/BB predominant pattern. B. BB/BB 2nd pattern.
C. Song of female duetting with BB/BB, note erratic distribution of energy.
D. BB/BB 3rd pattern (1970). Wide band graph (right) shows modulation frequency unresolvable at normal speed. E. BB/RR song. F. BB/BB 4th pattern.
G. Unmarked ♂ #3 H. BB/WW(1971) unlike any of 1970 patterns.

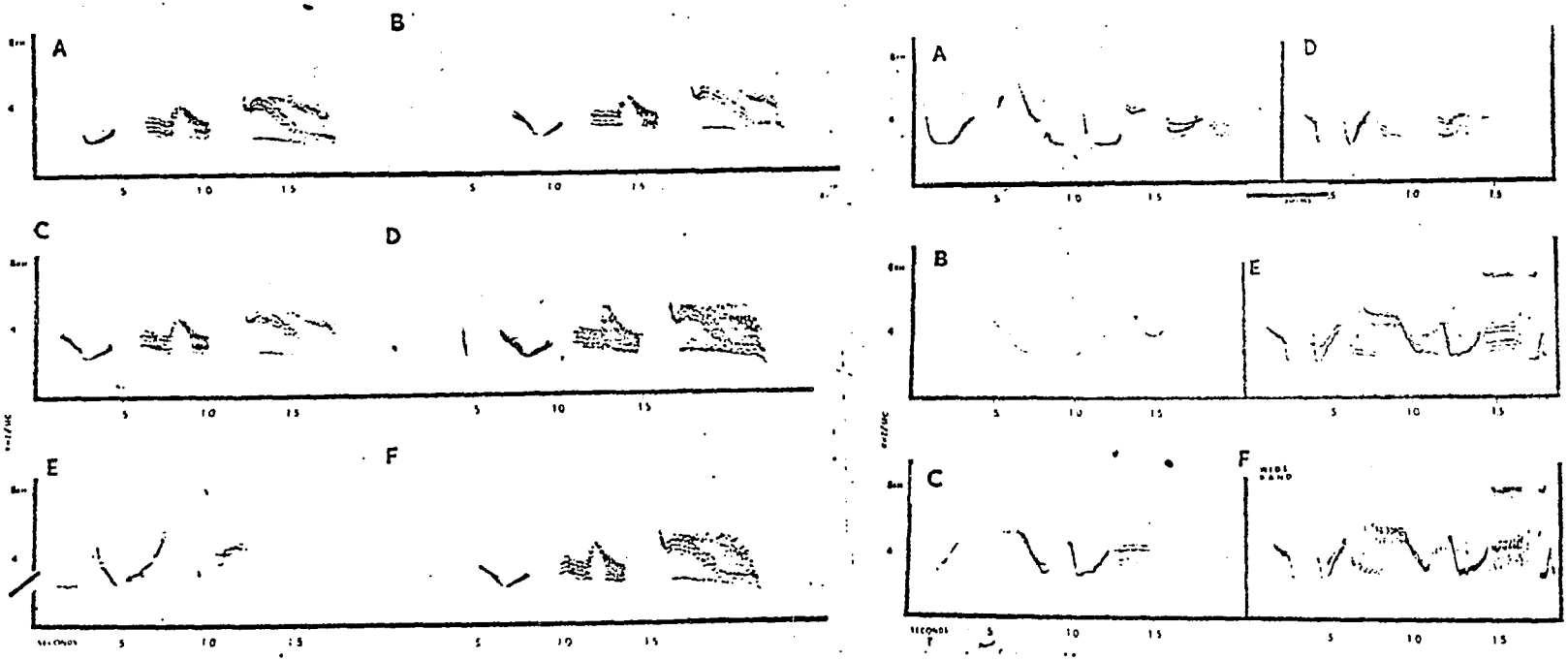


Plate 5. Primary songs of militaris GG/RR (Saudade, 18 Dec.1970). A,B,C and D represent essentially identical songs repeated in four song bouts of 13, 9, 7,and 16 songs. Song E given in response to playback of Bariloche militaris song. After about 7 renditions he reverted to original song type (see F).

Plate 6. Primary songs of two militaris males 25 km. southwest of Bahia Blanca (Umbucto). A,B,C given by male one. A is a complex double song with single buzz. D. given by male 2 in response to male 1. E. Duet with male 2 leading. F. Wide band of E.

Plate 7

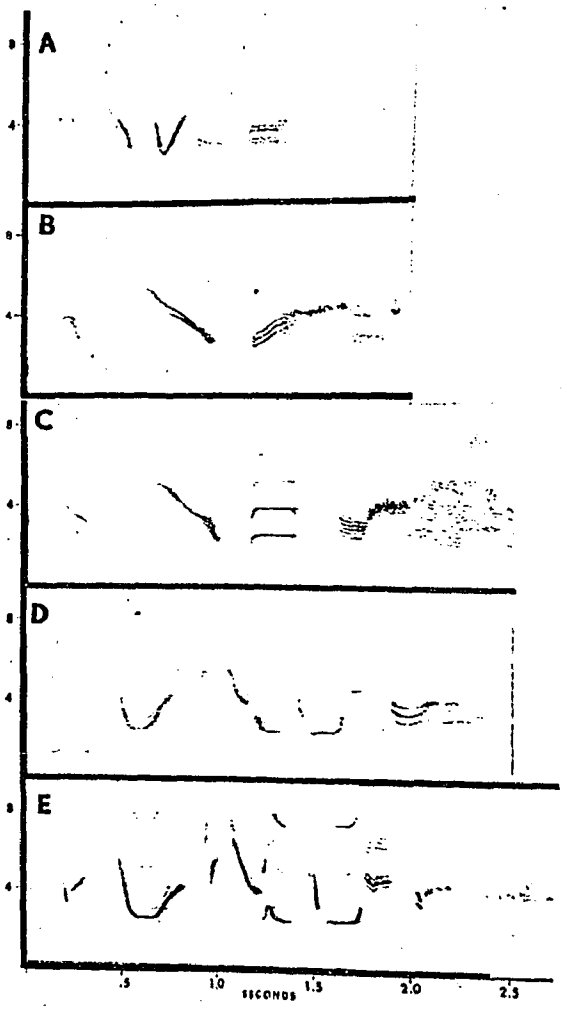


Plate 8

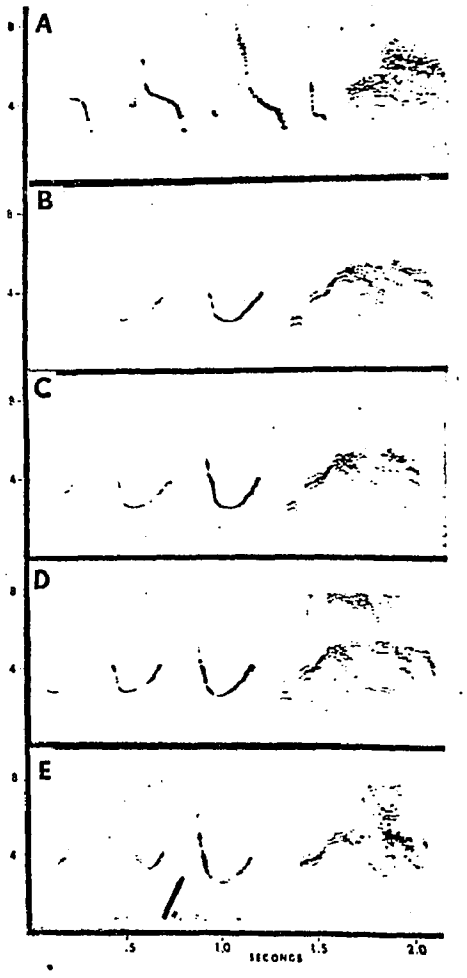


PLATE **7.** Primary songs of 3 militaris males near Umbucto, 25 km. southwest of Bahia Blanca.
A-B. Two song patterns of male 2. C. Song of male 3.
D. Complex song of male 1.
E. Complex song of male 2 given in duet with male 1. Note overall similarity in introductory notes, but different length of buzz.

PLATE **8.** Primary songs of 2 militaris males at kmp 742 (Route 3) 40 km. southwest of Bahia Blanca.
A. Song of male 1 characterized by 's' shapedintroductory notes.
B-E. Songs of male 2 characterized by 'u' shaped introductory notes.

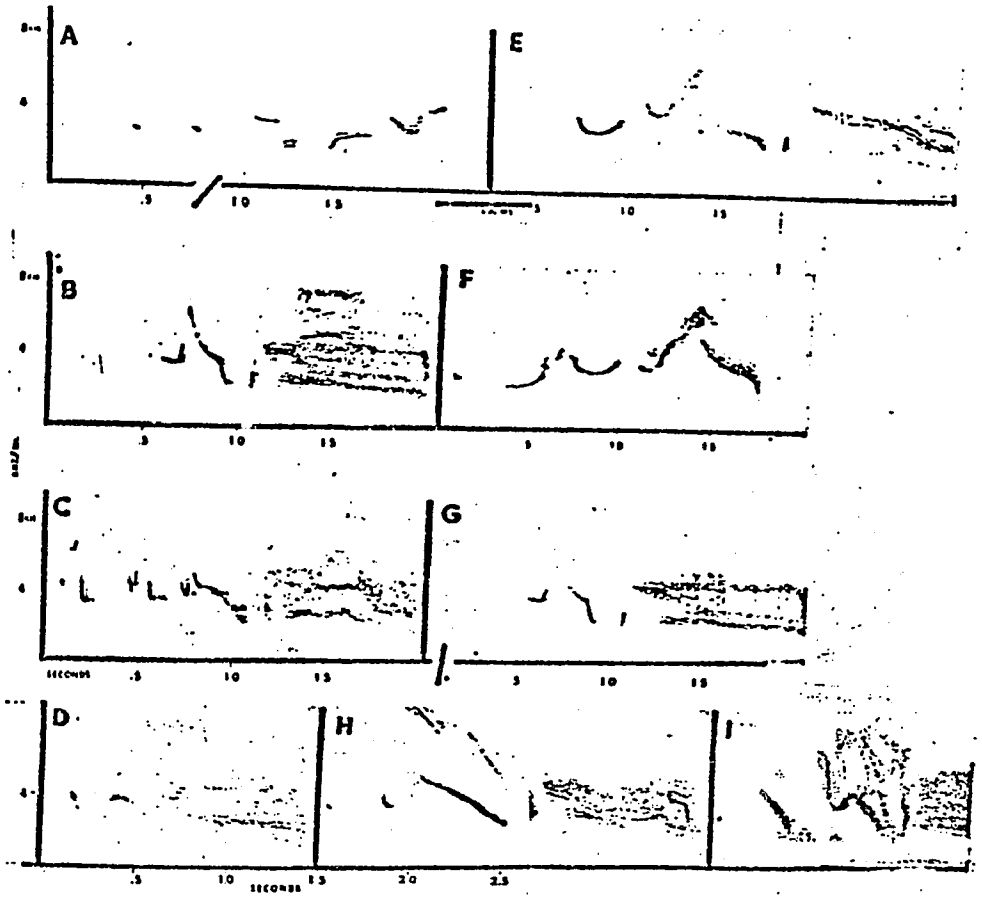


Plate 9. Primary songs of three militaris males near El Condor, Neuquen, Argentina, 28-29 November, 1970.
A. Male 3 song followed by female song. B. BB/GG primary song.
C. Complex song of male 3. D. Short song of male BB/YY.
E. Long song of BB/YY, F. Song of male BB/YY preceeding 7E.
G. 4th song pattern of BB/YY. Very weak introductory note is retouched. Second introductory note is very low (1900 hz). H. 5th song pattern of BB/YY including long introductory note lasting 450 msec.
I. 6th pattern of male BB/YY.

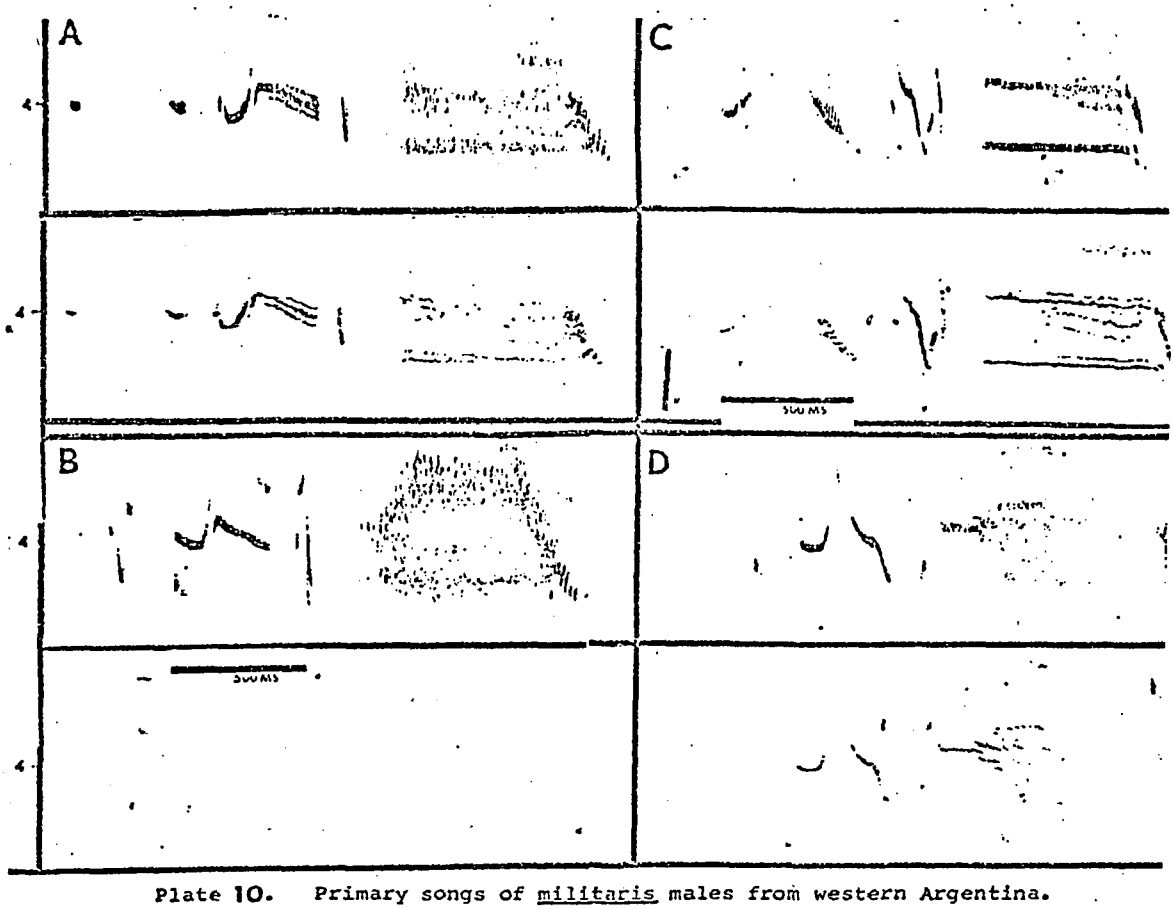


Plate 10. Primary songs of militaris males from western Argentina. A. 9km. east of San Carlos de Bariloche. This song was used for playback to birds on the pampas. B. Second song pattern of same bird as A. C. San Martin de los Andes. Very weak introductory note retouched. Note two dominant frequencies in buzz. D. El Condor, 12 km. southeast of San Carlos de Bariloche. Very faint introductory note is visible in the wide band figure. All songs have wide band over narrow band.

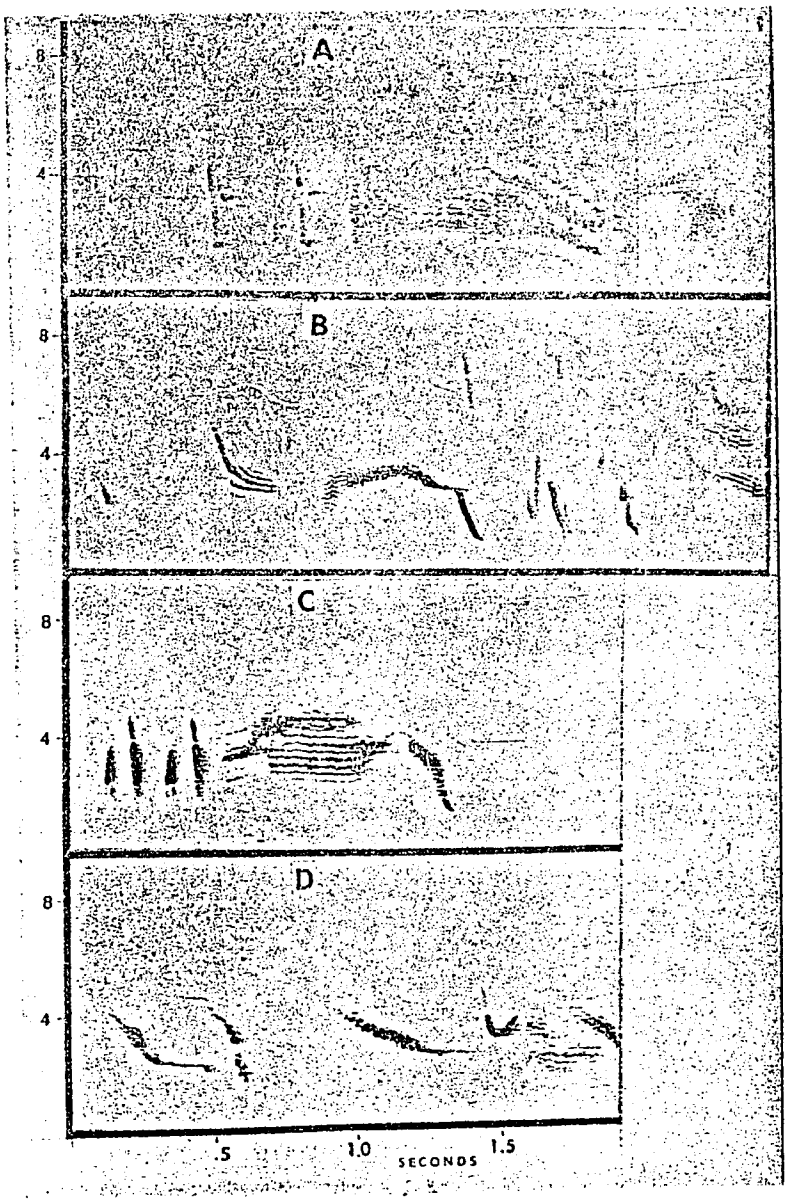


PLATE 11. Four primary songs of catamarcanus recorded from one or two unmarked males.

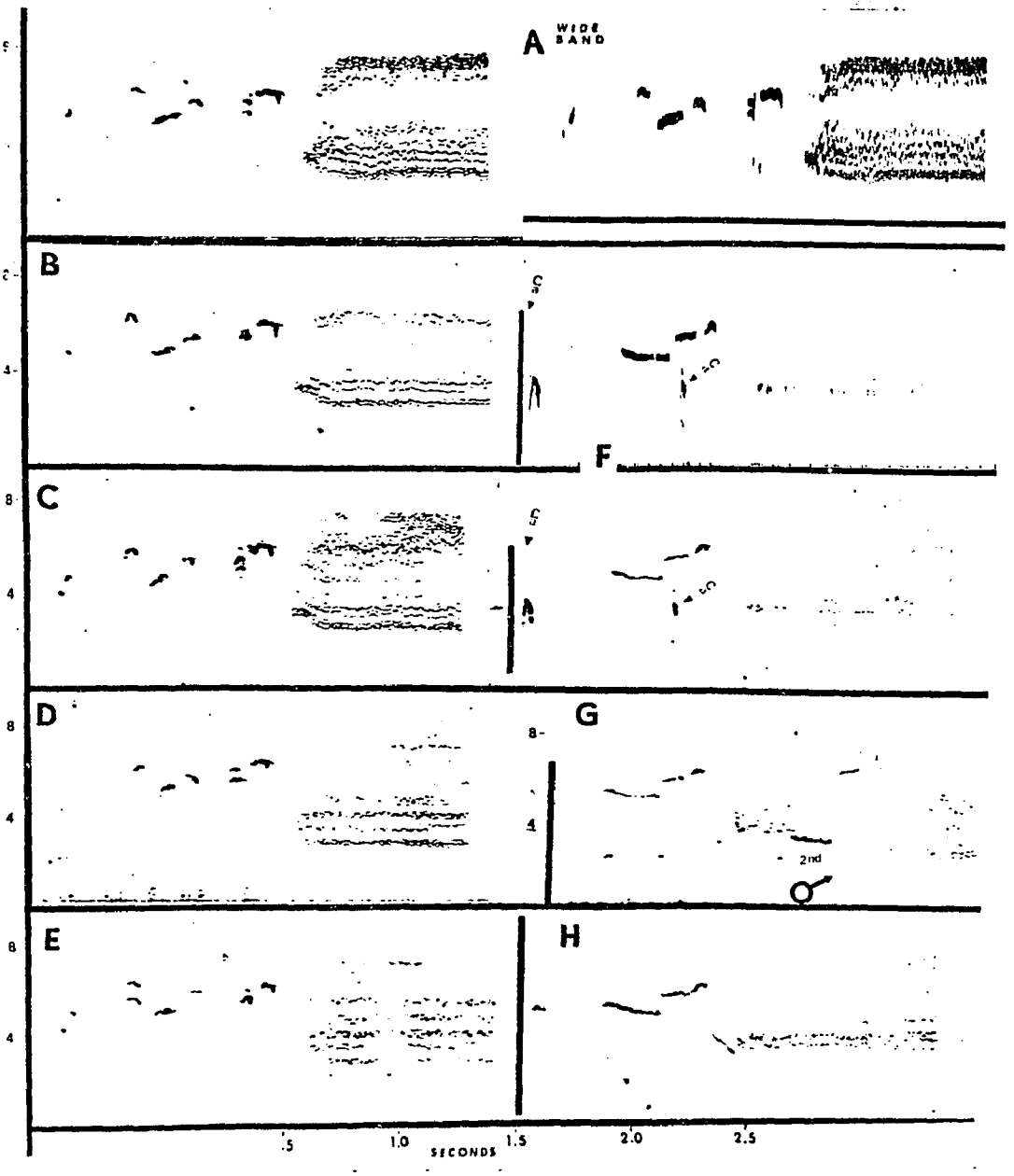


Plate 12. Primary songs of two defilippii males near Tres Picos, 48 km. north of Bahia Blanca, recorded 11 Nov. 1970.
A-E first male and F-H 2nd male. A. has wide band figure on right. A-E are essentially identical songs recorded over a period of two hours. No other song patterns obtained from this bird.
F. has wide band figure over narrow band figure (call is indicated by 'Ca'. G is same song pattern with another primary song overlapping it. H. is same song pattern with additional introductory note. No other song patterns were obtained from this male.

