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THE EFFECT OF LOCATION AND STAGE OF NESTING ON NEIGHBOR/STRANGER DISCRIMINATION IN THE HOUSE WREN

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THE EFFECT OF LOCATION AND STAGE OF NESTING ON NEIGHBOR / STRANGER DISCRIMINATION IN THE HOUSE WREN

by

PATRICIA A. GROVE

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.

1981

PATRICIA GROVE

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.

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INTRODUCTION

The concept of territory as a "defended area" was first developed through the observation of avian behavior by Altum (Mayr 1935) in the nineteenth century, and expanded by Howard (1920) in the early twentieth century. The form and extent of this defended area varies with the ecological and social requirements of the species. The area that is defended may range from a small distance around individual nests to large breeding areas within which nesting, courtship, mating, and most food seeking usually occur. The function of territory has been reviewed and discussed by Hinde (1956), Tinbergen (1957), Brown (1969), and Verner (1977).

Territorial behavior is the result of two distinct tendencies: site attachment and hostility (Tinbergen 1957). Hostility is directed toward others who would seek to share the resources of the defended area, be they conspecifics of the same sex as the territory owner, or in some cases members of other species. Any individual who would seek to share resources which the resident of the territory requires could be considered a potential rival, and denied access to the area.

As the territory holder's needs change through the nesting season, the threat posed by challengers fluctuates, and patterns of territorial defense also may shift (Ickes and Ficken 1970; Catchpole 1977). A territorial male would be expected to respond to conspecific challengers with differing intensities and behaviors. Of the many factors which may influence the response of a territorial male, I have examined three: the familiarity of the challenger to the resident, the location of the challenger with regard to the territory of the resident, and the stage of the nesting cycle.

Ownership of a territory is a prerequisite for breeding in most passerine species which nest, court, mate, and feed within the territory (Verner 1977). Although not all territory owners secure mates, males which lack a territory do not acquire mates for the nesting season. The female of many species travels from territory to territory, and seems to "judge" the attractiveness of a male largely on the basis of his behavior, appearance, and the resources his area has to offer (Kendeigh 1941; Orians 1961; Willson 1966; Best 1977). A male does not leave his territory to secure a mate. He must render himself conspicuous by occupying a position from which he can readily be seen, or by producing sounds which will direct the female.

In order to maintain ownership of an area, a "no vacancy" message must be proclaimed, and the physical presence of the resident carrying on daily activities within the territory is an effective deterrent to potential challengers to that ownership. The resident's presence is emphatically made known through visual and auditory displays, and information pertaining to an individual's species, sex, motivational state and identity may be transmitted.

The physical appearance of a bird may transmit much information. Many species are sexually dimorphic (Verner and Willson 1969) with intraspecific variability fostering individual as well as sexual identification. Adult males may possess structures or coloration lacking in subadults or juveniles, with postures and movements rendering these parts even more conspicuous. However, visually conveyed information requires proximity and visibility. At short distances, visual displays are extremely important, but their usefulness declines with increasing distances.

Auditory displays act to reinforce visual displays as well as act alone. The physical properties of sound impose few constraints on the transmission of auditory information, although the habitat may selectively alter the sound as it travels (Morton 1975; Marten and Marler 1977; Wiley and Richards 1978). Sound carries at a distance, and travels through vegetation and around obstacles while remaining localizable (Marler 1955). Vocalizations are independent of light levels, and are effective day or night.

Passerine vocalizations are generally categorized into two classes: call notes and songs (Thorpe 1961). The distinction between these classes is clearest, for the most part, among the Oscines, while for other groups the classes may not be clearly separable. _Call notes_ are usually mono- or disyllabic, of fewer than four or five notes. Call notes are used in various contexts by adults and immatures of both sexes throughout the year. There is a degree of variability among callers within a species which may code individual and group identity (Mundinger 1970). The role of call notes in territorial defense in passerine species has not received much attention. _Songs_ are composed of a series of notes, generally of more than one type, uttered in succession and so related as to form a recognizable sequence or pattern in time. Song is primarily under the control of sex hormones (Andrew 1969), and is confined in its most developed form to adults during the breeding season. In species that include more than one song in their repertoire, the composition and size of a repertoire may be a source of information about an individual (Kroodsma 1976b; Smith and Reid 1979; Yasukawa _et al._ 1980).