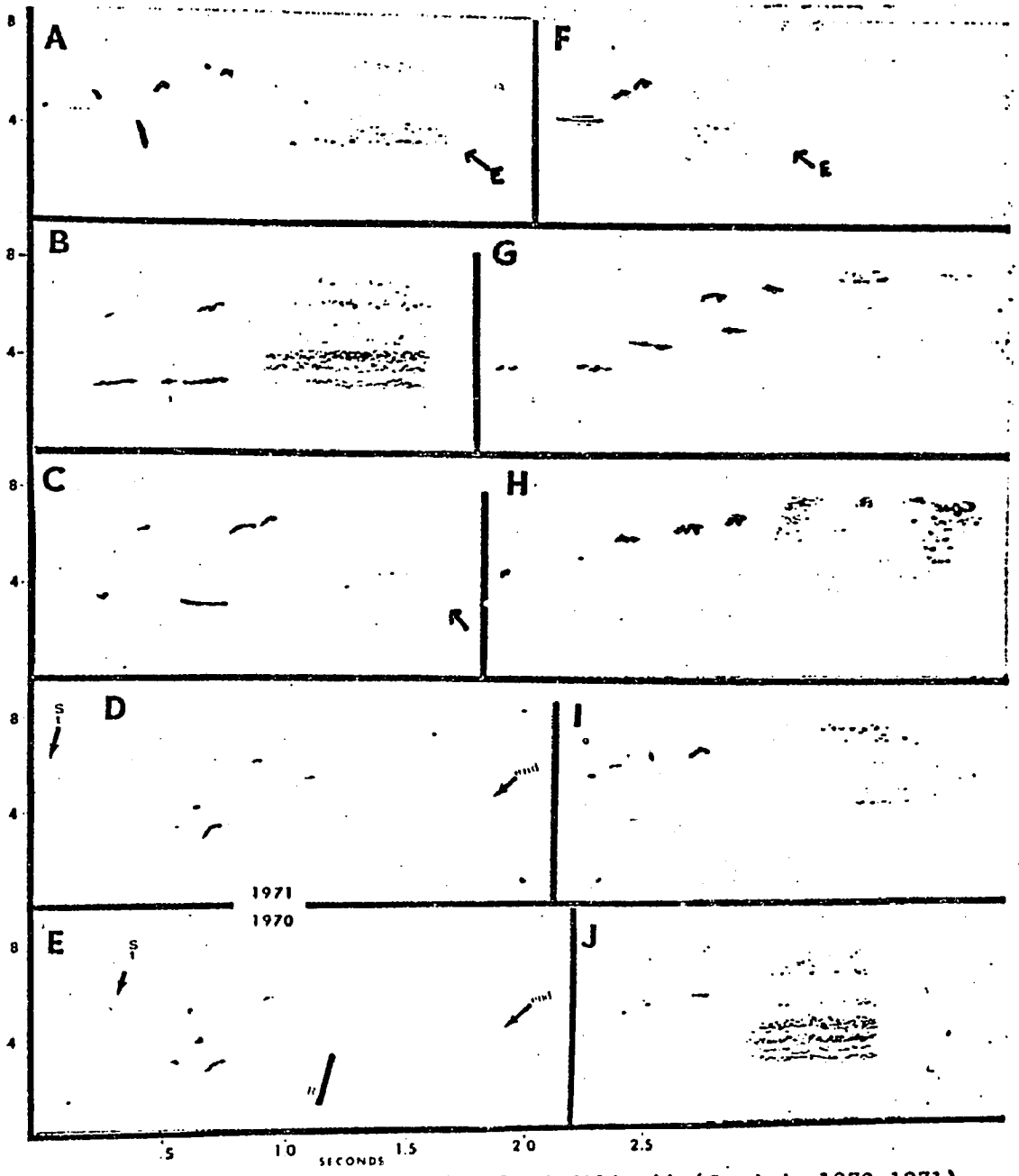


PLATE 13 . Primary songs of 9 male defilippii (Saudade 1970,1971). These songs indicate variability in energy distribution within the buzz and in arrangement of introductory notes.
A. Male E (Saudade 1971). B. Unmarked male (1970).
C. Male RR/RR (1971) D,E male BB/WB (1971 over 1970)identical. This song is the same for both seasons and was characterized by a very weak buzz, sometime inaudable at a range of 20 meters.
F. male D (1971) G. male RR/BB 'double singer' (1971).
H. 'triller' (1971). I. male RR/YY (given immediately after flight.
J. Unmarked male (1970). Pattern resembles I, but only three introductory notes and a shorter buzz.

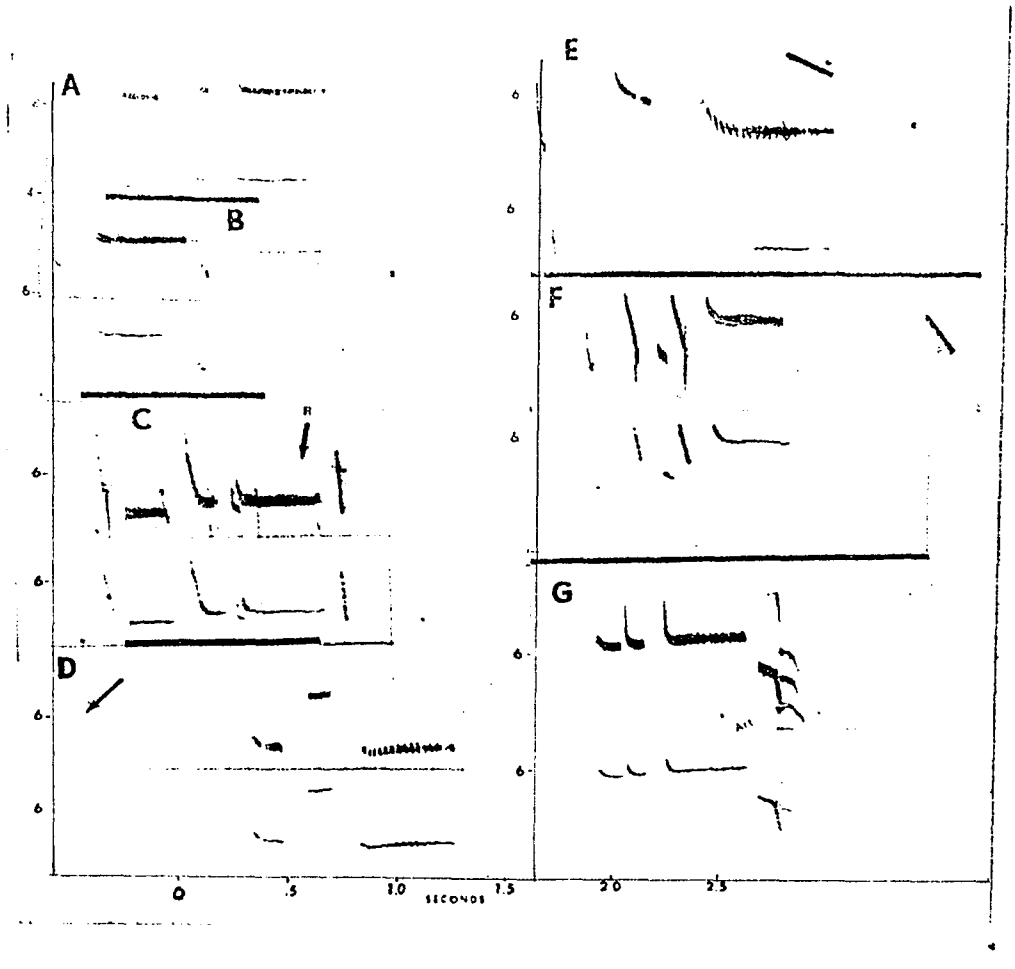


PLATE 14. Flight songs of defilippii males. (all have wide band sonogram mounted over narrow band)

A. Male RR/YY (Saudade 1971), 2 weak introductory notes were given occasionally.
B. Male RR/RR (Saudade 1971)
C. Male D (Saudade 1971), note similarity to G.
D. Male A (Saudade 1971) chasing an intruder, arrow indicates very weak introductory note
E. Unmarked male at Umbucto. Note long series of 't' notes.
F. Male G (Saudade 1971)
G. Male F (Saudade 1971)

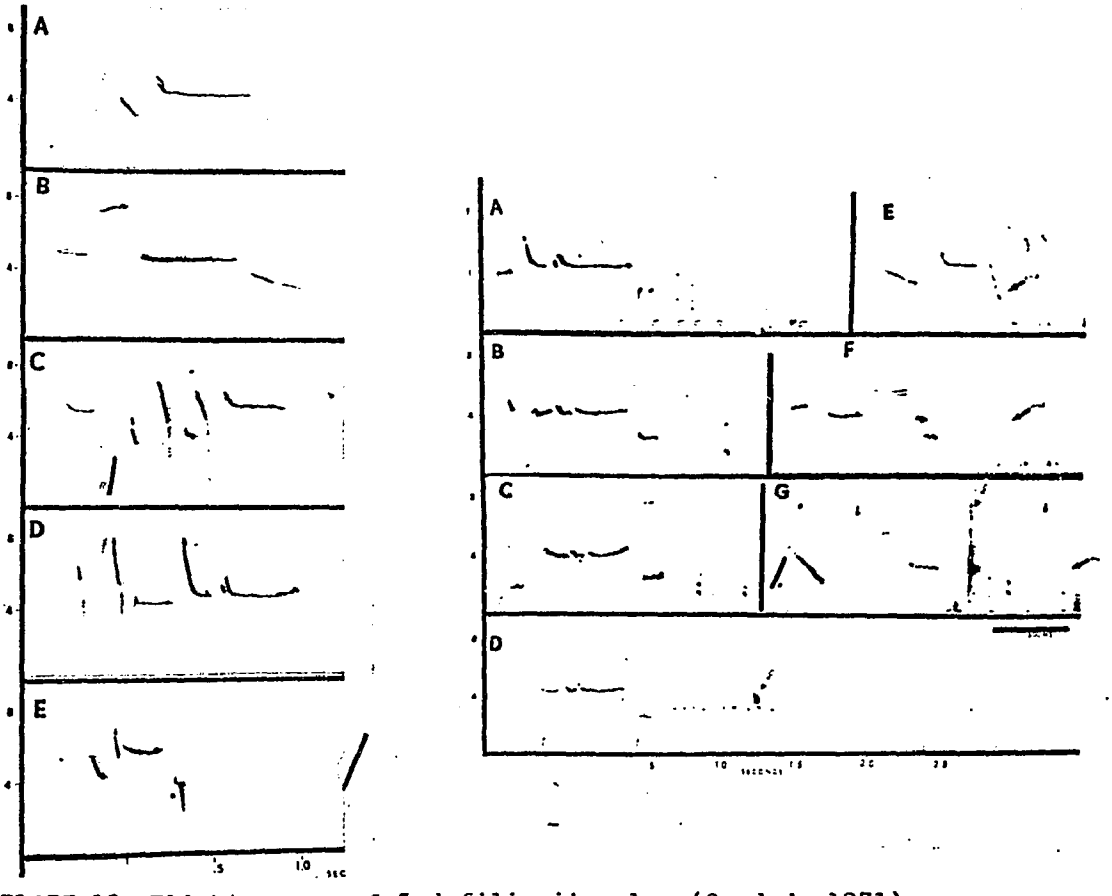


PLATE 15. Flight songs of 5 defilippii males (Saudade 1971).
A. RR/RR (similar to 14B) B. RR/BB ("Double-singer")
C. ♂G (similar to 14F) D. RR/YY (similar to 14A)
E. ♂D 2nd flight song pattern from this territory, but birds unmarked.

PLATE 16. Flight songs of 5 defilippii males (Tres Picos, 11 Nov.1970).
A. Song terminates with three different 't' notes.(arrow = artifact)
B. 2nd male with song similar to A. C. 2nd male, 2nd pattern.
D. 2nd male, 3rd pattern, all whistled notes on one pitch.(arrow = call).
E. Another male with a short 4-note whistle.
F. Another male with a 6-note whistle.
G. Another male with introductory element of 45° angle.
First arrow indicates retouching, 2nd indicates a call. 3rd = 'end'

Plate 17

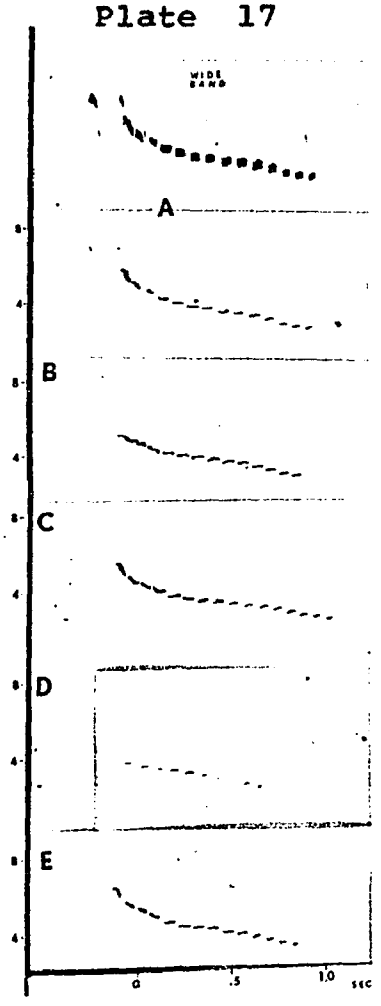


Plate 18

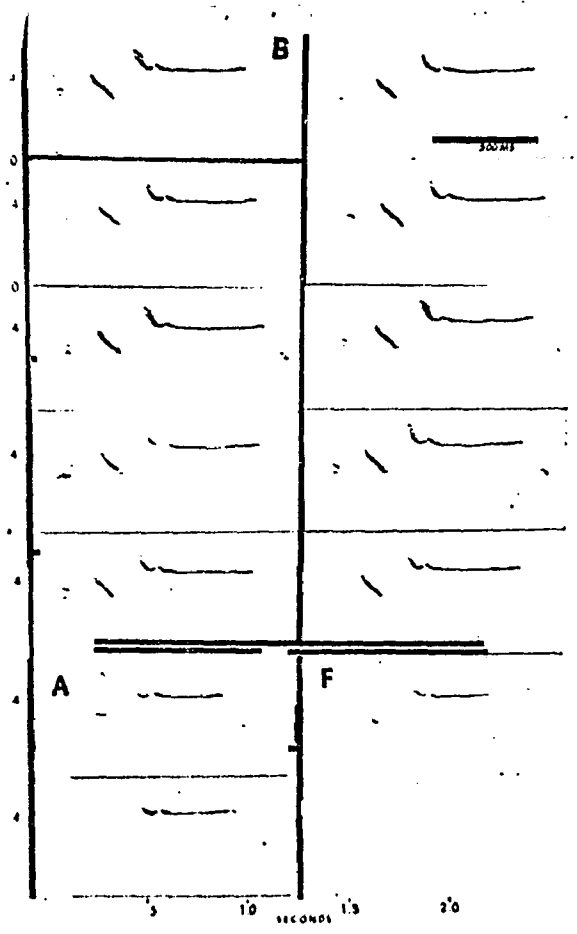


PLATE **17**. Flight songs of defilippii male "Triller"(Saudade,1971).
A. Has wide band graph mounted over narrow band.
A-E. Recorded 26 Oct. to 8 Nov. 1971.

PLATE **18**. Flight songs of 3 <u>defilippii</u> males (Saudade 1971)
These three birds share a common song pattern and held adjacent areas.
B. 10 songs of RR/RR (duration 1.065 ± .020 seconds).
A. 2 songs of ♂A. Middle whistle consistently shorter than for B.
F. 1 song of ♂F.

PLATE 19

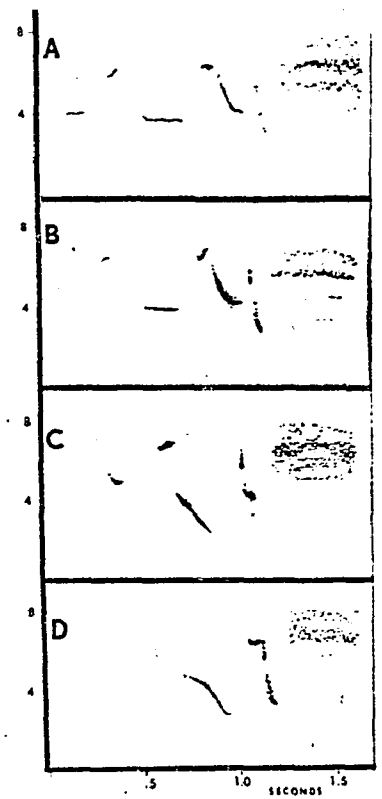


PLATE 20

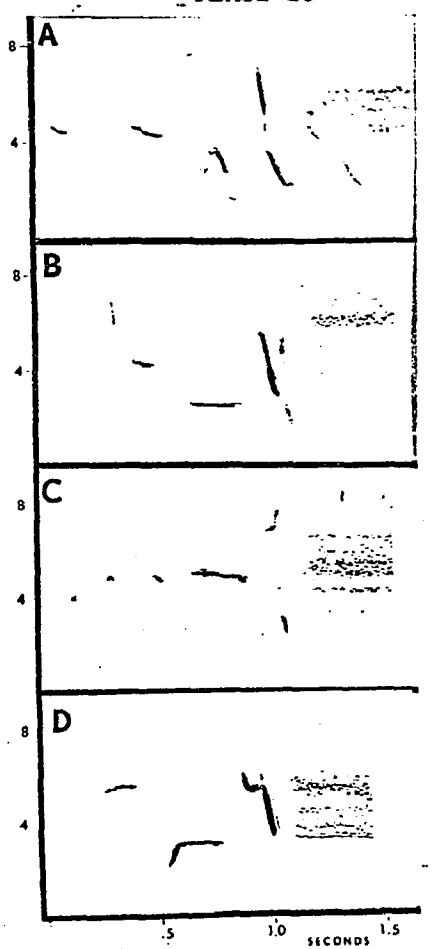
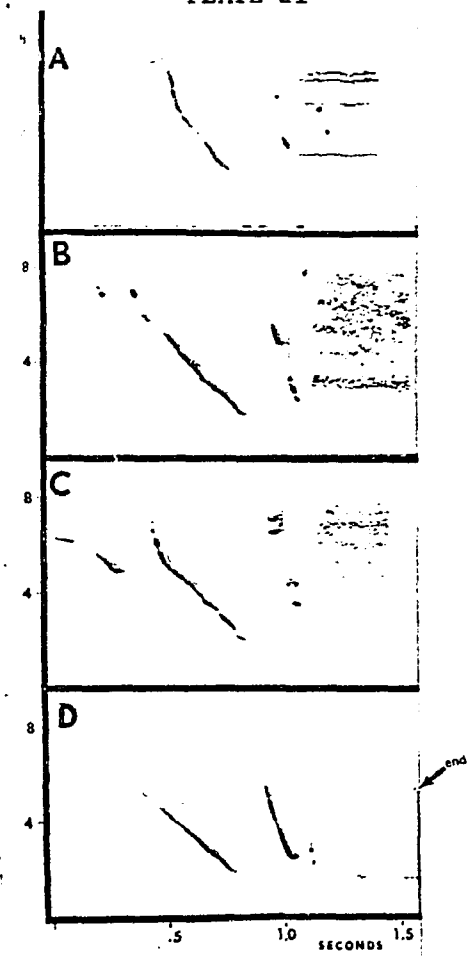


PLATE 21



PLATES 19-21 . Representative primary songs of bellicosa males.

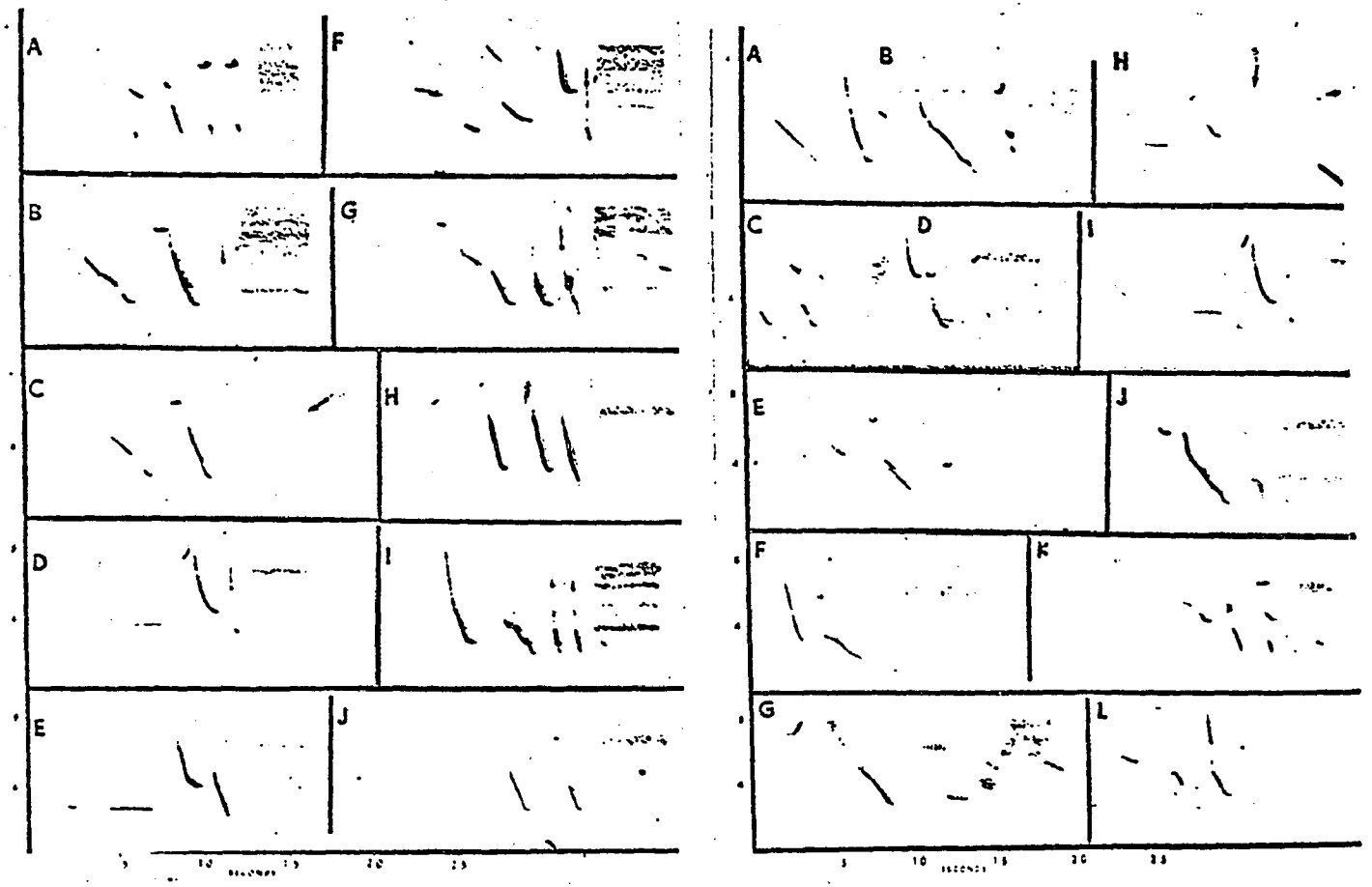


PLATE 22. Primary songs of bellicosa males with multiple steep elements.

PLATE 23. Primary songs of bellicosa males with single steep elements.

A-B and C-D represent primary song duets.

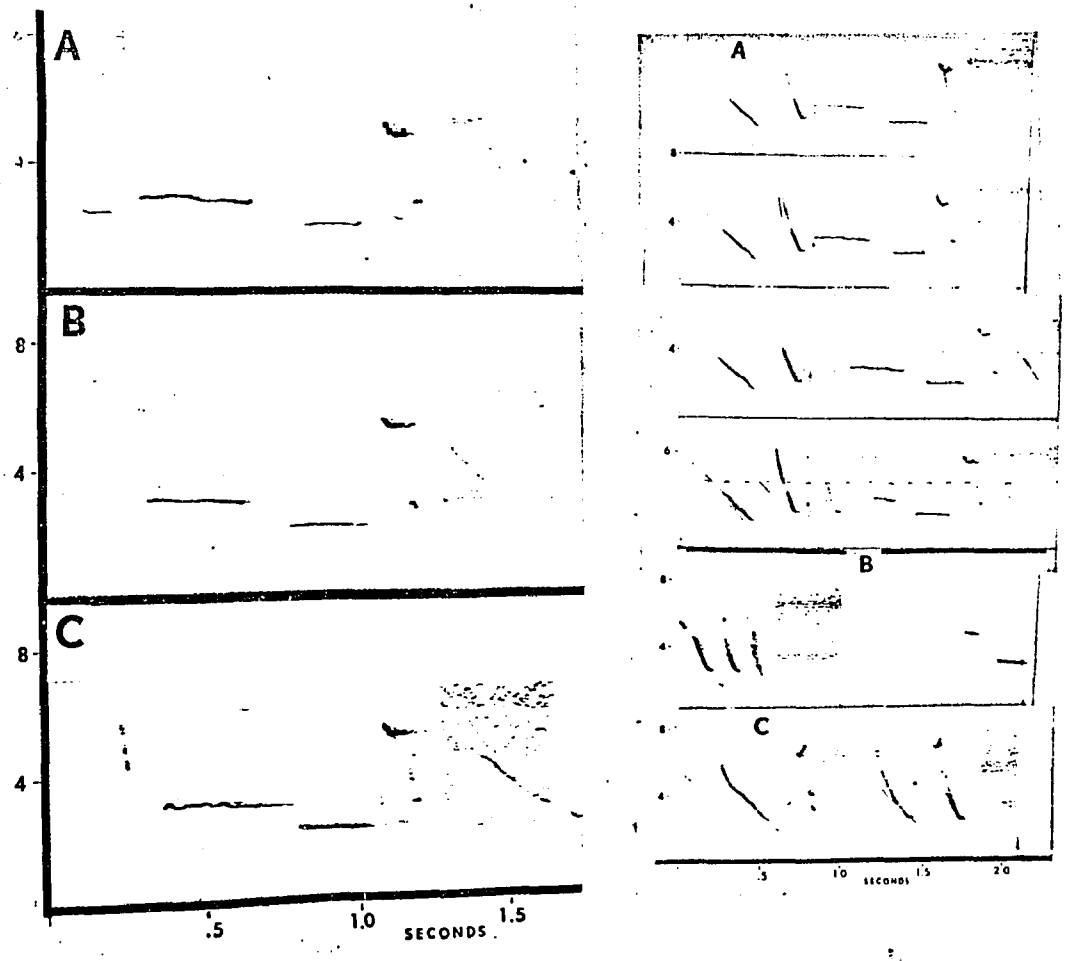


PLATE 24. Alternate-type primary song of bellicosa. A,B,C are three consecutive songs given by one bird in about 20 seconds while engaged in a vigorous primary song duet with neighbor. Note variation in introductory note.

PLATE 25. Primary song duets of bellicosa.
A. Four duets involving 3 individuals. (one gives alternate-type pattern).
B-C. Two other duets

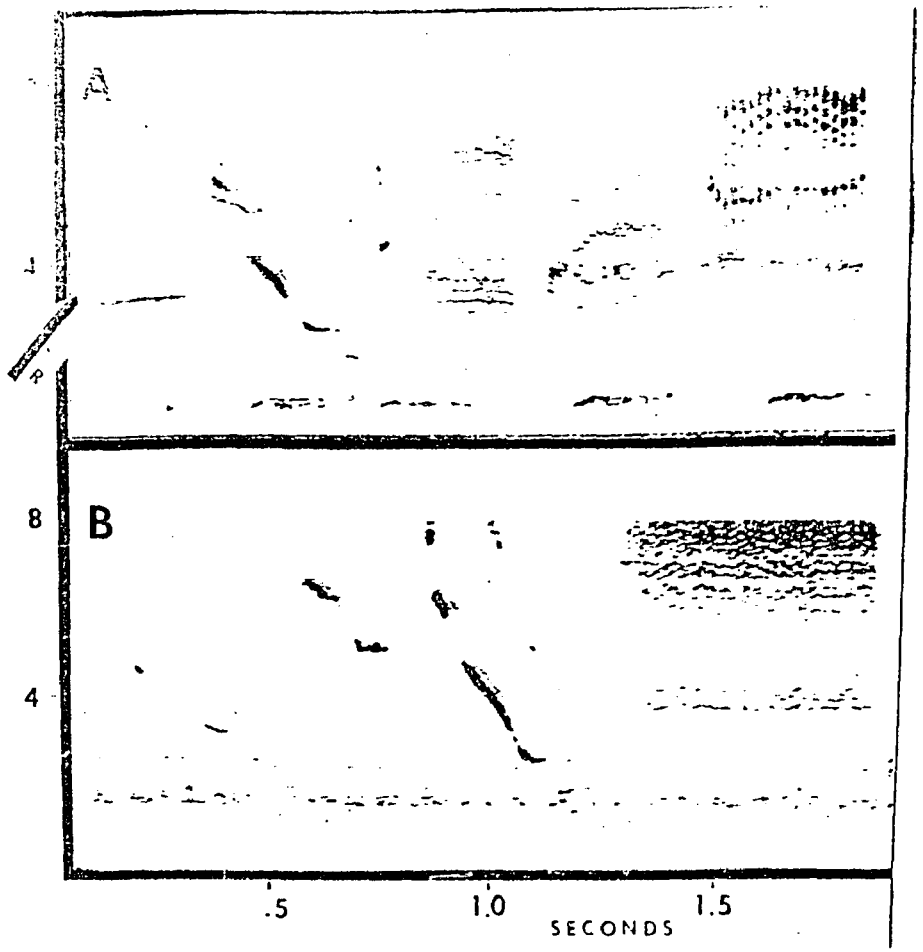


PLATE 26. Two primary songs of male bellicosa near Huanuco, Peru.

A. Complex song ending in rolled note, unlike any primary song from Bujama.

B. A more typical primary song, albeit with 6 or 7 introductory notes. Not distinguishable by ear from Bujama songs.

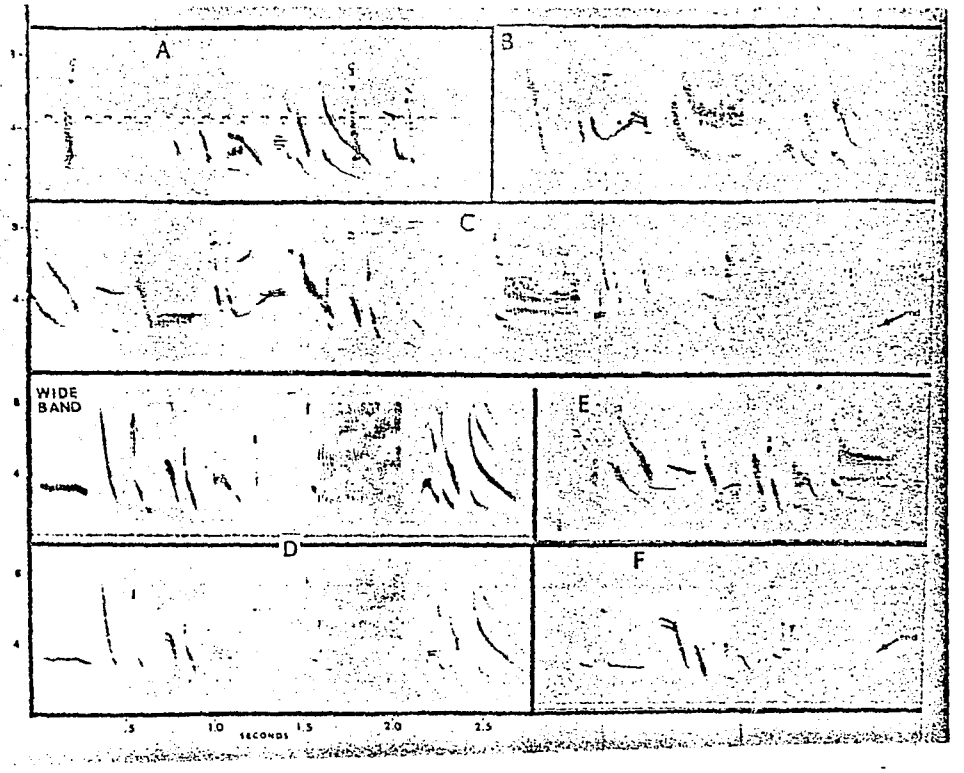


PLATE 27. Bellicosa flight songs

A. Male WR/BB
B. Flight-type song given from perch
C. Male WR/GR
D. Male WR/BR
E. Male E
F. Brief flight song of male F

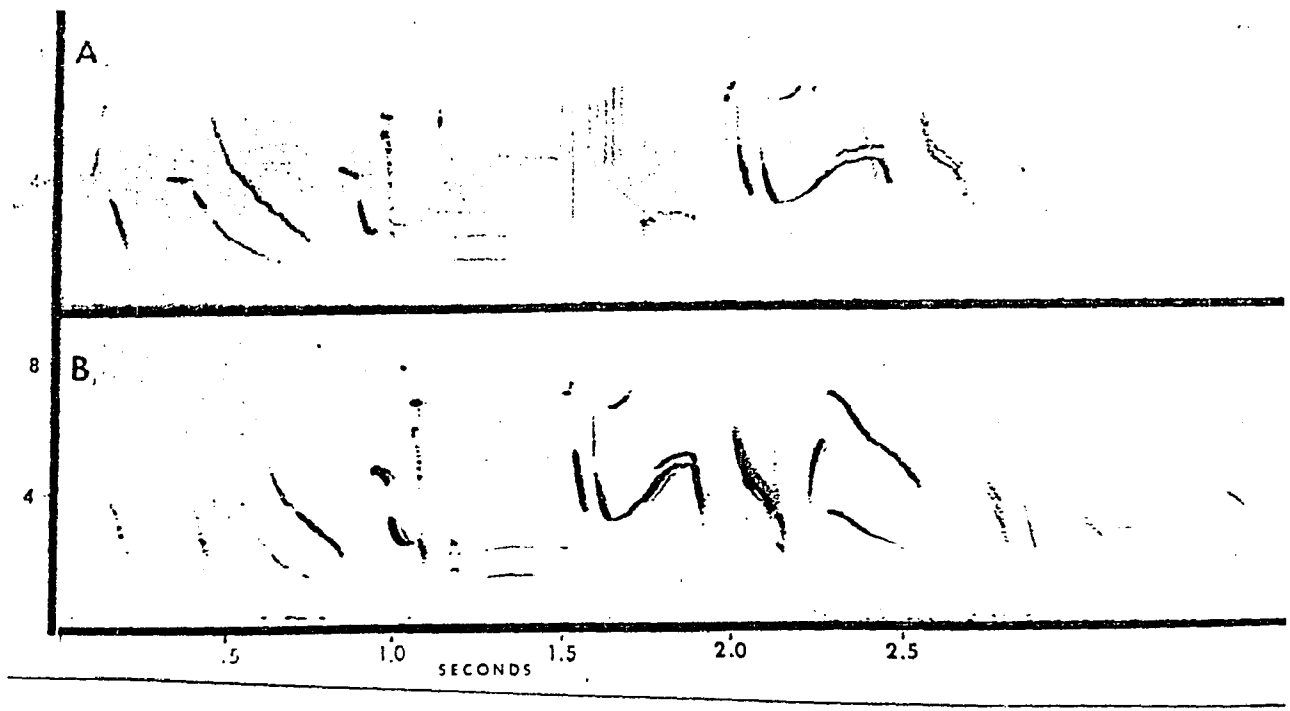
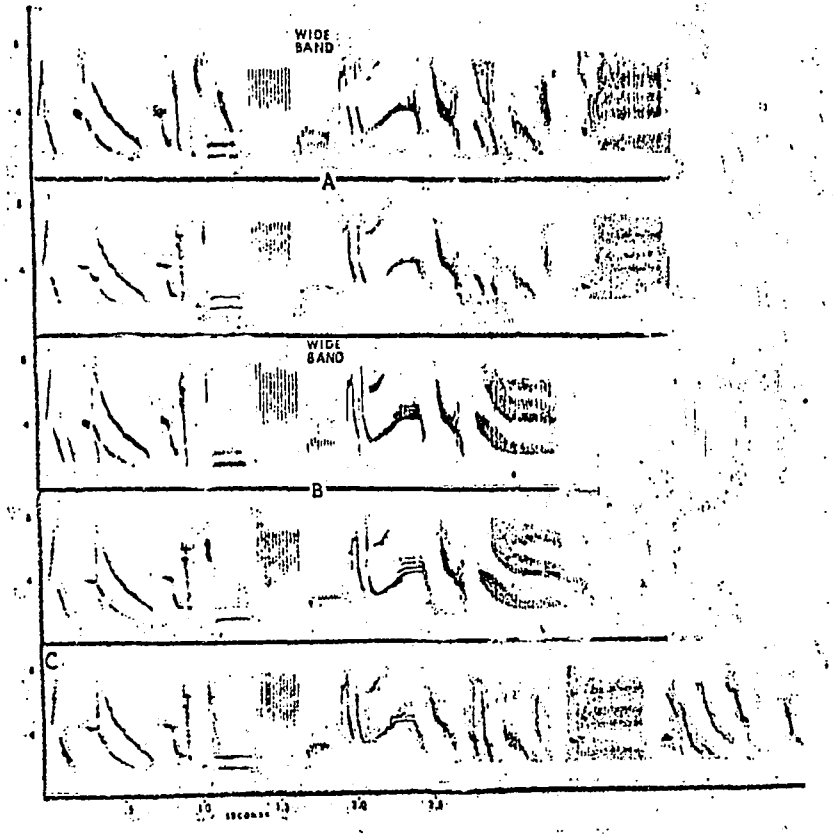
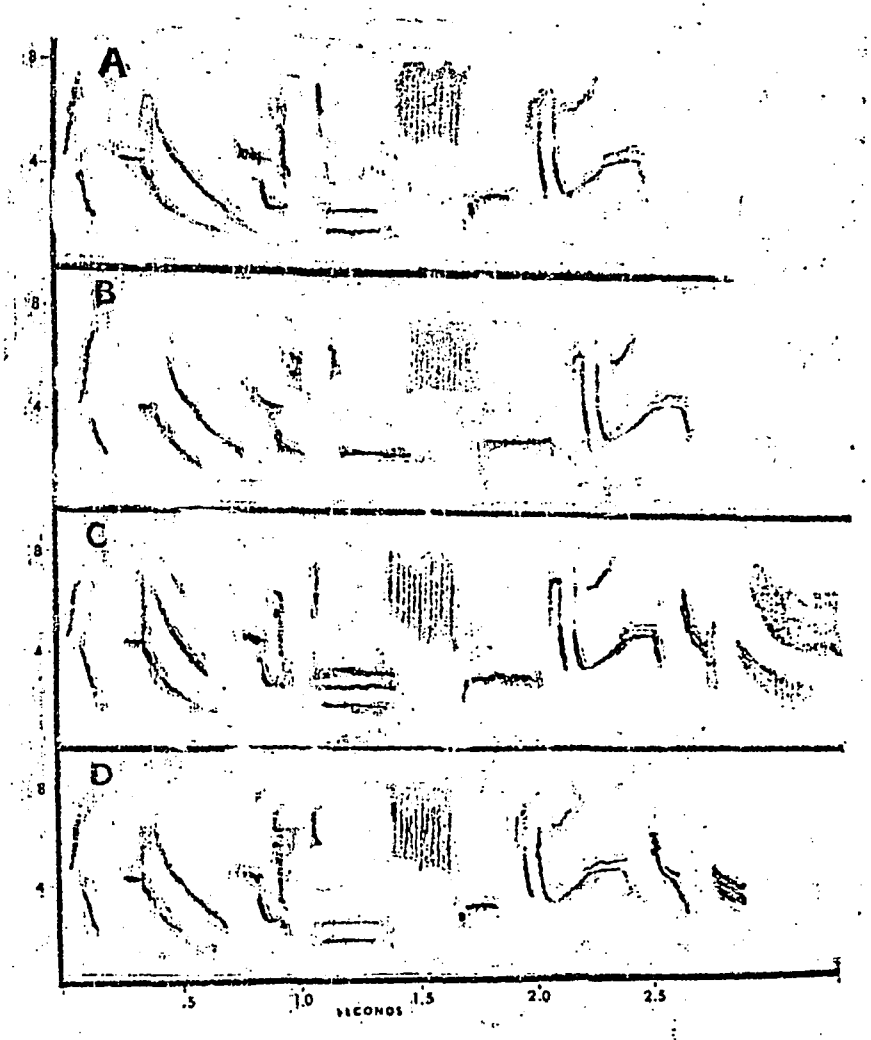


PLATE 28 . Bellicosa flight songs.