The set of behaviors of the territorial owner concerned with self-advertisement and defense of the area against potential rivals may be termed territorial maintenance activities. Territorial maintenance accounts for a substantial portion of an individual's time and energy budget (Verner 1965). It can be argued that individuals possessing methods which minimize the expenditure have a selective advantage (Weeden and Falls 1959). A territory holder can most efficiently allocate time and energy reserves by adjusting responsiveness to the magnitude of the threat posed by potential competitors. A Mockingbird (Mimus polyglottos), for example, responds to intrusions by members of other species proportionately to the degree of dietary overlap (Moore 1978). In a number of species, the territory owner responds less strongly to the presence and activities of neighboring conspecifics on their territories than to new birds in an area. This decrease in responsiveness to a monotonous stimulus has been attributed to habituation (Falls and Brooks 1966; Verner and Milligan 1971; Petrinovich and Peeke 1973).

As boundaries are established, the song of a neighbor on his territory may not hold the same implications as that of the song of an unfamiliar male who may be seeking to carve out an area of his own and thus acquire a mate. It has been shown in the White-crowned Sparrow (Zonotrichia leucophrys), for example, that although a certain amount of boundary shifting may occur among neighboring conspecifics, once the territories are established, they remain fairly stable through a nesting cycle (Patterson and Petrinovich 1978). The owner of a territory, then, must be able to discriminate between a neighbor and an unfamiliar conspecific who presumably poses a stronger threat to his territorial claim and hence to the nesting success of the pair. Species which have been shown to discriminate between unfamiliar conspecific and neighbor on the basis of song alone include the Chaffinch, Fringilla coelebs (Marler 1965b), Ovenbird, Seiurus aurocapillus (Weeden and Falls 1959), Great Tit, Parus major (Gompertz 1961; Krebs 1971), White-throated Sparrow, Zonotrichia albicollis (Falls 1969; Brooks and Falls 1975), Indigo Bunting, Passerina cyanea (Emlen 1971), Field Sparrow, Spizella pusilla (Goldman 1973), Song Sparrow, Melospiza melodia (Kroodsma 1976a), Stripe-backed Wren, Campylorhynchus nuchalis (Wiley and Wiley 1977), and Common Yellowthroat, Geothlypis trichas (Wunderle 1978).

The factor of dialect must be considered in the interpretation of neighbor/stranger response. Several species have a geographical variation in their vocalizations, and, as Lemon (1967) has shown for Cardinals (Cardinalis cardinalis), and Kreutzer (1974a) for the European, or Winter, Wren, (Troglodytes troglodytes), males respond strongest to songs of their own dialect. As dialects may change over rather short distances (Lemon and Harris 1974; Baptista 1975), care must be shown in selecting "strangers" in neighbor/stranger discrimination experiments. The additional variable of dialect confounds interpretation of a subject's responses as well as making cross species comparisons difficult.

The discrimination among neighbors and non-neighbors may be effected on a number of levels. The territory resident may "know" all of his neighbors auditorially as individuals, and thereby be able to pick out an unknown individual when that male makes his presence known. The individuality cue may well be the timbre (quality) of the vocalization. As Bertram (1970:171) has discussed,

> It is to be expected that syrinxes, like for example (sic) human fingerprints, differ slightly in different individuals, and that the vocalizations produced by

> these syrinxes will, therefore, differ slightly between individuals. Two vocalizations produced by a given syrinx cannot be expected to be absolutely identical. In order for individual recognition to be possible, the differences between the vocalizations of two individuals must be greater than the range of variation within each individual; they must be large enough for the bird to be able to detect; and they must be diverse enough to distinguish many different individuals.

The recognition may also be possible based upon the song repertoires of individuals, although as the repertoires become sizeable, discriminations made on this basis among individuals may be time consuming and difficult for the territorial males (Krebs 1976; Kroodsma 1976a).

Rather than knowing each male as an individual, the owner may recognize a neighbor only as a member of a class of familiar sounds, and be able to pick out a familiar individual. As discussed by Beer (1970), the species which have demonstrated the ability to perform neighbor/stranger discriminations have not necessarily demonstrated individual recognition.

The location of a conspecific as a cue in the performance of neighbor/stranger discriminations has been overlooked in many studies. A bird may be recognized as a neighbor only when the vocalizations are considered together with their source in space. A neighbor singing outside of his territorial borders may then be regarded as posing as large a threat to an owner of an adjacent territory as does a new conspecific male in the area. On the other hand, an unfamiliar conspecific singing from an established territory would indicate a change in ownership and a likely need for redefining borders. In either case, activity is required on the part of the holder of an adjacent territory. As Belcher and Thompson (1969:82) have discussed,

> It seems that this location effect may also be enough to override the need for individual song recognition ...(in) reducing the time spent in active territorial defense...Without individual song recognition, the territorial boundary would be maintained by the constancy of location from which the (bird) sings, thereby producing a constancy of direction from which each bird hears his neighbor's songs... Differentiation between the structure of the song of the neighbor and that of the intruder would not be necessary.

The biological reality of this "location effect" has been indicated for the White-throated Sparrow (Falls and Brooks 1975), the Stripe-backed Wren (Wiley and Wiley 1977), and the Common Yellowthroat (Wunderle 1978). In each of these species, the songs of neighbors and non-neighbors were played to territorial males from various locations in and around the territory. The difference between the responses to these two groups of songs changed with location, being largest when the speaker was placed along the border with the neighbor. At the normal boundary, a resident's response to stranger song was stronger than that to the song of a neighbor. At the opposite boundary, response to the two groups of songs were not significantly different. The response to neighbor's song changed with location.

Just as the needs of the mated pair change through a nesting cycle, different resources and areas within the territory are utilized to a greater or lesser degree (Yarrow 1970), and patterns of defense may change (Ickes and Ficken 1970; Verner and Milligan 1971; Petrinovich et al. 1976; Catchpole 1977). The role of the male in the care of eggs, nestlings, and fledglings varies within and between species (Verner and Willson 1969), but if the male assists in the care of the brood at any stage, it will affect the energy he can devote to territorial maintenance activities.

The response of a territorial male to the presence of a male conspecific will be affected by at least three factors:

1. The status of the male conspecific. A recognized neighbor singing on his own territory may be regarded differently than a new male singing in the area.

2. The location of the male conspecific. A territorial male may come to associate a neighbor with a particular area, and respond diffently to a neighbor on and off his territory. The neighbor/non-neighbor discrimination may change depending upon the location of the singing male.

3. The stage of the breeding cycle. Areas of the territory will be defended to a greater or lesser degree. Demands upon the male's time and energy will fluctuate through the period of development of the brood.

I chose the House Wren (Troglodytes aedon aedon) as a suitable species for this investigation. In the eastern United States, this species breeds from Maine to North Carolina during the summer months, and winters from the southern part of its range to Veracruz and south Florida (A.O.U. Checklist 1965). The breeding behavior of this species (Kendeigh 1941; Mc Cabe 1965), and the closely related European, or Winter Wren (Armstrong and Whitehouse 1977) has been well described. House Wrens are common in habitats near human dwellings, and are fairly tolerant of the presence of human observers.

The general behavior of an Ohio population described by Kendeigh (1941) is identical to that of the population I have studied. The male establishes a territory of approximately one acre (≈ 4047 m^2) in area, and defends it vigorously throughout the breeding season. The male uses several song types (Kroodsma 1977), and visual displays include flights toward an intruder, chases, wing extension and vibration, tail spreading, and feather erection.

The territory chosen by a male in the early spring usually contains several potential cavity nest-sites, and the male indicates possession of these sites by laying the rudiments of a nest. Nest boxes provide suitable nesting sites for the House Wren. The female travels from territory to territory, and is led to nest sites by the displaying male resident. Insertion of nest lining by the female indicates her choice of nest site and male.