A. Flight in territory E.

B. Flight of WR/GG





PLATES 29 & 30. Seven flight songs of bellicosa male WR/GG given over a three week period. 29 A and B include wide-band graphs. Compare also with B, a different pattern for same male.

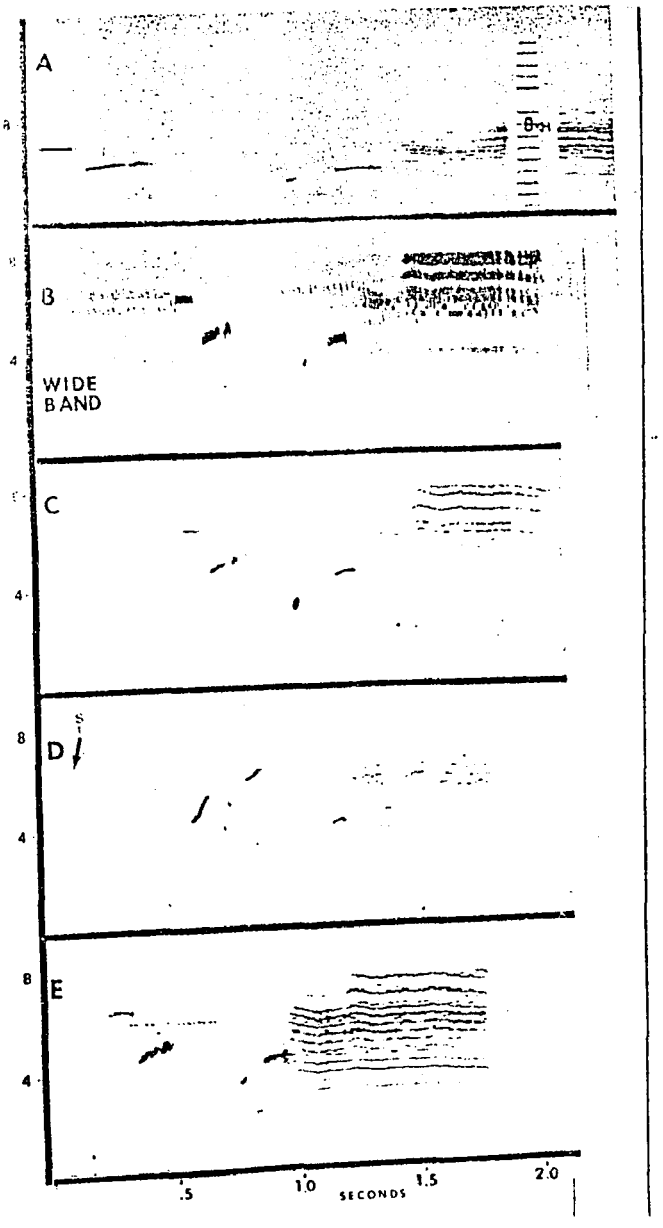


PLATE 31 . Songs of Leistes m. militaris.

A. Half-speed graph of primary song from 16 km. sdwest of Paramaribo. B &C. Standard speed graph of same song.

D. Primary song from 30 km. west of Paramaribo.

E. Song pattern similar to C.

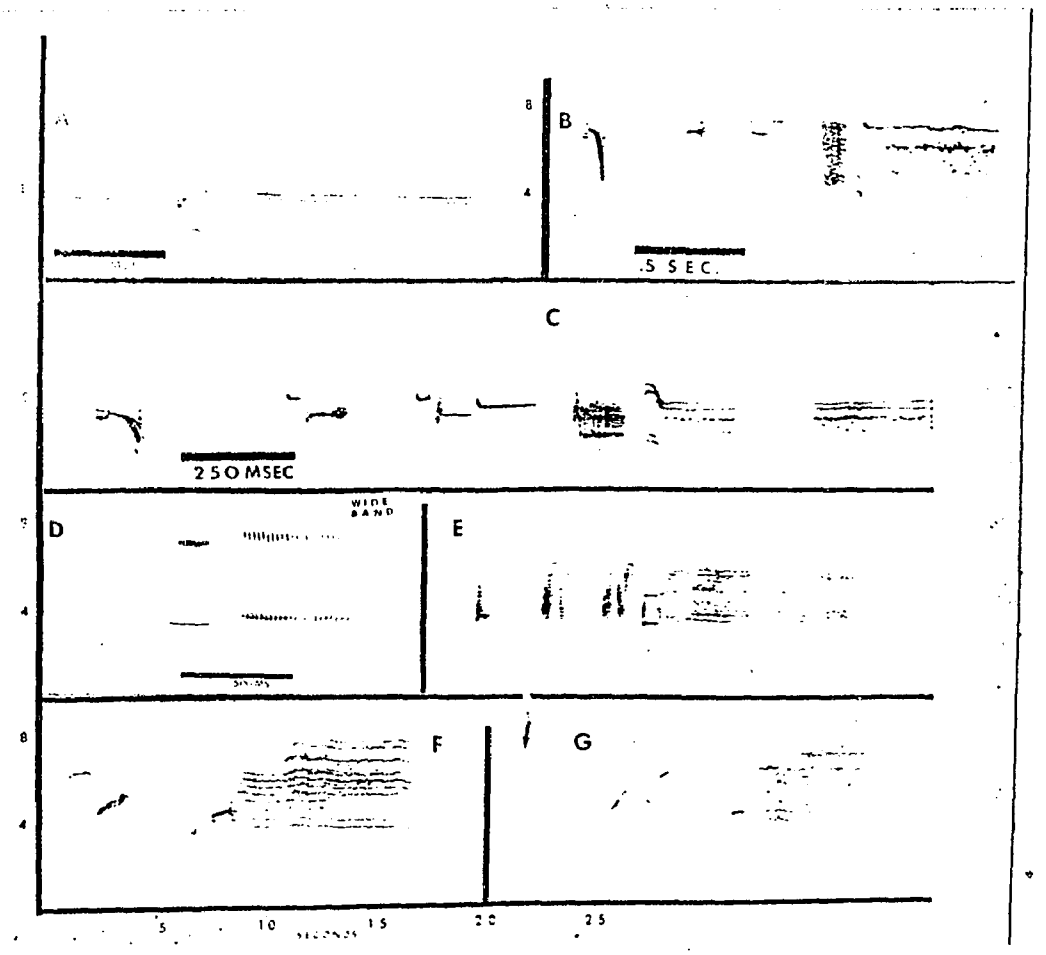


PLATE 32 | Primary songs of Leistes

A-C. superciliaris, Venado Tuerto, Argentina.

A. Half-speed graph. of one songg.

B & C. Standard and half-speed graph of second song.

D. Sao Paulo, Brazil. superciliaris song pattern resembling Myospiza humeralis.

E. L.m. militaris recorded in Panama.

F. L.m. militaris, 16 km west of Paramaribo, Surinam.

G. L.m. militaris, 30 km west of Paramaribo, Surinam.

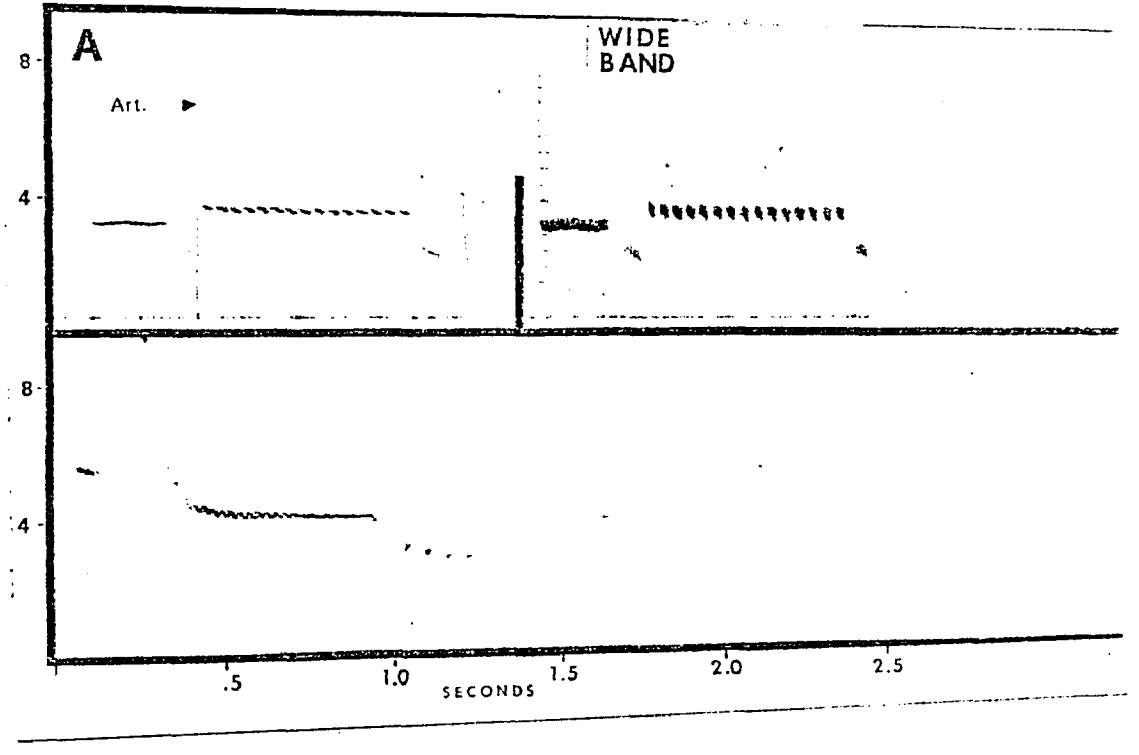
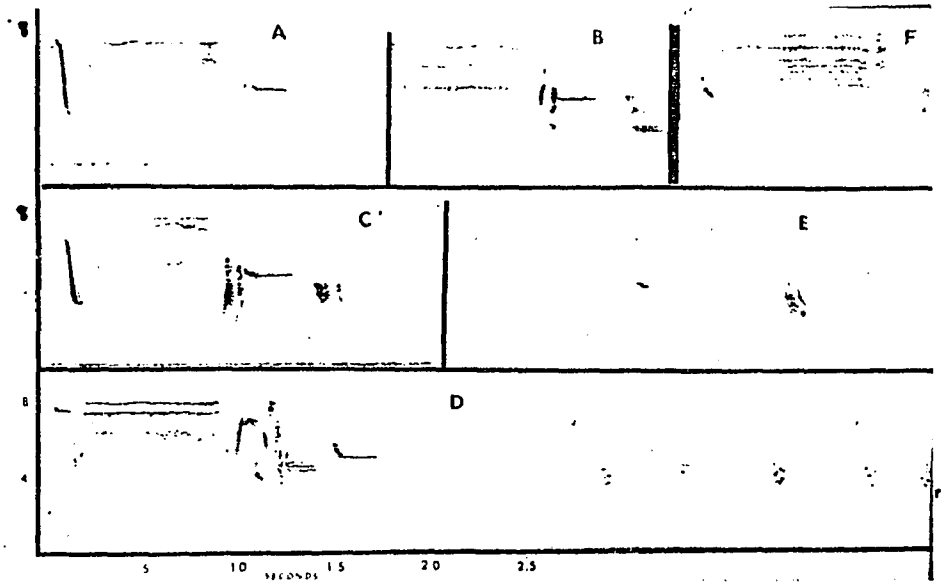


PLATE 33. Comparison of defilippii and superciliaris.
A. Narrow and wide band graphs of an unusual primary song recorded from superciliaris near Sao Paulo by Lanyon Song is similar to that of Myospiza humeralis.
Similar pattern recorded in northern Buenos Aires Prov. as well.

B. A flight song of defilippii



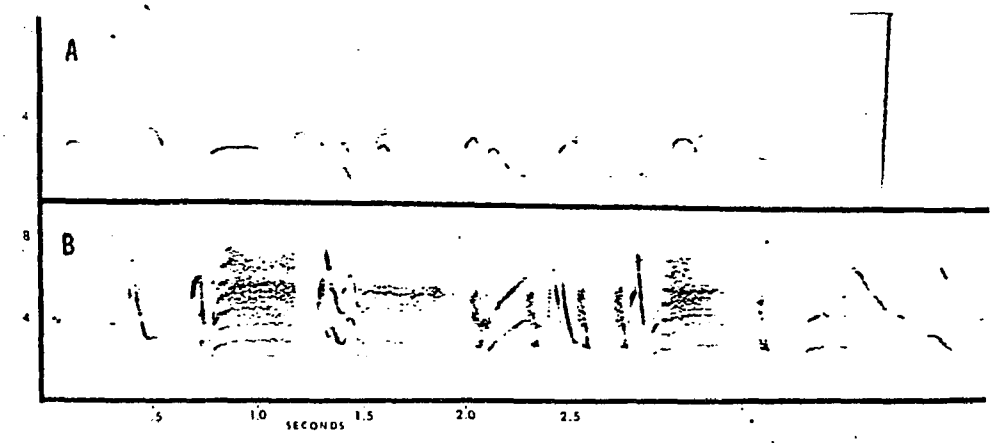


PLATE 34 . Flight songs of Leistes

A & B. superciliaris, Venado Tuerto

C & D. superciliaris, Saudade

E. superciliaris, Sao Paulo

F. L.m.militaris 30 km west of Paramaribo

PLATE 35 . "Rehearsed" song of superciliaris

A. "rehearsed" song from perch

B. Excited notes given during sex chase

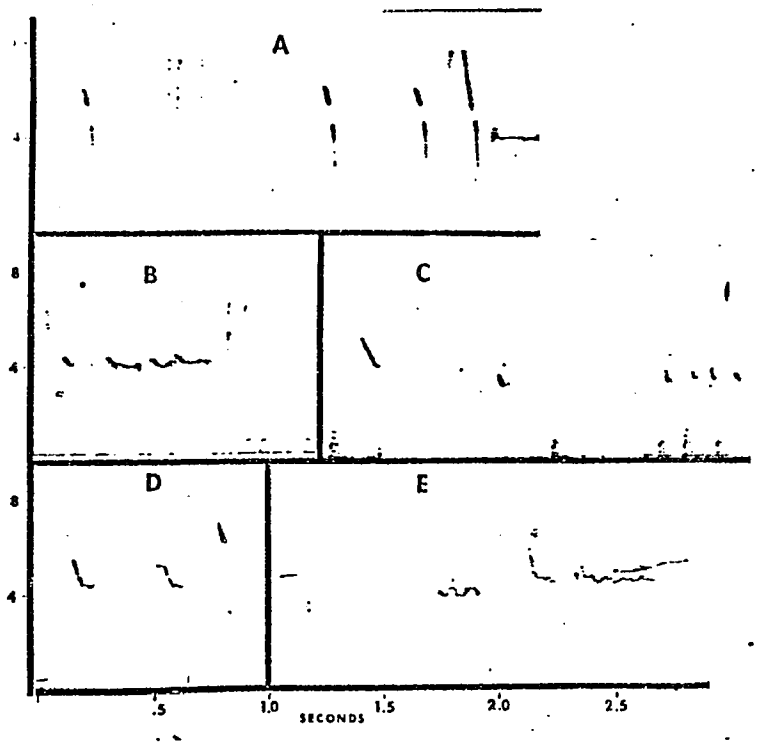


PLATE **36.** Miscellaneous vocalizations of defilippii.

A. RR/YY quasi-flight song given during sex chase. Male utters 'd d d d' notes similar to those of female.

B. Another male's flight song given during sex chase, overlapping "jt-jt" notes of female.

C. "Tseyu","chip" and rattle "d-d-d-d" notes recorded from a group of non-territorial males engaged in primary song duets within a group.

D. Squeaky notes given by one male confronting another.

E. Excited whistled chase notes given by male chasing a male.

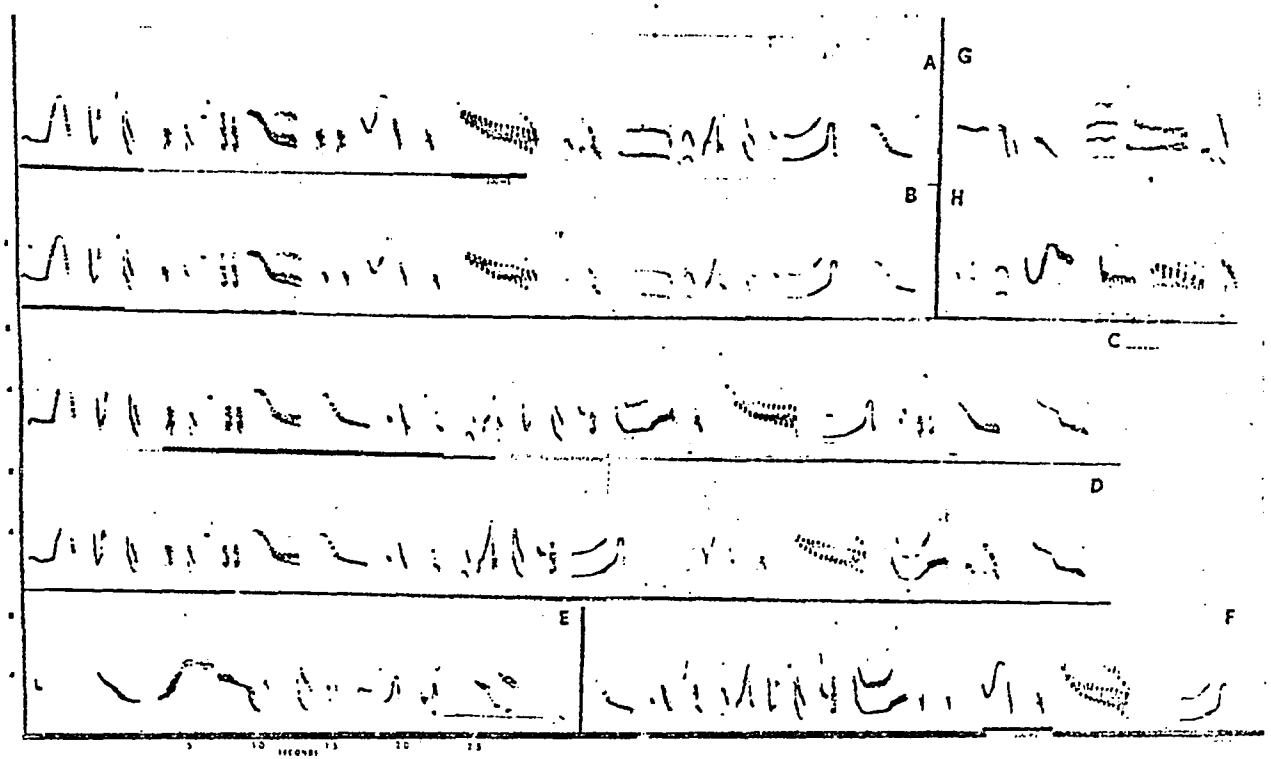


PLATE 37. Flight songs of P.m.catamarcanus recorded by W.E.Lanyon along the Rio Santa Maria, near Amaicha del Valle, Tucuman Province, Argentina, 27 Nov. 1970. One or two males represented. Introduction to A,B,C, D is identical. A and B are identical (duration 6.3 sec). B and C are very similar but with some variation in element sequence. G and H are abortive. Longest duration is 7.5 sec for C and D.

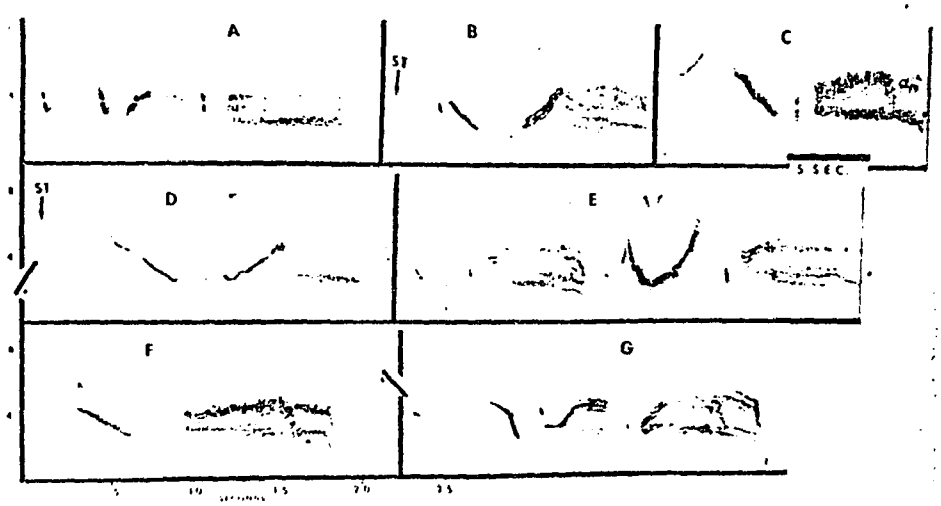


PLATE 38. Primary songs of militaris male GG/GG

A-F Six primary song types given on 9 December 1970.