The territory is essential to the successful breeding of the House Wren. Nesting cavities play a role in mate acquisition, and provide the location for the nest and shelter for the developing brood. Insect food material for adults and young are gleaned from within the territory. Foliage provides song perches, foraging areas, and shelter for parent and fledged young. The territory and its resources are utilized and defended throughout the nesting season.

The density of mated pairs in an area is determined by the number and distribution of potential nesting sites (Kendeigh 1941). A territory may adjoin several conspecific territories at different points along its border. Territorial disputes are common, especially early in the season. As Kendeigh (1941:36) observed, "The concept of territorial relations in this species should be a dynamic one with individuals often in strife to adjust their space relations best to meet the prevailing demands." Expansion and contractions are slight through a nesting cycle, but extensive changes may occur when mating for second broods.

Several aspects of the behavior of the House Wren, which include the use of a repertoire of songs, the reported incidence of polygyny, the two successive nesting cycles, and the highly aggressive defense of the territory throughout the breeding season, render this species an important extension of the neighbor/stranger work cited previously. Additionally, observations indicate that neighbors may pose a strong threat to territorial integrity (Kendeigh 1941). Habituation to the activities of neighbors could be of questionable adaptive value.

MATERIALS AND METHODS

Study Areas

Study sites included several areas in Westchester County, NY and Fairfield County, CT. The large part of the experimental work was done with the House Wren populations found at the Greenburgh Nature Center, Scarsdale, NY (26 pairs, 1978-1980, with five males returning two seasons), the Audubon Center, Greenwich, CT (7 pairs, 1979 and 1980), and Nevis Laboratories, Irvington, NY (4 pairs, 1978 and 1979). In these areas, the wrens, with three exceptions, used nest boxes rather than natural cavities. Other study sites in which House Wren activities were monitored throughout the breeding season included several areas near private homes in Westchester and Fairfield counties.

Banding

Both U.S. Fish and Wildlife serialized aluminum bands and plastic color bands were used to make individual and sex discrimination of the monomorphic adults possible under field conditions. Adults were sexed behaviorally, and by the presence or absence of a brood patch. Nestlings were banded with a serialized band and a color band to indicate natal territories, but were not sexed. Mist netting, capturing with a small net at the entrance to the nest, and trapping within the nest box were the methods used to catch the House Wrens. Playbacks were not used in the netting activities. All banding was done when the nesting was well under way so as to minimize danger of desertion.

Mapping of Territory

Territory was defined as the area used and defended by a male during the breeding season. Territories were mapped by plotting each male's location on a map of the area during several hours of observation. Particular attention was paid to those areas encompassing neighboring territorial boundaries. Occasional boundary disputes served further to delineate the borders. The territory of each male was remapped in this manner at each stage of the nesting cycle before any playbacks were attempted.

Experimental Conditions

In order to facilitate comparisons between the findings of this study and studies cited previously, the experimental conditions have been kept similar to those described in the playback literature. Scotch-brand audio tapes were recorded and played at 19 cm/sec (7.5 ips). A Uher 4200S tape recorder was used with a Dan Gibson electronic parabolic microphone for recording, and a Realistic 10 cm speaker with a 25 m lead for playbacks. All recordings were made between the hours of dawn and 11 a.m. E.D.T., and playbacks between 6 and 9 a.m. E.D.T. so as to coincide with the House Wren's period of maximal song activity. Playbacks were not performed in windy or rainy weather.

Playback tapes were constructed from recordings of males singing on territory. New tapes were constructed for each nesting stage, with either four minute segments used in whole, or shorter segments rerecorded to total four minutes. The factors considered in selecting the section of tape which was to comprise the four minute recordings were rate of singing and minimal extraneous noise. Since recognition of particular birds was being tested, and not the function of different song types, the playback tapes were representative of the activities of a bird and commonly consisted of several song types. Though not all wrens in an area were in stage synchrony at a particular time, the neighbor for a playback was always at the same stage as the experimental male. The same stranger tape was used for all birds tested in an area at a particular stage to simulate a new bird in the area seeking to establish a territory. The males recorded for use as strangers were breeding approximately one kilometer from the experimental sites. One kilometer is far enough from the territory to be beyond the flying range of residents during the breeding season, yet close enough to minimize a potential dialect difference. Lemon (1967) and Kreutzer (1974a) have found that similarity of dialect of song playback and resident influenced the response. Although Kreutzer (1974b) has described dialect differences in widely separated populations of the European Wren, the presence or absence of a dialect in the House Wren has not been ascertained. However, an analysis of the song types found on the test-tapes showed as large a variation in song types used and apparent repertoire size between individual residents as between residents and strangers in an area. This analysis will be discussed further at a later point.

A sample of resident males was exposed to playbacks at each of the following seven stages of the nesting cycle: Mating I, Egg Laying I, Incubation I, Nestling I, Fledgling I / Mating II / Egg Laying II, Incubation II, Nestling II. The stages separated by a slash in the listing overlapped considerably, and were difficult to separate in the field without frequent examination of the nest. For this reason, the mid-season transition period was treated as a single stage for purposes of analysis.

Each experimental bird fulfilled the condition diagrammed in Figure 1. The experimental bird (I) had a territorial boundary generalized here as a polygon ABCDEFGH. This boundary was shared with conspecific II at the arc BCD. Arc BCD was the normal boundary between the birds. Arc FGH was the boundary opposite to it. This arc could be a part of another conspecific's territory (Bird III), but none of the experimental males chosen had a conspecific neighbor on this boundary. Experimental birds were subject to playbacks of neighbor (Bird II) or stranger songs from the boundary locations described above at each stage of the nesting cycle; however, not every bird was tested at each stage, or subjected to all playback conditions. The speaker sites chosen for a given male at each stage remained the same for all playbacks to that male at that stage. The sites were chosen on the basis of proximity to the boundary and availability of perching sites.

Although "normal" and "opposite" boundary locations are not applicable to the stranger males, the terms will be used to facilitate discussion of response to different playbacks at a particular location. "Normal" and "opposite" are always with reference to the location of the neighbor's territory.

The playback tapes were coded, and test sequences arranged by someone other than myself, such that the administration was double blind. In the field, although location (normal vs. opposite boundary) was of course known to me, the identity of the male on the tape (neighbor vs. stranger) was not.

The overall design of the experiments is diagrammed in Figure 2. The details of only one stage and condition are shown. This design allowed employment of a nested analysis of variance as one of the statistical treatments of the data. Four types of playbacks were done: neighbor from the normal boundary (NN), neighbor from the opposite boundary (NO), stranger from the "normal" boundary (SN), and stranger from the "opposite" boundary (SO). A bird chosen to be tested at a stage received no more than four playbacks, but those playbacks might be all different (NN,NO,SN,SO), or include one or more replicates (NO, SN,SO,NO). Replicates (same tape, same location; total N = 38) were done at each stage to several birds, and this method enabled assessment of the consistency of a bird's response over time. Lack of significance at a lower level allowed pooling of data and analysis at the next higher level. The sequence of playback types for each bird at each stage was different (For example, Bird A schedule: Day 1, NO, Day 2, NN, Day 3, SO. Day 4, SN; Bird B schedule: Day 1, NN, Day 2, SO, Day 3, SN, Day 4, NO).

Experimental Procedure

The speaker was hung between one and two meters above the ground, either in some shrubbery or from a tree, and the wires stretched across the ground to a semisecluded area where the tape recorder was positioned. The speaker was directed toward the center of the resident's territory. During the experiment, the observer was seated under overhanging shrubs and/or behind trees or other foliage, and remained at least 13 m from the speaker while visually monitoring the subject's activities. During the early testing sessions, markers were placed 3 and 10 m from the speaker to facilitate distance estimation.

Each playback consisted of three parts: a silent pre-play period, a playback period, and a silent post-play period, each four minutes in length. During these periods, the territory resident's activities were monitored for vocalizations, flights of more than 1 m in length, approaches to within 3 and 10 m of the speaker, postures, and general activity.