G Song pattern given on 13 November 1971.

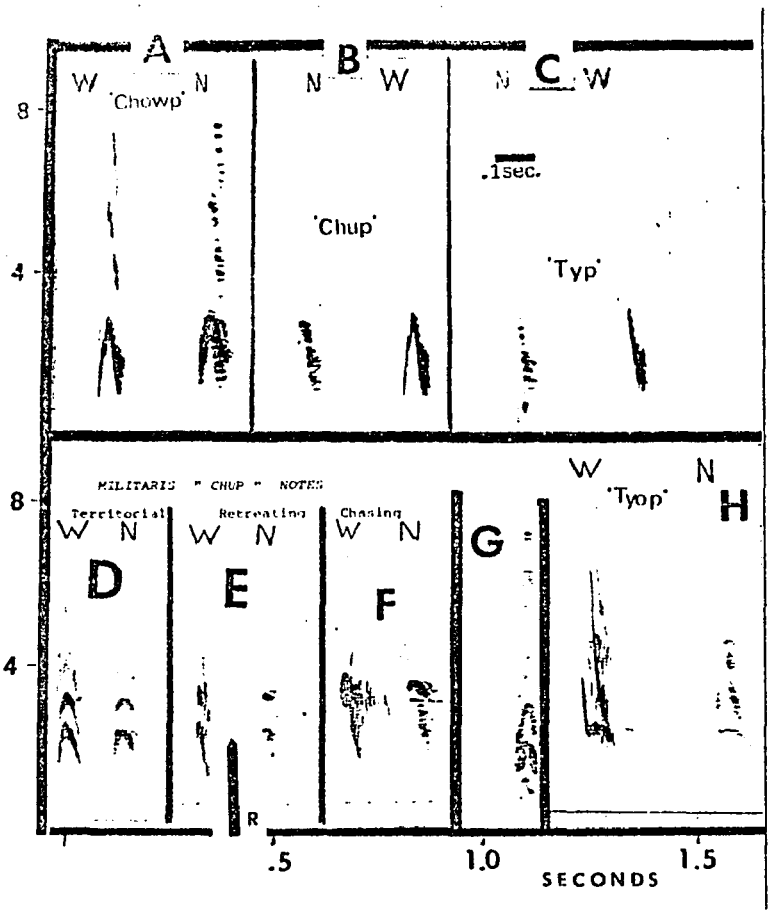


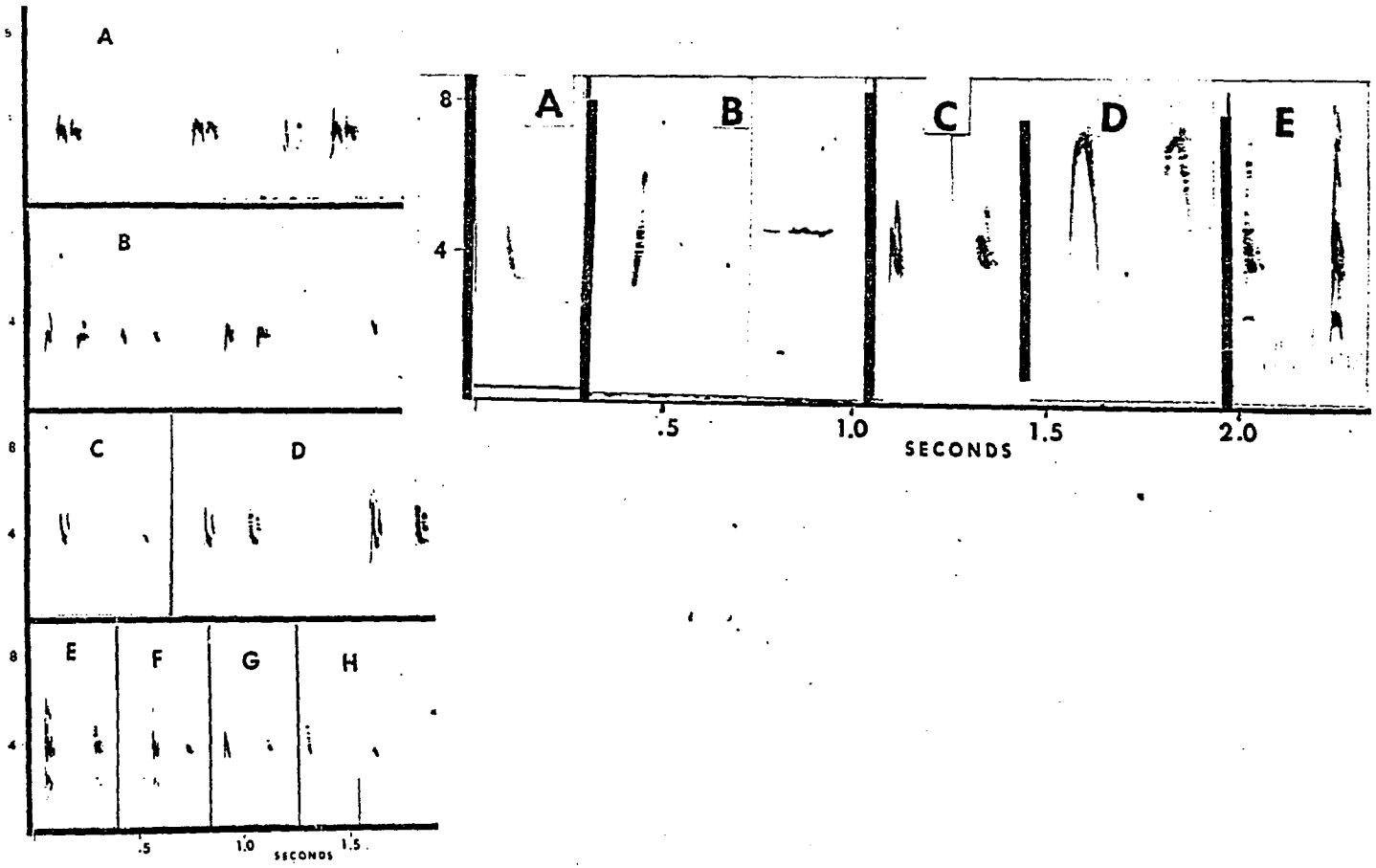
PLATE 39. Call notes of militaris

A-C, G & H recorded on pampas

D-F recorded in northwestern Argentina

All seem to be variants of the "chup"
Phonetic rendition is indicated on graphs

W and N refer to wide and narrow band analyses



CALLS OF DEFILIPPII MALES

PLATE 40. A "pit" B. various "chup" notes. C. "pesh" D. "peet-peet"
E-G Alarm "chuk" notes H. Alternating calls of two males at boundary.

PLATE 41. A. "tsut" B. "Twee" and "seet" notes of RR/YY. C. "chut" notes D. "Kye k"
E. "tup" note given in alarm.

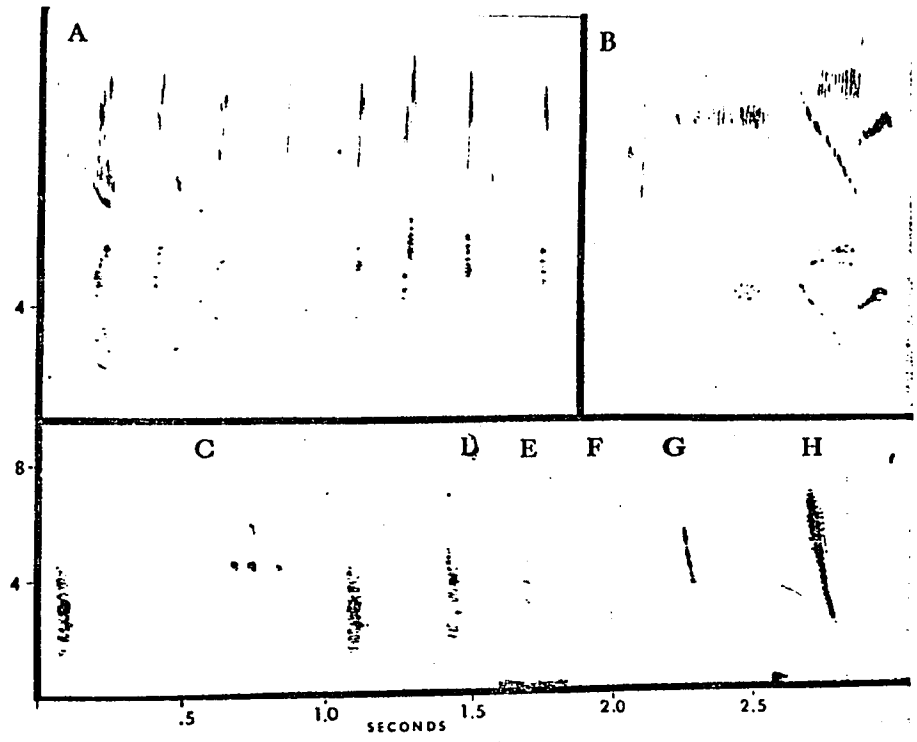


PLATE 42 . Samples of bellicosa call notes.

A. Series of "jt jt" notes of female given during sex chase.

B. "Tsee-seet" calls given by female during flight display.

C. "Chup" of male and "d-d" of female given during sex chase.

D. "Chip" note or low intensity "chup" of male.

E. "Chch" note or low intensity "chup" of male.

F. "Sh" note of female.

G. "Tip" note given by both sexes.

H. "Tseyu" note.

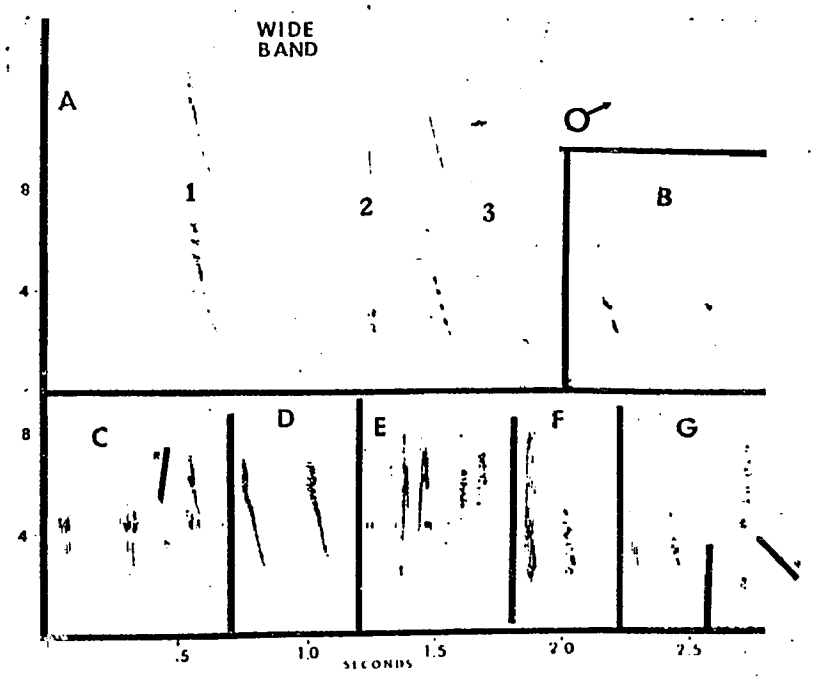


PLATE 43 . Call notes of bellicosa.

A. 1. is "tsyep" note of male which seemed to be in response to a sex chase of an adjacent pair. 2. is "chup" of male chasing a female. 3. "jt-jt" notes of female in sex chase.

B. "chip" and "chch" notes given by male while warbling from perch.

C. "cluk" notes from group of birds going to roost.

D. "Tsu" notes of male.

E. "pfit-tit" notes uttered by male in flight.

F. "Dzip" note of male.

G. "Tzut" call of unmarked male intruder, followed by call of WR/GG given during chase.

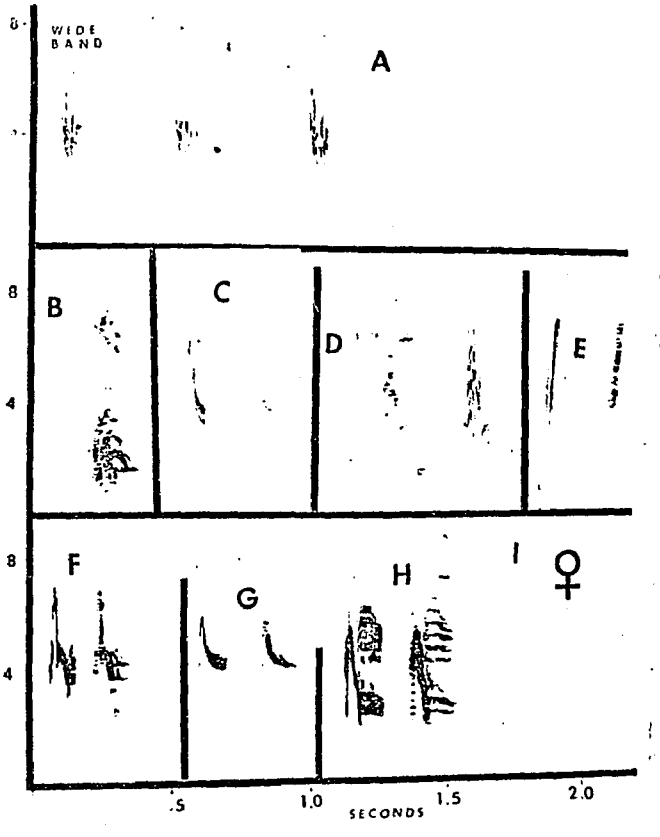


PLATE 44 . Call notes of Leistes.

A. "tsuk" notes given by male superciliaris in flight.

B-I. Miscellaneous notes of L.m.militaris.

B Loud "tup" given at decoy. C "tsu" note

D "chlk" call E "wsst" harsh note,alarm.

F,G,H. "teyu","tyu","tyop" notes of different males.

The context of most of these notes could not be determined.

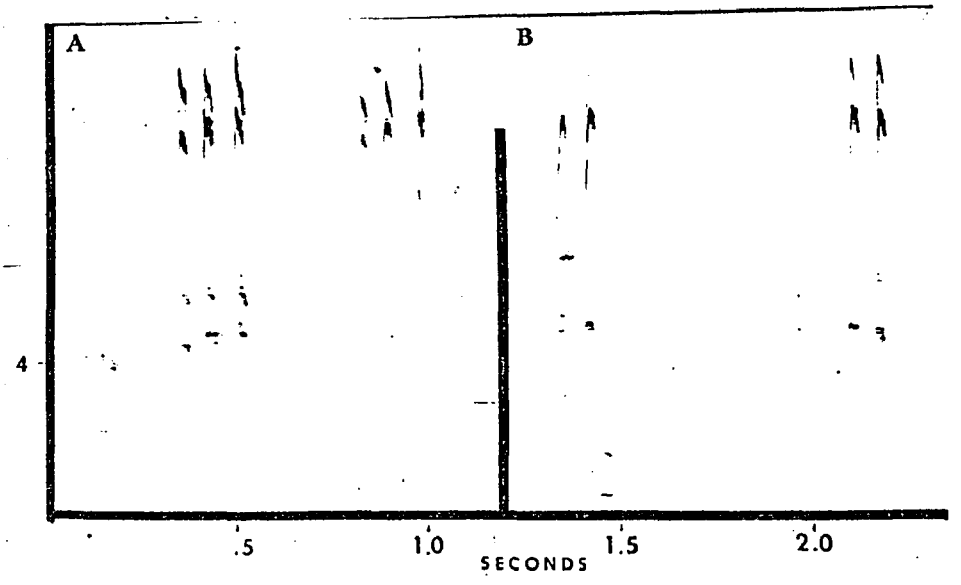
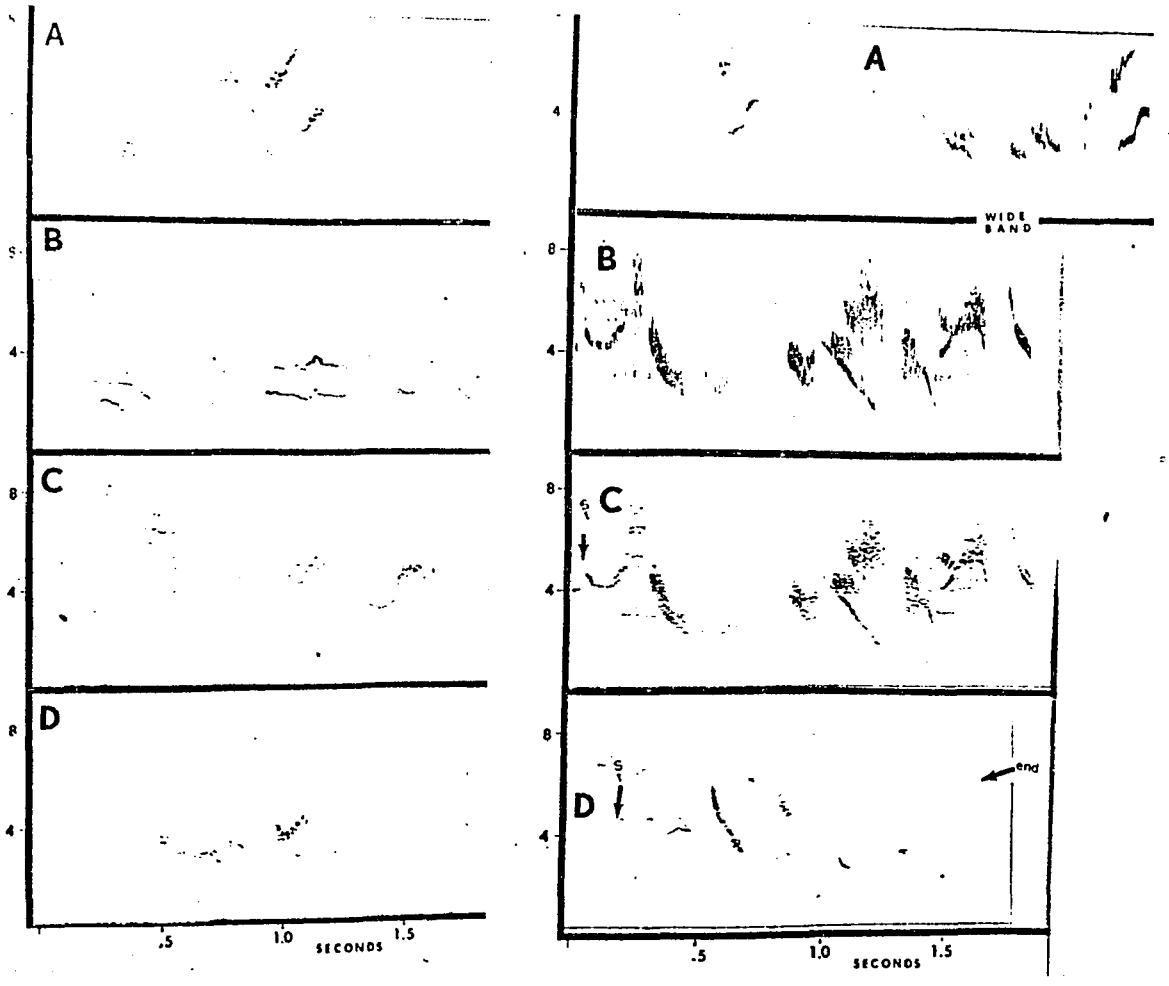


PLATE 45. Solicitation notes of bellicosa females.

A and B. "jt jt" notes of two different females.



PLATES 46 & 47. Flight display vocalizations of bellicosa females
Note extensive frequency modulations in most elements.
All notes have very buzzy quality.

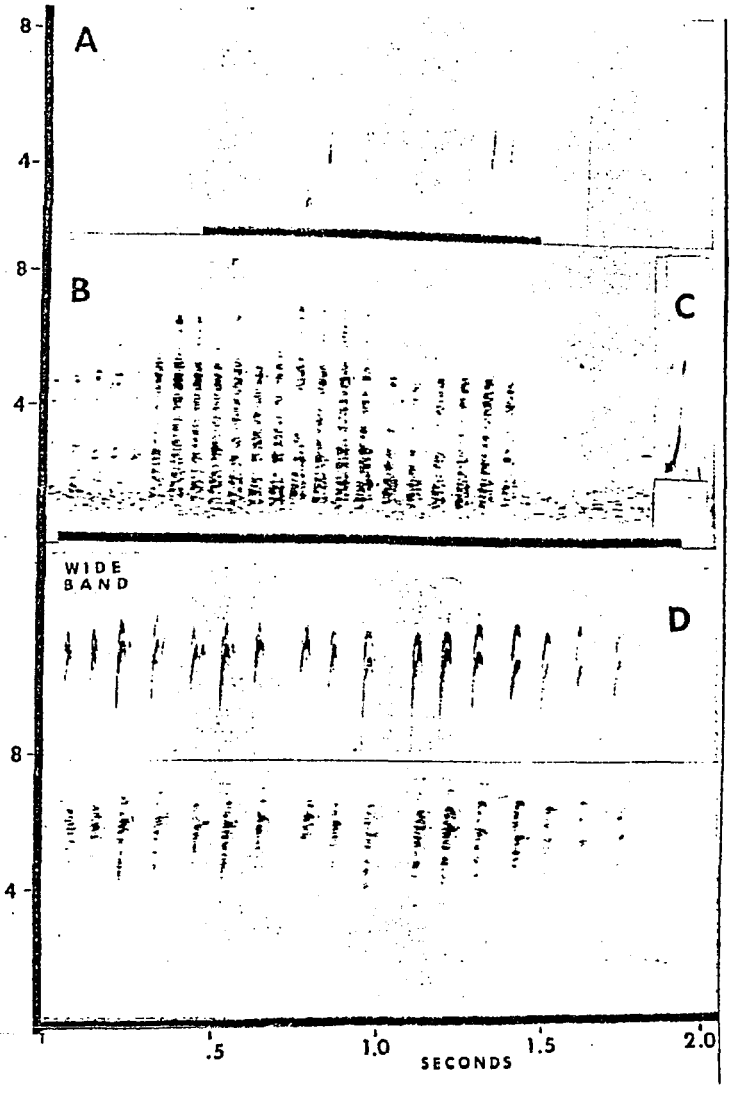


PLATE 48 . Rattle-type notes.

A. "jt jt jt jt" of female defilippii during sex chase

B. Loud rattle of female militaris near Bariloche. This call was not heard elsewhere.

C. "tsis", soft note given by female militaris on perch immediately after rattle.

D. Slower rattle of female L.m.militaris in Surinam. (compare with bellicosa notes on Plate 42A)

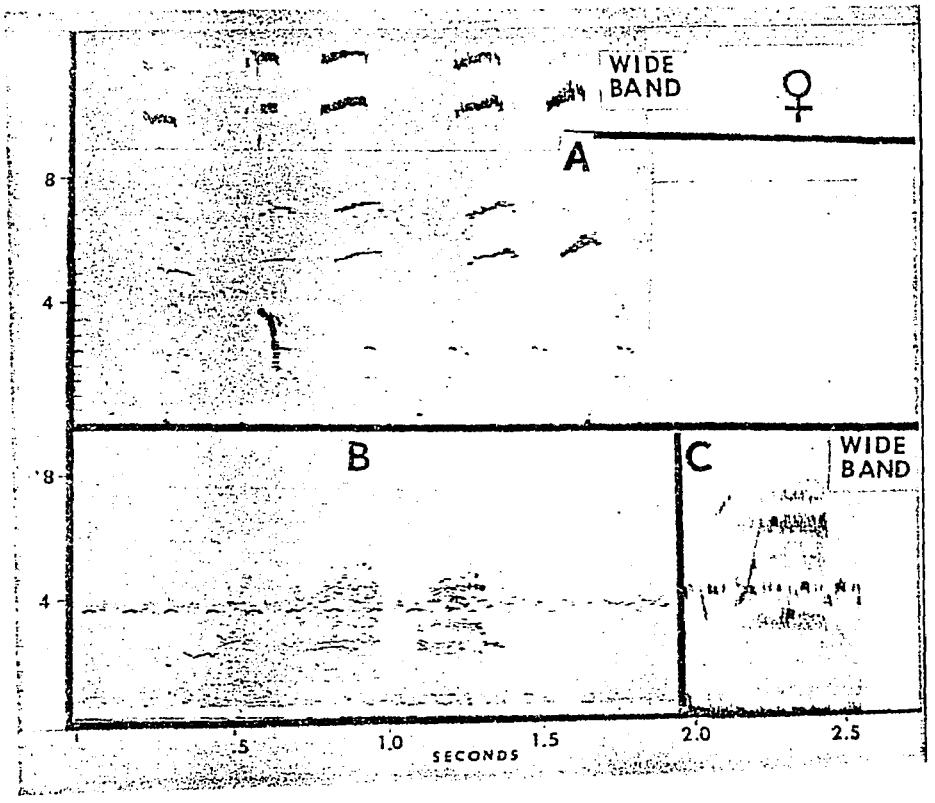


PLATE 49. Notes of female Pezites

A. "see-see" of defilippii in sex chase.
Single note is a "tyuk" given by ♂ chasing her.

B. "zhe-zhee-shee" of bellicosa in flight display.

C. Loud harsh "shee" of bellicosa

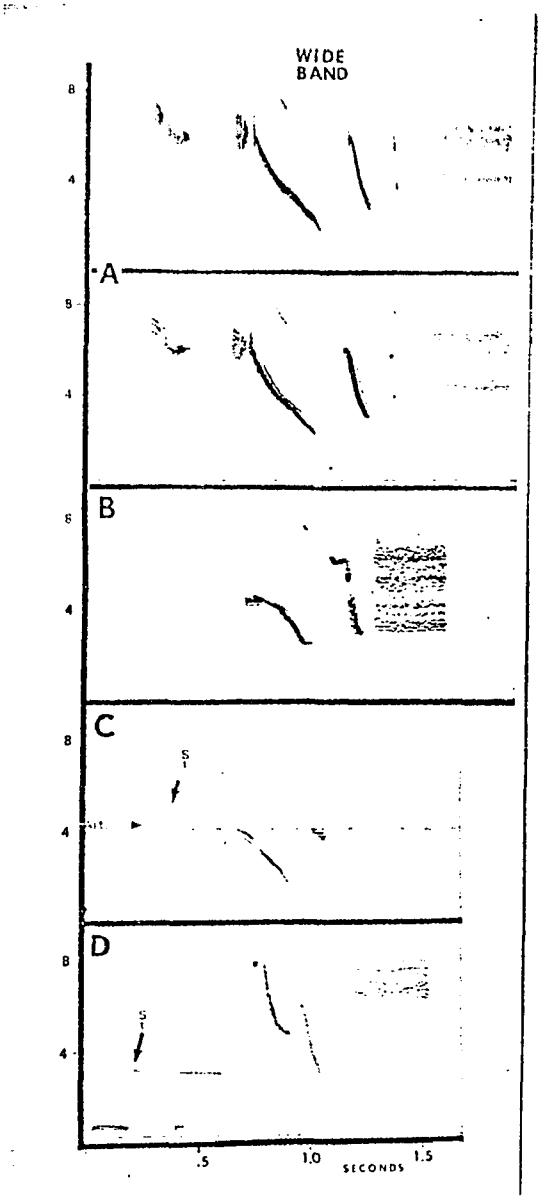


PLATE 50. Four primary songs of bellicosa ♂ WR/GG

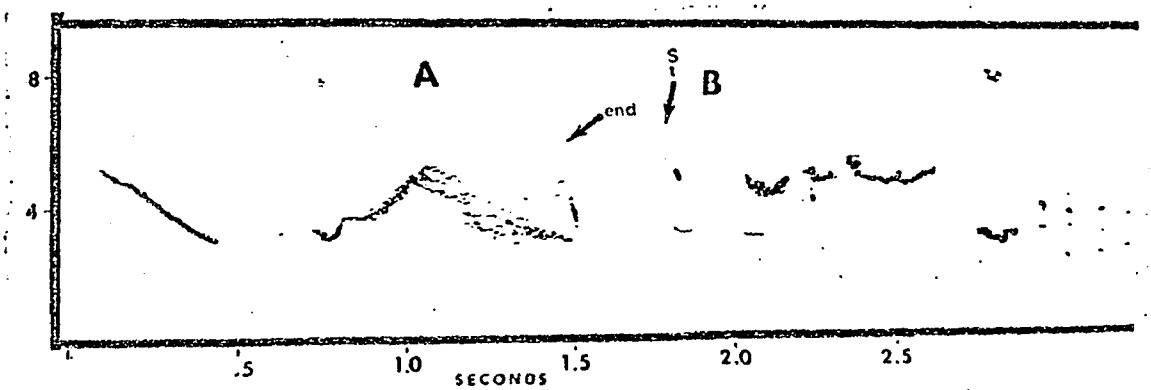
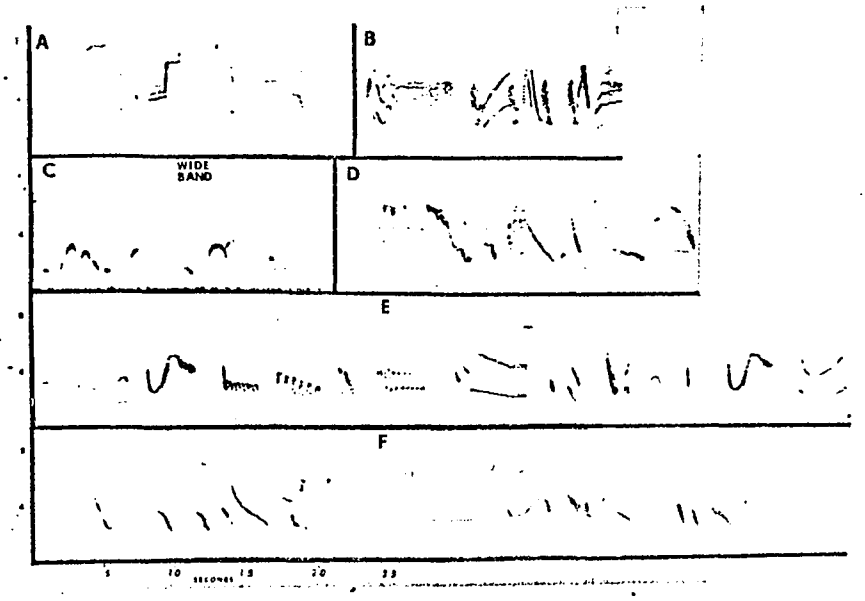


PLATE 51. Primary song of militaris ♂ YY/RR followed by a flight-type song from an unmarked ♂ defilippii which duetted repeatedly with this bird in a typically territorial manner. The flight-type notes appear to indicate a high-level of excitement.



52. Flight and "rehearsed" songs.

A

B. superciliaris male, during sex chase

C.

D. bellicosa non-territorial male from perch

E. militaris male GG/RR (Saudade 1970) in flight
Compare with similar notes from catamarcanus, Plate 37.

F. bellicosa male WR/GG in flight.

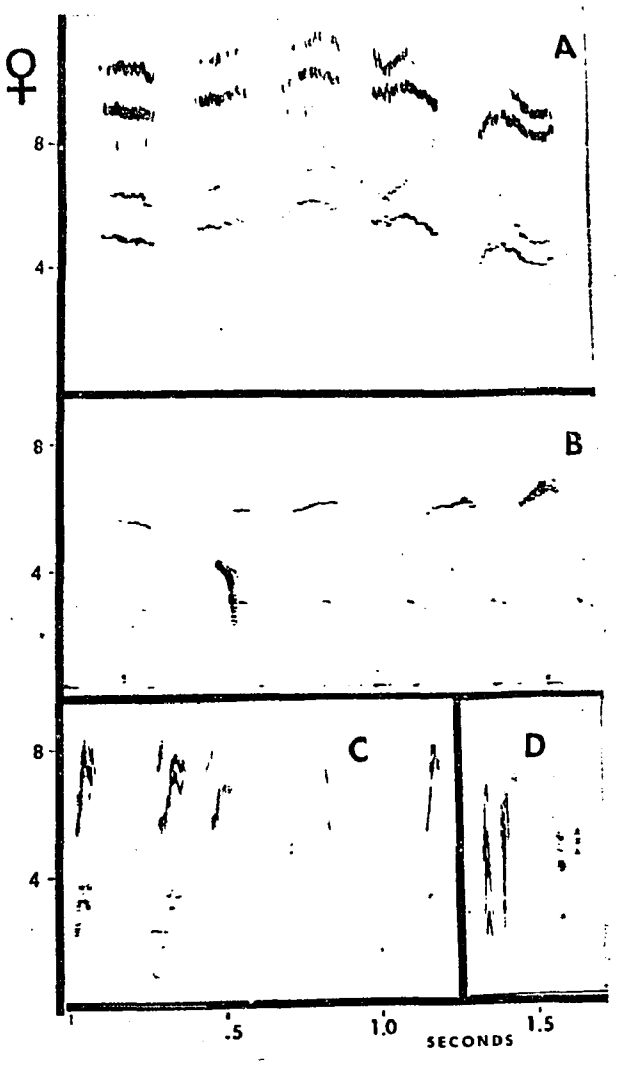


PLATE 53. Call notes of defilippii females

A. "Scree-cree" given in sex chase

B. "See-see" given in sex chase, with male chase note included

C. "weet-weet" given by overflying female.

D. "tup" note of female.

APPENDIX II MEADOWLARK SPECIMENS COLLECTED

Dates are listed as month/day/year. Number following hyphen refers to the number of the specimen collected on that date.

Abbreviations: BA = Buenos Aires Province
LR = La Rioja RN = Rio Negro SJ = San Juan
CAT= Catamarca Co = Corrientes L = Lima (Peru)

(except for Lima, all specimens were collected in Argentina)

DATE	LOCALITY	WEIGHT	SEX	COMMENTS
	PEZITES MILITARIS MILITARIS			
11/27/70-2	RN: El Condor(Bariloche)	116g	♂	
12/ 9/70-8	BA: Saudade	89g	♂	
12/19/70-1	BA: Sierra Ventana		♂	
12/19/70-2	BA: " "		♂	
12/19/70-3	BA: " "		♂	
12/21/70-5	BA: " "	91g	♂	
12/30/70-1	SJ: San Juan		♂	
12/30/70-2	SJ: " "	102g	♂	
12/31/70-1	SJ: 18 km W of San Juan	108g	♂	
12/31/70-2	SJ: Niviquil	102g	♂	
1/ 1/71-1	LR: Villa Union	108g	♂	
1/ 1/71-2	LR: " "	111g	♂	
1/ 3/71-1	CA: Tinogasta	102g	♂	
1/ 4/71-2	CA: "	97g	♂	intermediate
1/ 4/71-4	CA: "	91g	♂	
1/ 4/71-5	CA: "	106g	♂	
1/ 5/71-2	CA: 70 km SW of Sta Maria	110g	♂	
10/20/71-3	BA: Dufaur		♂	
10/20/71-4	BA: 7 km E of Bahia Blanca		♂	
11/ 7/71-4	BA: 22km W of Medanos	90g	♂	
11/ 7/71-5	BA: 50km SW Bahia Blanca	95g	♂	
11/ 7/71-6	BA: " " "	91g	♂	
11/ 7/71-7	BA: " " "	93g	♂	
11/ 7/71-10	BA: " " "	93g	♂	
11/ 7/71-11	BA: " " "	87g	♂	
11/ 7/71-13	BA: " " "	96g	♂	
12/21/70-4	BA: Sierra Ventana	71g	♀	
12/21/70-6	BA: " "	71g	♀	
12/22/70-3	BA: Saudade	82g	♀	
1/ 4/71-1	CA: Tinogasta	93g	♀	
1/ 4/71-3	CA: "	91g	♀	
10/20/71-2	BA: Dufaur	87g	♀	
11/ 7/71-3	BA: 22km W of Medanos	68g	♀	
11/ 7/71-8	BA: 50km SW Bahia Blanca	85g	♀	
11/ 7/71-9	BA: " " "	90g	♀	
11/ 7/71-12	BA: " " "	79g	♀	

(Appendix II con't)

DATE	LOCALITY	WEIGHT	SEX	COMMENTS
	PEZITES MILITARIS CATAMARCANUS			
1/ 6/71-2	CA: 55 km SW Santa Maria	108g	♂	int.
1/ 6/71-3	CA: " " "	110g	♂	
1/ 6/71-4	CA: " " "	103g	♂	int.
1/ 6/71-5	CA: " " "	104g	♂	
1/ 6/71-7	CA: " " "	117g	♂	int.
1/ 6/71-8	CA: 110 kmg SW " "	108g	♂	int.
1/ 6/71-10	CA: 100 km SW " "	122g	♂	int.
1/ 9/71-1	CA: 4 km N " "	112g	♂	
1/ 5/71-1	CA: Corral Quemado	96g	♀	int.
1/ 6/71-1	CA: 55 km SW Santa Maria	95g	♀	
1/ 6/71-6	CA: " " "	93g	♀	
1/ 9/71-2	CA: 4 km N " "	93g	♀	
1/ 6/71-11	CA: 55 km SW Santa Maria	106g	♀	
1/ 6/71-9	CA: 55 km SW Santa Maria	109g	♂	juv
	PEZITES DEFILIPPII			
12/ 9/70-2	BA: Sierra Ventana	69g	♂	molt
12/ 9/70-3	BA: " "	70g	♂	
12/ 9/70-4	BA: Saudade	72g	♂	
12/21/70-1	BA: "	77g	♂	
12/21/70-2	BA: "	71g	♂	
12/21/70-7	BA: "	79g	♂	
12/21/70-8	BA: "	71g	♂	
12/ 9/70-6	BA: "	69g	♂	
11/ 1/71-4	BA: 60km SW Bahia Blanca		♂	
11/14/71-3	BA: Saudade			
11/15/71-1	BA: "	74g	♂	
11/15/71-2	BA: "	78g	♂	
11/15/71-3	BA: "	76g	♂	
11/15/71-5	BA: "		♂	
12/21/70-3	BA: "		♀	juv
11/15/71-4	BA: "	58g	♀	
12/28/70-2	BA: Sierra Ventana	77g	♂	
12/28/70-4	BA: Sierra Ventana	77g	♀	
	LEISTES M. SUPERCILIARIS			
12/ 9/70-5	BA: Saudade	52g	♂	molt
12/ 9/70-7	BA: Saudade	52g	♂	
1/25/71-2	Co: Ito Ibate	39g	♀	
10/17/71-1	BA: Juarez	51g	♂	
1/25/71-1	Co: Ito Ibate	40g	♀	

(Appendix II con't)

DATE	LOCALITY	WEIGHT	SEX	COMMENTS
	PEZITES BELLICOSA			
8/ 2/72-1	L: Bujama	85g	♂	
9/28/72-1	L: "	91g	♂	
9/28/72-2	L: "	89g	♂	molt
9/29/72-2	L: "	78g	♂	
9/29/72-3	L: "	89g	♂	
9/30/72-1	L: "	86g	♂	
9/ 2/72-1	L: Bujama		♀	
9/ 4/72-1	L: "	58g	♀	
9/ 5/72-4	L: "		♀	skel.
9/27/72-2	L: "	60g	♀	
9/28/72-3	L: "	61g	♀	
9/28/72-4	L: "	67g	♀	molt
9/28/72-5	L: "	62g	♀	
9/28/72-6	L: "	68g	♀	molt

APPENDIX II. (addendum)

PEZITES MILITARIS MILITARIS

11/25/70-1	RN: 30km E of Junin de los Andes	105g	♂
12/18/70-3	BA: Sierra Ventana	76g	♀
1/ 1/71-3	LR: Villa Union	82g	♀

PEZITES DEFILIPPII

12/28/70-2	BA: Sierra Ventana	77g	♂
12/28/70-4	BA: Sierra Ventana	77g	♀

APPENDIX III THE BUJAMA CORN BORER SUPPLY

Since adult bellicosa of both sexes did much feeding off territory in the two cornfields, and since nestlings and fledglings were apparently fed almost entirely on corn borers in certain territories (including those more than 1 km from the corn), it seemed reasonable to estimate the abundance of the corn borers. An adult probing through the corn husk, often appeared to eat corn as well as borers, but examination of the corn did not allow me to separate damage caused by the borers from damage caused by the birds.

I examined 11 corn ears that had not been probed and 13 that had been probed. All had borers or evidence of borers.

NUMBER OF LARVAE PER EAR

Unprobed	1 1 1 1 2 2 2 2 2 3 4	Total=21	ave. =1.909
Probed	0 0 0 1 1 1 1 2 2 2 2 2 3	Total=17	ave. =1.308

Mann-Whitney U=39, $p < .05$

The corn was planted in rows about 70 cm apart, which would give about 20818 plants/hectare. There were 3.89 ears on 50 plants I sampled, (total of 80983.4 ears/ hectare or 154597 borers per hectare). The total area planted to corn in the valley was 0.55 hectares giving a total population of 85337.5 borers available on the day

of sampling (excluding those already removed by birds).

Since borers have a turnover rate, and since ears of corn have a turnover rate, the number available in the course of a season is probably far greater.