A cassette tape recorder was switched on at the beginning of the pre-play period, and ran continuously for the next twelve minutes until the end of the post-play period. Observations were recorded orally onto this tape, and were transcribed at a later time onto data sheets. A stop watch was used during the transcription process to subdivide the field observations into fifteen second intervals.

The sequence of individuals tested was determined randomly at the beginning of the testing series at a stage, then retained through that stage. The playbacks to a particular male were each separated by at least twenty-four hours. Playback volume was subjectively judged to match that of usual singing behavior.

Measures of Response

Several measures of response were extracted from the field observations of boundary encounters. These were used to assess strength of auditory and visual displays of the resident male during the playback experiments. The measures were as follows, with possible ranges indicated.

Play Period (Tape running, 4 min.)

Songs Raw -- number of songs sung by resident male during period. All songs were considered to be of equal value, regardless of volume or length. (Range: 0 to $+\infty$)

Songs Corrected -- number of songs sung during play period minus number sung during pre-play period. (Range: $-\infty$ to $+\infty$)

Churrs -- number of bouts during period when one or more of these call notes were uttered rapidly. Bouts are separated by a time interval which exceeds that between notes in a series. (Range: 0 to $+\infty$)

Flights -- number of flights of the resident exceeding 1 m in length. Since some flights were hidden by the foliage, this represents a minimum value. (Range: 0 to $+\infty$)

Approach 10 -- number of 15 sec intervals during which male was closer than 10 m to the speaker during any part of that interval. (Range: 0 to 16)

Approach 3 -- number of 15 sec intervals during which male was closer than 3 m to the speaker during any part of that interval. (Range: 0 to 16)

Latency 10 -- mumber of 15 sec intervals before bird approached to within 10 m of the speaker. If bird did not approach, maximum latency was assigned. (Range: 0 to 16)

Latency 3 -- number of 15 sec intervals before bird approached to within 3 m of the speaker. If bird did not approach to this distance, maximum latency was assigned. (Range: 0 to 16)

Latency Song Total -- number of 15 sec intervals before bird sang. If bird did not sing, maximum latency was assigned. (Range: 0 to 16)

Latency Song 10 -- number of 15 sec intervals before bird sang after and while it has approached to within 10 m of speaker. If bird did not approach, or sing upon approach, maximum latency was assigned. (Range: 0 to 16)

Song Intervals -- number of 15 sec intervals during which resident sang at least one song. (Range: 0 to 16)

<u>Post-Play Period</u> (Tape not running, 4 min.)

Songs Raw -- number of songs sung by resident male during period. All songs were considered to be of equal value, regardless of volume or length (Range: 0 to $+\infty$)

Songs Corrected -- number of songs sung during the post-play period minus number sung during pre-play period. (Range: $-\infty$ to $+\infty$)

Churrs -- number of bouts during period when one or more of these call notes were uttered rapidly. Bouts are separated by a time interval which exceeds that between notes in a series. (Range: 0 to $+\infty$)

Latency to Leave 10 -- number of 15 sec intervals after tape stopped (*i.e.* end of play period) before bird left its position within 10 m of speaker. (Range: 0 (departure within 15 sec) to 16 (no departure through 4 min)

Song Intervals -- number of 15 sec intervals during which resident sang at least one song. (Range: 0 to 16)

Analysis of Data

1. Parametric Tests; Analysis of Replicates and Pooling

One-way analysis of variance for unequal sample sizes was first applied to the replicate playbacks at every stage. The measures of response listed above were analyzed separately at each stage. When none of the replicates were found to be significant ($\alpha = 0.05$) for any of the males, measures, or stages, the data were pooled for further analysis. The responses of all of the males tested at a particular stage and with the same experimental condition (*i.e.* NN, NO, SN or SO) were pooled for analysis.

The data were first examined for homoscedasticity using the F-max and/or Cochran's C tests. Since significant departures from homoscedasticity were found, the date were subjected to a square-root transformation before the ANOVA was applied. The square-root transformation removed departures from homoscedasticity, and was selected as a less severe alternative than a logarithmic transformation.