Assuming that each adult could make 5 trips per hour (they don't) and feed continuously for 12 hours (they don't seem to), the 25 nests estimated for the valley would receive a total of 3000 borers/day and the number of borers estimated would last (if fully utilized and unrenewed) for 29 days.

I noted that it took between 1.5 and 3.0 minutes for an adult to extract a borer from a fresh ear, and often took more than a minute even if the ear had been previously probed. Although these observations were casual, they reveal the feasibility of studying the relative contribution of cornborers to the bellicosa diet, since many birds feed together in a small area, and since they make long conspicuous flights with the vorers to their nests. It was also interesting that when feeding in the corn, even known territorial birds showed no aggression to nearby birds, except in one instance when a bird tried to land on an already occupied plant. In this case it was a male that was chased by a female. Thus the time required to extract a borer may be of such magnitude compared with the abundance of borers, that it is not advantageous to either defend or trespass.

APPENDIX IV TABLE OF MORPHOMETRIC DATA

This appendix provides tables of basic descriptive statistics (means, range, standard deviation, standard error of mean, 95% confidence limits around mean, and coefficient of variation) for all forms of red-breasted meadowlarks examined. Where sample sizes were adequate I subdivided specimens into geographical groups (not populations). Four basic measurements: wing, tail, bill and culmen length are tabulated in this appendix.

STATISTICAL SUMMARIES FOR WING LENGTH

LOCATION	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
PEZITES MILITARIS MALES									
Non-pampas birds									
Falkland Is. (falklandicus)	19	129.95	3.3245	.7627	128.351	131.544	2.56	123.00	136.00
Tierra del Fuego & Santa Cruz Prov.	35	129.54	3.9656	.6703	128.189	130.897	3.06	120.00	139.00
Southern Andes (Chubut)	27	125.59	2.9905	.5755	124.412	126.774	2.38	119.00	131.00
Mendoza to Bariloche	13	126.77	3.3949	.9416	124.735	128.803	2.68	120.00	132.00
San Juan & La Rioja	9	126.67	4.0311	1.3437	123.630	129.703	3.18	121.00	131.00
S. Catamarca (intermediate area)	6	131.33	1.7512	.7149	129.582	133.085	1.33	129.00	134.00
N. Catamarca-Jujuy (catamarcanus)	10	131.20	2.1499	.6799	129.684	132.716	1.64	128.00	134.00
Pampas birds									
31-35.3° S. Lat (northern pampas)	21	124.05	4.1890	.9141	122.146	125.949	3.38	118.00	132.00
36-36.3° S Lat (central pampas)	14	118.71	1.9779	.5286	117.578	119.851	1.67	116.00	122.00
Estancia Saudade	15	122.07	2.9873	.7713	120.424	123.710	2.45	117.00	126.00
Bahia Blanca	7	121.29	2.4976	.9440	119.058	123.514	2.06	116.00	123.00
Panhandle 39-40° S. latitude	12	120.17	2.6227	.7571	118.516	121.817	2.18	116.00	124.00
Coastal Rio Negro-Chubut (43-48° S).	7	128.57	3.4087	1.2884	125.531	131.612	2.65	125.00	134.00
No locality information	10	127.60	3.6878	1.1662	124.999	130.201	2.89	122.00	133.00
TOTAL: 14 groups of P. militaris ♂♂	205	126.08	4.9502	.3457	125.405	126.761	3.93	116.00	139.00
Chile 29-30° S. Latitude	9	121.89	3.6893	1.2298	119.110	124.668	3.03	117.00	129.00
Chile 32-34° S. Latitude	17	121.35	3.2199	.7809	119.705	123.001	2.65	115.00	127.00
Chile 34-38° S. Latitude	13	120.15	3.6707	1.0181	117.955	122.353	3.06	113.00	125.00
Chile 38-40° S. Latitude	17	120.47	3.3933	.8230	118.734	122.207	2.82	117.00	129.00
Chile 41-42° S. Latitude	10	119.40	2.8752	.9092	117.372	121.428	2.41	115.00	124.00
Chile 50° and southward	2	125.50	.7071	.5000	123.348	127.651	.56	125.00	126.00
Chile No locality information	12	121.75	2.4168	.6977	120.229	123.271	1.99	117.00	124.00
TOTAL: 7 groups of P.militaris ♂♂	80	120.95	3.3052	.3695	120.215	121.685	2.73	113.00	129.00

PEZITES M. MILITARIS MALES TAIL LENGTH

LOCATION	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
CUT-MALES FALKLAND IDS.	19	94.26	2.5351	.5816	93.046	95.480	2.69	89.00	99.00
MALES TIERRA DEL FUEGO	35	94.66	5.3958	.9121	92.815	96.499	5.70	74.00	102.00
MALES S.ANDES--W. CHUBUT	27	95.07	3.7099	.7140	93.609	96.539	3.90	88.00	103.00
MALES MENDOZA-BARILOCHE	13	94.23	4.6575	1.2918	91.441	97.021	4.94	85.00	99.00
MALES SAN JUAN - LA RIOJA	9	94.44	4.6667	1.5556	90.929	97.960	4.94	84.00	101.00
MALES CATAMARCA--INTERMED.	6	97.17	1.6021	.6540	95.564	98.769	1.65	95.00	99.00
NOR-MALES. CATAMARCA-JUJUY	10	94.90	3.6347	1.1494	92.337	97.463	3.83	89.00	99.00
MALES PAMPAS 31 - 35.3 S	21	92.67	3.4108	.7443	91.119	94.215	3.68	88.00	99.00
MALES PAMPAS 36-36.3	14	88.07	2.4326	.6501	86.674	89.469	2.76	85.00	92.00
MALES PAMPAS--SAUDADE	15	91.20	3.1893	.8235	89.446	92.954	3.50	86.00	96.00
MALES PAMPAS--BAHIA BLANCA	7	88.86	2.8536	1.0785	86.312	91.402	3.21	84.00	93.00
MALES B.A.PAN-HANDLE, 39-40	12	87.83	4.0639	1.1731	85.276	90.391	4.63	81.00	94.00
MALES NO LOCATION	10	94.50	4.0069	1.2671	91.674	97.326	4.24	90.00	102.00
MALES COAST- 43 - 48 S LAT	7	96.43	2.6367	.9966	94.077	98.781	2.73	93.00	100.00
MALES CHILE--29-30 S LAT	9	92.44	4.1866	1.3955	89.291	95.598	4.53	87.00	99.00
MALES CHILE 32 - 33.5 S L	16	91.06	5.8818	1.4705	87.945	94.180	6.46	79.00	100.00
MALES CHILE- 34-37.5 S LAT	13	88.85	4.4879	1.2447	86.158	91.535	5.05	83.00	99.00
MALES CHILE 38-39.5 S LAT	17	90.24	3.7338	.9056	88.325	92.146	4.14	85.00	98.00
MALES CHILE- 41-42 S LAT	10	88.90	4.7714	1.5089	85.535	92.265	5.37	83.00	98.00
MALES CHILE -SOUTH 50 S L	2	95.00	2.8284	2.0000	86.394	103.606	2.98	93.00	97.00
MALES CHILE--NO LOCALITY	12	91.00	3.9080	1.1282	88.541	93.459	4.29	84.00	100.00

PEZITES MILITARIS MILITARIS MALES BILL LENGTH

LOCATION PEZITES MILITARIS MALES	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Non-pampas birds									
Falkland Is. (falklandicus)	18	29.65	2.6001	.6128	28.363	30.937	8.77	26.80	35.60
Tierra del Fuego & Santa Cruz Prov.	35	24.77	1.9813	.3349	24.092	25.445	8.00	19.50	28.70
Southern Andes (Chubut)	27	23.16	1.5680	.3018	22.540	23.778	6.77	20.20	27.10
Mendoza to Bariloche	13	23.33	1.3256	.3677	22.537	24.125	5.68	21.30	26.80
San Juan & La Rioja	9	23.08	1.0414	.3471	22.293	23.862	4.51	21.40	24.60
S. Catamarca (intermediate area)	6	22.68	.5672	.2315	22.116	23.251	2.50	22.00	23.40
N. Catamarca-Jujuy (catamarcanus)	10	23.10	1.1643	.3682	22.279	23.921	5.04	21.10	25.30
Pampas birds									
31-35.3° S. Lat (northern pampas)	21	23.12	1.0925	.2384	22.623	23.615	4.73	21.20	25.10
36-36.3° S Lat (central pampas)	14	22.11	1.1072	.2959	21.478	22.750	5.01	20.90	24.20
Estancia Saudade	15	22.66	1.5426	.3983	21.812	23.508	6.81	19.90	25.10
Bahia Blanca	6	21.58	1.9364	.7905	19.647	23.520	8.97	19.20	24.20
Panhandle 39-40° S. latitude	12	21.97	.9764	.2819	21.352	22.581	4.44	20.00	23.70
No locality information	10	25.29	1.5920	.5034	24.167	26.413	6.29	23.00	29.00
Coastal Rio Negro-Chubut (43-48° S).	7	24.10	2.3707	.8960	21.985	26.215	9.84	21.00	27.90
Chile 29-30° S. Latitude	9	23.41	1.2534	.4178	22.467	24.355	5.35	21.70	25.50
Chile 32-34° S. Latitude	17	23.99	1.7695	.4292	23.083	24.894	7.38	21.00	26.70
Chile 34-38° S. Latitude	13	24.20	2.0716	.5746	22.959	25.441	8.56	20.80	27.80
Chile 38-40° S. Latitude	17	25.19	1.7311	.4199	24.308	26.080	6.87	22.00	29.00
Chile 41-42° S. Latitude	10	26.45	2.3100	.7305	24.821	28.079	8.73	23.20	30.00
Chile 50° and southward	2	25.15	.0707	.0500	24.935	25.365	.28	25.10	25.20
Chile No locality information	12	23.58	1.7827	.5146	22.461	24.705	7.56	20.40	27.40

PEZITES MILITARIS males TARSUS LENGTH

LOCATION PEZITES MILITARIS MALES	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Non-pampas birds									
Falkland Is. (falklandicus)	19	36.23	1.0578	.2427	35.724	36.739	2.92	33.50	37.60
Tierra del Fuego & Santa Cruz Prov.	35	35.74	1.0754	.1818	35.373	36.107	3.01	32.20	37.90
Southern Andes (Chubut)	27	36.29	.8421	.1621	35.960	36.625	2.32	34.20	37.50
Mendoza to Bariloche	13	35.72	.9236	.2562	35.162	36.269	2.59	34.50	37.60
San Juan & La Rioja	9	36.24	1.3078	.4359	35.259	37.230	3.61	33.20	37.50
S. Catamarca (intermediate area)	6	36.60	.6132	.2503	35.987	37.213	1.68	35.80	37.50
N. Catamarca-Jujuy (catamarcanus)	10	36.62	.8954	.2832	35.989	37.251	2.45	34.40	37.70
Pampas birds									
31-35.3° S. Lat (northern pampas)	21	35.18	1.0644	.2323	34.693	35.659	3.03	33.30	37.60
36-36.3° S Lat (central pampas)	14	34.42	1.1040	.2950	33.787	35.056	3.21	32.60	36.40
Estancia Saudade	15	34.35	1.5240	.3935	33.515	35.191	4.44	30.90	36.80
Bahia Blanca	7	34.27	1.0950	.4139	33.295	35.248	3.20	32.60	35.30
Panhandle 39-40° S. latitude	11	33.79	1.0968	.3307	33.063	34.519	3.25	31.00	35.00
No locality information	10	36.48	.6088	.1925	36.051	36.909	1.67	35.40	37.30
Coastal Rio Negro-Chubut (43-48° S).	7	36.13	.6237	.2357	35.572	36.685	1.73	35.40	37.40
Chile: 29 - 30° South lat.	9	33.87	1.7464	.5821	32.551	35.182	5.16	31.10	36.50
Chile: 32 - 33.5° South lat.	15	35.09	1.5647	.4040	34.226	35.947	4.46	32.80	37.80
Chile: 34 - 37.5° South lat.	13	34.42	1.5550	.4313	33.484	35.347	4.52	31.80	36.70
Chile: 38-- 39.5° South lat.	17	34.89	.8215	.1992	34.468	35.309	2.35	33.40	36.50
Chile: 41 - 42° South lat.	10	34.31	.8875	.2807	33.684	34.936	2.59	32.90	35.60
Chile: 50° S. lat. and southward	2	34.90	.8485	.6000	32.318	37.482	2.43	34.30	35.50
Chile: no locality information	12	34.75	.9239	.2667	34.169	35.331	2.66	33.60	36.80

PEZITES MILITARIS FEMALES

WING LENGTH

LOCATION	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
PEZITES MILITARIS FEMALES									
Falkland Is. (falklandicus)	17	120.47	2.0346	.4935	119.429	121.512	1.69	115.00	124.00
Tierra del Fuego	20	119.30	4.1789	.9344	117.351	121.249	3.49	111.00	128.00
Bariloche & Chubut	13	116.85	2.6092	.7236	115.283	118.409	2.23	111.00	120.00
Mendoza to Catamarcana (Andean)	9	119.44	3.3353	1.1318	116.887	122.002	2.84	115.00	126.00
Catamarcana-Jujuy (catamarcanus)	10	121.20	3.9665	1.2543	118.403	123.997	3.27	116.00	131.00
Pampas	20	112.50	3.6721	.8256	110.778	114.222	3.28	107.00	121.00
Chile	21	113.19	3.3109	.7226	111.688	114.693	2.93	107.00	118.00

TAIL LENGTH

LOCATION	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
PEZITES MILITARIS FEMALES									
Falkland Is. (falklandicus)	17	86.18	2.7211	.6600	84.784	87.569	3.16	82.00	91.00
Tierra del Fuego	20	87.25	3.9719	.8882	85.397	89.103	4.55	76.00	97.00
Bariloche & Chubut	13	87.69	2.2871	.6343	86.322	89.062	2.61	83.00	91.00
Mendoza to Catamarcana (Andean)	8	89.00	4.5981	1.6257	85.245	92.755	5.17	81.00	95.00
Catamarcana-Jujuy (catamarcanus)	10	90.20	5.3292	1.6852	86.442	93.958	5.91	80.00	102.00
Pampas	20	83.00	3.4489	.7712	81.391	84.609	4.16	76.00	91.00
Chile	21	86.57	4.9957	1.0902	84.304	88.839	5.77	78.00	96.00

BILL LENGTH

LOCATION	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
PEZITES MILITARIS FEMALES									
Falkland Is. (falklandicus)	15	25.93	1.9977	.5158	24.828	27.025	7.71	22.40	30.40
Tierra del Fuego	20	22.04	2.2371	.5002	21.001	23.088	10.15	19.10	29.10
Bariloche & Chubut	13	19.92	1.0566	.2930	19.282	20.548	5.31	17.70	21.50
Mendoza to Catamarcana (Andean)	9	21.60	1.3491	.4497	20.534	22.666	6.25	18.50	23.50
Catamarcana-Jujuy (catamarcanus)	9	21.73	.8832	.2944	21.068	22.399	4.06	20.40	23.20
Pampas	19	23.51	1.2301	.2822	20.920	21.201	5.97	18.30	29.10
Chile	20	22.30	1.2386	.2770	21.727	22.873	5.55	20.40	29.10

TARSUS LENGTH

LOCATION	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
PEZITES MILITARIS FEMALES									
Falkland Is. (falklandicus)	17	34.82	1.2407	.3009	34.189	35.458	3.56	31.30	37.30
Tierra del Fuego	19	34.61	.7982	.1831	34.222	34.988	2.31	33.50	36.20
Bariloche & Chubut	13	34.90	.7874	.2184	34.428	35.372	2.26	33.70	36.70
Mendoza to Catamarcana (Andean)	8	35.25	1.1032	.3901	34.449	36.151	3.13	31.50	36.40
Catamarcana-Jujuy (catamarcanus)	10	34.92	1.2300	.3890	34.093	35.787	3.52	33.80	36.10
Pampas	20	32.85	1.2902	.2885	32.248	33.452	3.93	30.30	35.20
Chile	21	33.10	1.0141	.2213	32.635	33.565	3.06	31.20	34.80

WING LENGTH

PEZITES BELLICOSA MALES	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		Cv	MINIMUM	MAXIMUM
No locality information	5	116.00	3.3912	1.5166	112.101	119.899	2.92	111.00	120.00
Ecuador	43	118.98	5.7531	.8789	117.210	118.743	5.01	101.00	128.00
Northern Peru	37	116.35	3.6824	.6055	115.128	117.575	3.17	107.00	125.00
Central Peru (Lima, Bujama)	30	113.63	2.6844	.4901	112.633	114.634	2.36	108.00	118.00
Southern Peru and Chile	13	116.38	3.3050	.9166	114.405	118.365	2.84	110.00	122.00
Peruvian Andes	19	119.37	3.9470	.9055	117.473	121.264	3.31	112.00	127.00

WING LENGTH

TAIL LENGTH

	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		Cv	MINIMUM	MAXIMUM
No locality information	5	71.60	3.2863	1.4697	67.821	75.379	4.59	67.00	76.00
Ecuador	43	71.09	4.5346	.6915	69.703	72.483	6.38	64.00	85.00
Northern Peru	37	71.73	3.1767	.5222	70.675	72.785	4.43	66.00	79.00
Central Peru (Lima, Bujama)	29	68.66	3.7059	.6882	67.248	70.062	5.40	61.00	76.00
Southern Peru and Chile	13	70.38	2.1809	.6049	69.078	71.691	3.10	67.00	74.00
Peruvian Andes	20	73.55	2.2355	.4999	72.507	74.593	3.04	70.00	77.00

TAIL LENGTH

BILL LENGTH

	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
No locality information	5	19.28	.9859	.4409	18.146	20.414	5.11	18.10	20.50
Ecuador	43	18.52	1.1443	.1745	18.172	18.874	6.18	16.60	21.50
Northern Peru	35	18.62	1.0435	.1764	18.266	18.979	5.60	17.00	21.50
Central Peru (Lima, Bujama)	29	19.08	1.0419	.1935	18.680	19.471	5.46	17.40	21.80
Southern Peru and Chile	13	20.10	1.3051	.3620	19.318	20.882	6.49	18.40	22.30
Peruvian Andes	20	21.36	11.5888	2.5913	15.954	25.766	54.25	16.90	70.50

BILL LENGTH

TARSUS LENGTH

	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
No locality information	5	35.88	1.4446	.6461	34.219	37.541	4.03	34.20	37.80
Ecuador	43	35.66	1.5522	.2382	35.182	36.139	4.38	29.30	38.50
Northern Peru	37	35.47	1.2705	.2089	35.051	35.895	3.58	32.70	38.50
Central Peru (Lima, Bujama)	30	35.42	1.0040	.1833	35.049	35.798	2.83	33.80	37.60
Southern Peru and Chile	12	33.17	1.2198	.3521	34.399	35.934	3.47	32.30	37.40
Peruvian Andes	20	36.40	1.0397	.2325	35.915	36.885	2.86	34.20	38.50

TARSUS LENGTH

WING LENGTH

LOCATION PEZITES BELLICOSA FEMALES	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Ecuador---sea level	13	95.46	2.5369	.7036	93.942	96.981	2.66	90.00	100.00
N. Peru below 1000 m; north of 8° S.	10	99.60	4.0066	1.2667	96.775	102.425	4.02	94.00	108.00
C. Peru (Lima, Bujama)	7	97.14	7.6251	2.8820	90.341	103.944	7.85	82.00	106.00
Southern Peru and Chile	8	100.37	3.5025	1.2383	97.614	103.236	3.49	95.00	105.00
Ecuador---above 2000 m.	6	105.40	3.2094	1.4353	101.710	109.090	3.04	100.00	108.00
N. Peru above 1800 m.	11	102.27	3.0361	.9154	100.258	104.288	2.97	98.00	105.00
	54	99.48	4.9613	.6751	98.131	100.832	4.99	82.00	108.00

TAIL LENGTH

PEZITES BELLICOSA FEMALES	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Ecuador---sea level	13	56.85	2.6092	.7236	55.283	58.409	4.59	51.00	62.00
N. Peru below 1000 m; north of 8° S.	10	59.40	2.1187	.6700	57.906	60.894	3.57	55.00	62.00
C. Peru (Lima, Bujama)	7	59.00	5.8878	2.2254	53.748	64.252	9.98	51.00	65.00
Southern Peru and Chile	8	59.75	4.6522	1.6448	55.951	63.549	7.79	53.00	67.00
Ecuador---above 2000 m.	5	65.20	1.9235	.8602	62.988	67.412	2.95	63.00	68.00
N. Peru above 1800 m.	11	62.00	3.1305	.9439	59.923	64.077	5.05	56.00	66.00

PEZITES BELLICOSA FEMALES

BILL LENGTH

PEZITES BELLICOSA FEMALES	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Ecuador---sea level	13	15.63	.6223	.1726	15.258	16.004	3.98	14.80	17.10
N. Peru below 1000 m; north of 8° S.	10	15.09	.4818	.1524	15.750	16.430	2.99	15.40	15.90
C. Peru (Lima, Bujama)	7	16.63	1.8117	.6848	15.013	18.245	10.90	13.50	19.30
Southern Peru and Chile	8	16.10	1.4462	.5113	14.919	17.281	8.98	12.70	17.20
Ecuador---above 2000 m.	5	17.00	.6245	.2793	16.282	17.718	3.67	16.10	17.70
N. Peru above 1800 m.	11	16.47	.8076	.2435	15.937	17.009	4.90	14.80	17.90
	54	16.21	1.0550	.1436	15.926	16.500	6.51	12.70	19.30

BILL LENGTH

TARSUS LENGTH

PEZITES BELLICOSA FEMALES	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Ecuador---sea level	13	32.92	.6581	.1825	32.521	33.310	2.00	31.50	33.90
N. Peru below 1000 m; north of 8° S.	10	31.94	1.1384	.3600	31.137	32.743	3.56	30.70	33.30
C. Peru (Lima, Bujama)	7	32.40	3.1225	1.1802	29.515	35.185	9.64	26.70	36.50
Southern Peru and Chile	8	32.70	.8502	.3006	32.006	33.394	2.60	31.30	33.90
Ecuador---above 2000 m.	5	33.22	.8438	.3774	32.250	34.190	2.54	32.30	34.20
N. Peru above 1800 m.	11	31.62	1.4764	.4451	30.638	32.598	4.67	28.10	33.30

TARSUS LENGTH

PEZITES DEFILIPPII MALES

WING LENGTH

PEZITES DEFILIPPII MALES	N	MEAN	ST. DEV.	ST. ERROR	95% CONF. LIMIT		CV	MINIMUM	MAXIMUM
North Argentina 32-34° South Lat.	9	122.89	3.0596	1.0199	120.584	125.194	2.49	117.00	126.00
Northern pampas 34-36° South Lat.	21	123.00	2.7019	.5896	121.774	124.226	2.20	119.00	130.00
Central pampas 36-37° South lat.	9	123.22	3.7342	1.2447	120.409	126.035	3.03	120.00	130.00
Southern pampas 37-38° South Lat.	22	123.82	2.9054	.6194	122.536	125.100	2.35	116.00	129.00
No locality information	3	123.67	3.5119	2.0276	117.215	130.118	2.84	120.00	127.00

TAIL LENGTH

	N	MEAN	ST. DEV.	ST. ERROR	95% CONF. LIMIT		CV	MINIMUM	MAXIMUM
North Argentina 32-34° South Lat.	9	76.56	4.3906	1.4635	73.248	79.863	5.74	71.00	85.00
Northern pampas 34-36° South Lat.	21	74.95	3.3388	.7286	73.437	76.468	4.45	69.00	83.00
Central pampas 36-37° South lat.	9	77.33	4.3012	1.4337	74.093	80.574	5.56	71.00	83.00
Southern pampas 37-38° South Lat.	23	75.39	4.3457	.9061	73.516	77.267	5.76	68.00	88.00
No locality information	3	74.67	2.0817	1.2018	72.842	80.491	2.72	75.00	79.00

BILL LENGTH

	N	MEAN	ST. DEV.	ST. ERROR	95% CONF. LIMIT		CV	MINIMUM	MAXIMUM
North Argentina 32-34° South Lat.	9	20.67	.9874	.3291	19.923	21.411	4.78	19.10	21.90
Northern pampas 34-36° South Lat.	21	20.24	.7201	.1571	19.911	20.565	3.56	18.90	22.20
Central pampas 36-37° South lat.	9	21.13	.9887	.3296	20.369	21.878	4.68	19.90	22.50
Southern pampas 37-38° South Lat.	22	20.58	1.4790	.3153	19.924	21.230	7.19	17.40	24.50
No locality information	3	20.87	.5860	.3383	19.790	21.943	2.81	20.20	21.30

TARSUS LENGTH

	N	MEAN	ST. DEV.	ST. ERROR	95% CONF. LIMIT		CV	MINIMUM	MAXIMUM
North Argentina 32-34° South Lat.	9	32.00	1.0198	.3399	31.232	32.768	3.19	30.50	33.80
Northern pampas 34-36° South Lat.	21	32.36	1.0264	.2240	31.891	32.823	3.17	30.10	33.80
Central pampas 36-37° South lat.	9	32.10	1.2329	.4110	31.171	33.029	3.84	30.10	33.40
Southern pampas 37-38° South Lat.	23	31.73	1.6350	.3409	31.025	32.436	5.15	27.60	34.50
No locality information	3	31.53	1.1930	.6888	29.342	33.725	3.78	30.20	32.50

LOCATION

PEZITES DEFILIPPII FEMALES

	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Northern pampas 34-36° South Lat.	13	109.62	5.0915	1.4121	106.565	112.666	4.64	105.00	123.00
Central pampas 36-37° South lat.	13	109.85	3.1532	.8759	107.954	111.738	2.88	103.00	116.00
Southern pampas 37-38° South Lat.	7	106.29	1.6066	.6061	104.855	107.716	1.51	105.00	108.00
No locality information	7	110.14	1.4639	.5533	108.837	111.449	1.33	107.00	111.00

	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Northern pampas 34-36° South Lat.	13	69.00	4.5461	1.2608	66.277	71.723	6.59	63.00	77.00
Central pampas 36-37° South lat.	13	69.00	2.5166	.6980	67.492	70.508	3.65	65.00	73.00
Southern pampas 37-38° South Lat.	7	62.29	2.1381	.8081	60.379	64.193	3.43	61.00	67.00
No locality information	7	69.29	7.0407	2.6611	63.005	75.566	10.16	61.00	82.00

	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Northern pampas 34-36° South Lat.	13	17.86	1.3805	.3829	17.034	18.689	7.73	16.20	21.10
Central pampas 36-37° South lat.	13	17.72	.7650	.2122	17.265	18.181	4.32	16.70	19.40
Southern pampas 37-38° South Lat.	7	16.24	.2879	.1088	15.986	16.500	1.77	16.00	16.80
No locality information	7	17.51	.6594	.2492	16.926	18.102	3.76	16.50	18.10

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	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Northern pampas 34-36° South Lat.	13	29.88	1.0764	.2985	29.232	30.522	3.60	27.80	31.30
Central pampas 36-37° South lat.	13	29.94	.5650	.1567	29.600	30.277	1.89	29.00	30.70
Southern pampas 37-38° South Lat.	7	29.83	.6370	.2407	28.260	29.397	2.21	28.40	30.20
No locality information	7	29.71	1.1796	.4458	28.662	30.766	3.97	27.80	31.70

LEISTES MILITARIS SUPERCILIARIS MALES

WING LENGTH

LOCATION LEISTES M. SUPERCILIARIS MALES	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Central Brazil	7	102·86	1·6762	·6335	101·309	104·352	1·63	101·00	106·00
Sao Paulo & Adolpho	6	102·67	1·7512	·7149	100·915	104·418	1·71	101·00	105·00
Matto Grosso	4	99·50	2·0817	1·0408	96·611	102·389	2·09	97·00	102·00
Bolivia	25	99·08	3·3779	·6756	97·688	100·472	3·41	93·00	107·00
North & N.W. Argentina	14	97·86	2·3487	·6277	96·508	99·207	2·40	93·00	101·00
Paraguayan Chaco	30	100·10	2·7336	·4991	99·081	101·119	2·73	94·00	105·00
Corrientes (Argentina)	17	101·53	2·3748	·5760	100·314	102·745	2·34	98·00	105·00
Uruguay	7	101·00	2·7689	1·0465	98·530	103·470	2·74	96·00	104·00
Entre Rios etc.(Argentina	10	100·00	3·8873	1·2293	97·259	102·741	3·89	95·00	105·00
La Plata & northern Buenos Aires	18	99·83	2·4555	·5788	98·618	101·049	2·46	96·00	105·00
Southern Pampas	4	99·50	3·8730	1·9365	94·124	104·876	3·89	94·00	103·00

TAIL LENGTH

LEISTES M. SUPERCILIARIS MALES	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Central Brazil	7	63·57	1·6183	·6117	62·128	65·015	2·55	62·00	67·00
Sao Paulo & Adolpho	6	63,83	1,9408	,7923	61,892	65,775	3,04	61·00	66,00
Matto Grosso	4	60·00	1·4142	·7071	58·037	61·963	2·36	58·00	61·00
Bolivia	24	58·04	3·7005	·7554	56·483	59·601	6·38	48·00	64·00
North & N.W. Argentina	14	59·00	3·9223	1·0483	56·746	61·254	6·65	52·00	64·00
Paraguayan Chaco	30	61·03	2·9535	·5392	59·932	62·134	4·84	53·00	65·00
Corrientes (Argentina)	17	63·24	2·8401	·6888	61·782	64·689	4·49	59·00	68·00
Uruguay	7	60·00	4·1633	1·5736	56·286	63·714	6·94	56·00	67·00
Entre Rios etc.(Argentina	10	62·00	2·9570	·7454	60·338	63·662	3·80	59·00	66·00
La Plata & northern Buenos Aires	18	59·67	2·2492	·5301	58·553	60·780	3·77	55·00	63·00
Southern Pampas.	4	61·25	1·2583	·6292	59·303	62·997	2·05	60·00	63·00

LEISTES MILITARIS SUPERCILIARIS

BILL LENGTH

LOCATION LEISTES M. SUPERCILIARIS MALES	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Central Brazil	7	13.67	.4608	.1742	13.260	14.082	3.37	13.00	14.20
Sao Paulo & Adolpho	6	14.08	1.0515	.4293	13.032	15.135	7.47	12.30	15.30
Matto Grosso	4	13.10	1.0424	.5212	11.653	14.547	7.96	11.70	14.20
Bolivia	25	12.79	.8511	.1702	12.437	13.139	6.66	11.10	14.70
North & N.W. Argentina	14	12.71	.5051	.1350	12.424	13.005	3.97	11.70	13.70
Paraguayan Chaco	30	12.98	.4992	.0911	12.794	13.166	3.85	11.50	13.70
Corrientes (Argentina)	17	13.06	.3868	.0936	12.861	13.256	2.95	12.40	13.70
Uruguay	7	12.80	.5568	.2104	12.303	13.297	4.35	11.70	13.50
Entre Rios etc.(Argentina	9	12.94	.6766	.2255	12.435	13.454	5.23	12.00	13.80
La Plata & northern Buenos Aires	17	12.91	.5739	.1392	12.612	13.200	4.45	11.90	14.00
Southern Pampas	4	13.97	.9912	.4956	12.599	15.351	7.09	13.30	15.40

TARSUS LENGTH

LEISTES M. SUPERCILIARIS MALES	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Central Brazil	7	30.87	.5080	.1924	30.417	31.325	1.65	30.20	31.60
Sao Paulo & Adolpho	6	30.83	1.1742	.4793	29.659	32.008	3.81	29.30	32.40
Matto Grosso	4	28.90	.5715	.2858	26.107	29.693	1.98	28.20	29.50
Bolivia	25	30.37	.9715	.1943	29.972	30.772	3.20	28.20	31.70
North & N.W. Argentina	14	30.39	1.0855	.2901	29.762	31.009	3.57	28.20	32.50
Paraguayan Chaco	30	30.24	.5654	.1032	30.029	30.451	1.87	29.10	31.80
Corrientes (Argentina)	17	30.36	.7771	.1885	29.961	30.756	2.56	29.10	31.70
Uruguay	7	29.89	.7669	.2899	29.202	30.570	2.57	29.00	31.00
Entre Rios etc.(Argentina	8	29.95	.7464	.2639	29.340	30.560	2.49	29.20	31.70
La Plata & northern Buenos Aires	18	30.09	1.0169	.2397	29.586	30.592	3.38	28.40	32.00
Southern Pampas	4	30.27	1.0500	.5250	28.818	31.732	3.47	29.40	31.80

LEISTES MILITARIS SUPERCILIARIS FEMALES

WING LENGTH

LOCATION LEISTES MILITARIS SUPERCILIARIS ♀♀	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
East-central Brasil (2-3° South lat.)	4	91.50	.5774	.2887	90.699	92.301	.63	91.00	92.00
Sao Paulo to Argentine pampas	6	89.33	1.9664	.8028	87.367	91.300	2.20	87.00	92.00
Northwestern Argentina	6	92.17	6.9113	2.8215	86.254	99.079	7.50	86.00	101.00
Bolivia (300 - 2700 m.)	13	89.54	3.1784	.8815	87.634	91.443	3.55	85.00	95.00

TAIL LENGTH

LEISTES MILITARIS SUPERCILIARIS ♀♀	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
East-central Brasil (2-3° South lat.)	4	56.50	4.0415	2.0207	50.890	62.110	7.15	53.00	60.00
Sao Paulo to Argentine pampas	6	55.83	2.4833	1.0138	53.350	58.317	4.45	51.00	58.00
Northwestern Argentina	6	55.00	4.2825	1.7512	50.710	59.290	7.80	51.00	60.00
Bolivia (300 - 2700 m.)	13	53.23	2.3507	.6520	51.823	54.639	4.42	50.00	56.00

BILL LENGTH

LEISTES MILITARIS SUPERCILIARIS ♀♀	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
East-central Brasil (2-3° South lat.)	4	12.20	1.1547	.5774	10.397	13.803	9.46	11.20	13.20
Sao Paulo to Argentine pampas	5	11.52	.7563	.3382	10.650	12.390	6.57	10.70	12.20
Northwestern Argentina	6	12.58	1.3091	.5344	11.274	13.893	10.40	11.10	14.40
Bolivia (300 - 2700 m.)	13	11.67	.6750	.1872	11.265	12.074	5.78	11.00	12.70

TARSUS LENGTH

LEISTES MILITARIS SUPERCILIARIS ♀♀	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
East-central Brasil (2-3° South lat.)	4	28.50	.2309	.1155	28.179	28.821	.81	28.30	28.70
Sao Paulo to Argentine pampas	6	28.45	.6626	.2705	27.787	29.113	2.33	27.50	29.20
Northwestern Argentina	6	28.90	.5177	.2113	28.382	29.418	1.79	28.00	29.40
Bolivia (300 - 2700 m.)	13	28.38	1.0971	.3043	27.720	29.034	3.87	26.80	29.90

WING LENGTH

LEISTES MILITARIS MILITARIS MALES	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Panama-Colombia-NW Venezuela	25	94.16	2.7031	.5406	93.046	95.274	2.87	89.00	98.00
Southern Venezuela (Orinoco)	25	96.48	2.2002	.4402	95.573	97.387	2.28	94.00	100.00
Trinidad	14	93.50	1.7867	.4775	92.473	94.527	1.91	92.00	97.00
Surinam and Cayenne	21	97.00	2.7568	.6016	95.749	98.251	2.84	90.00	101.00
Guyana	23	96.43	2.4463	.5101	95.379	97.491	2.54	93.00	100.00
Miscellaneous Amazonian sites	31	98.55	3.5293	.6339	97.262	99.835	3.58	90.00	106.00
Mouth of the Rio Andira (Amazonian)	15	100.27	2.7637	.7136	98.747	101.787	2.76	91.00	103.00
Rio Tapajoz (near confluence)	13	102.00	2.2730	.6304	100.638	103.362	2.23	98.00	105.00
Eastern Ecuador	4	94.50	1.9149	.9574	91.842	97.158	2.03	92.00	96.00
East-central Brazil	5	99.20	1.3038	.5831	97.701	100.699	1.31	98.00	101.00

TAIL LENGTH

LEISTES MILITARIS MILITARIS MALES	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Panama-Colombia-NW Venezuela	25	57.96	2.2635	.4527	57.027	58.893	3.91	54.00	62.00
Southern Venezuela (Orinoco)	25	60.04	2.5573	.5115	58.986	61.094	4.26	54.00	65.00
Trinidad	14	58.00	2.0755	.5547	56.807	59.193	3.58	55.00	63.00
Surinam and Cayenne	21	62.05	1.9869	.4336	61.146	62.949	3.20	57.00	65.00
Guyana	23	61.00	2.0869	.4356	60.098	61.902	3.42	56.00	66.00
Miscellaneous Amazonian sites	31	62.55	4.6536	.8358	60.852	64.248	7.44	55.00	70.00
Mouth of the Rio Andira (Amazonian)	15	64.73	1.7915	.4626	63.748	65.719	2.77	62.00	69.00
Rio Tapajoz (near confluence)	13	65.00	1.7795	.4935	63.934	66.066	2.74	62.00	68.00
Eastern Ecuador	4	61.75	3.5940	1.7970	56.762	66.738	5.82	57.00	65.00
East-central Brazil	5	62.00	2.0000	.8944	59.700	64.300	3.23	60.00	65.00

LEISTES MILITARIS MILITARIS MALES

BILL LENGTH

LOCATION LEISTES MILITARIS MILITARIS MALES	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Panama-Colombia-NW Venezuela	25	13.81	.6218	.1244	13.552	14.064	4.50	12.90	15.10
Southern Venezuela (Orinoco)	25	14.09	.6797	.1359	13.808	14.368	4.82	12.60	15.20
Trinidad	13	14.78	1.0175	.2522	14.167	15.386	6.89	13.70	17.90
Surinam and Cayenne	21	15.11	.9066	.1978	14.698	15.521	6.00	14.00	16.90
Guyana	22	14.30	.6658	.1420	14.002	14.589	4.66	13.00	15.40
Miscellaneous Amazonian sites	30	14.65	.9054	.1653	14.309	14.984	6.18	12.40	16.50
Mouth of the Rio Andira (Amazonian)	15	15.09	.5194	.1341	14.801	15.372	3.44	14.00	16.00
Rio Tapajoz (near confluence)	13	15.14	.4445	.1233	14.872	15.405	2.94	14.40	16.00
Eastern Ecuador	4	15.27	1.3048	.6524	13.464	17.086	8.54	13.90	17.00
East-central Brazil	5	13.48	.3114	.1393	13.122	13.838	2.31	13.20	14.00

TARSUS LENGTH

LEISTES MILITARIS MILITARIS MALES	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Panama-Colombia-NW Venezuela	25	29.54	.7489	.1498	29.235	29.852	2.53	28.10	30.80
Southern Venezuela (Orinoco)	25	29.21	.9153	.1831	28.835	29.589	3.13	27.60	31.20
Trinidad	10	29.09	1.1100	.3510	28.307	29.873	3.82	27.20	31.50
Surinam and Cayenne	19	29.57	1.2698	.2913	29.206	30.185	4.26	27.10	32.40
Guyana	22	29.75	.8900	.1897	29.389	30.174	2.99	28.30	31.40
Miscellaneous Amazonian sites	26	30.31	1.1589	.2272	29.836	30.784	3.86	28.50	32.80
Mouth of the Rio Andira (Amazonian)	15	31.29	.7398	.2644	30.854	31.733	2.36	29.90	33.20
Rio Tapajoz (near confluence)	13	31.22	1.3361	.3754	30.423	32.023	4.28	28.00	33.50
Eastern Ecuador	4	30.07	1.2066	.6033	28.400	31.750	4.01	28.90	31.70
East-central Brazil	5	30.40	1.1979	.5357	29.023	31.777	3.94	28.70	31.80

LEISTES MILITARIS MILITARIS FEMALES

WING LENGTH

LEISTES MILITARIS MILITARIS FEMALES	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Panama-Colombia-Venezuela-Ecuador	8	83.50	2.0702	.7319	81.809	85.191	2.48	81.00	88.00
Trinidad-Guyanas-E. Venezuela	23	84.65	1.8705	.3906	83.844	85.461	2.21	82.00	88.00
Amazonian Brasil	15	85.67	3.1773	.8204	83.919	87.414	3.71	82.00	92.00

TAIL LENGTH

	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Panama-Colombia-Venezuela-Ecuador	8	51.12	2.6969	.9531	48.923	53.327	5.27	48.00	55.00
Trinidad-Guyanas-E. Venezuela	23	53.39	2.0832	.4344	52.492	54.290	3.90	50.00	57.00
Amazonian Brasil	15	54.47	3.0675	.7920	52.780	56.154	5.63	50.00	60.00

BILL LENGTH

	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Panama-Colombia-Venezuela-Ecuador	8	12.42	.3955	.1398	12.102	12.748	3.18	11.90	13.10
Trinidad-Guyanas-E. Venezuela	23	13.07	.5638	.1176	12.822	13.309	4.31	12.00	14.50
Amazonian Brasil	15	12.59	.7941	.2050	12.157	13.030	6.31	11.10	13.70

TARSUS LENGTH

	N	MEAN	ST.DEV.	ST.ERROR	95% CONF.LIMIT		CV	MINIMUM	MAXIMUM
Panama-Colombia-Venezuela-Ecuador	8	27.59	.6244	.2207	27.078	28.097	2.26	26.30	28.50
Trinidad-Guyanas-E. Venezuela	21	27.73	1.0340	.2256	27.259	28.198	3.73	25.80	29.60
Amazonian Brasil	13	28.97	1.0570	.2932	28.336	29.602	3.65	27.20	30.70

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