2. Non-parametric Tests

Additionally, the Mann-Whitney U test was done on the untransformed measures of response. This analysis permitted direct comparison of response between like tapes at different locations (NO - NN; SO - SN) and different tapes at the same location (NN - SN; NO - SO), and enabled assessment of response trends which were not indicated by the overall ANOVA'S.

The chi-square goodness of fit test was used to evaluate the effects of test-tape repertoire size on resident response. The test tapes were grouped according to number of song types, and the responses of all males exposed to those tapes averaged. The result was a mean measure of response for each song-type number category. These means were then analyzed using a chi-square, with the expected values being the overall mean for each measure of response. Response categories were pooled in some cases so as to generate expected values greater than or equal to five.(Sokal and Rohlf 1969). The null hypothesis was no difference among the song-type categories.

The significance level for the results of all of the analyses is indicated as less than or equal to 10%, 5%, and 1%. Since sample sizes were small for the analyses, the $\alpha=0.1$ value was included along with the conventional values of $\alpha = 0.05$ and $\alpha = 0.01$. It is believed that with larger sample sizes, such measures would likely have achieved the $\alpha = 0.05$ level of significance.

RESULTS

The Territories

By the start of incubation, the territorial boundaries of the nesting House Wren pairs had become fairly stable. Figure 3 and Figure 4 illustrate the territories at two study sites during this stage of the 1979 season. The "X" within each territory indicates the nest cavity chosen by the female. Figure 5 and Figure 6 illustrate the territories during the incubation of the second brood.

Several aspects of the breeding behavior of the species are evident from an examination of these illustrations. Several males established territories within each of the study areas shown. The territories of adjacent pairs do not touch -- that is, there is commonly a "border area" of seven to ten meters in width which neither male resident uses. Nest cavities are usually (N = 40/46) near the center of the territory. Males which nested in the area more than one season often established territories partially or completely overlapping the one held in a previous season (N = 4/5).

Most of the males which had mated and fledged young during the first half of the breeding season attempted to renest. In 12 of 15 cases, the nest cavity chosen by the female was not the one which had been used with the first brood, regardless of whether the male remated with the same or another female. The territories established by the males commonly contained more than one suitable nest site, but the center of activity of the territory during the nesting depended upon the utilized cavity. This fact, together with boundary disputes between neighboring conspecifics, led to some shifting of boundaries early in the season.

Additionally, there is indication that changes do occur throughout the nesting period. The feeding areas utilized by the pair change, and I suspect that this reflects changes in insect availability. Kendeigh (1941) reports that the female, by feeding in areas outside the limits of the territory, may induce the male to add to his defended area. If a nest is destroyed early "in the nesting," the pair renests at another site in the territory, and centers of activity shift. This is shown in Figure 6, where the initial nest of the east-central pair suffered egg predation, and they renested in another cavity to the north.

New females were observed in several instances visiting boxes within a previously mated male's territory. Only one male was successful in attracting more than one female to nest in his territory. When this occurred, additional area was utilized and defended by the male for the second female's activities. In a densely populated area, such new additions must come from a neighbor's holdings, and may occur at any time in the season. In my study area, the additional area had not been a part of another conspecific's territory at the time of acquisition.

New males enter the area throughout the summer, and attempt to establish a territory and attract a female (N = 11, 1978-1980). Figure 3 shows just such a situation in the western portion. A male sang for several days from an area within another male's territory. The original resident initially responded agonistically, then shifted his activities northward. The new male was unable to attract a female, and stopped singing in the area.

The largest influx of new males occurs at the end of the first nesting (N = 8). Whether these be first nesters or males unsuccessful in another area during the early part of the summer is unknown. The activities of these males together with those of the residents lead to much boundary instability during this period of the season.

Late in the summer, there is another influx of males which I suspect are first-year males (N = 2). These vocalize using subsong (Thorpe 1961), and establish a small territory. One of these males banded at the end of the 1979 season nested in the area during the second nesting of 1980.

Temporal Distribution of Nesting Stages Through a Season

House Wrens may be found in the New York area April through October. Nesting activities are confined for the most part, however, to the span May through August. Figure 7a, Figure 7b, and Figure 8 illustrate the stage of nesting for males in the two major study sites during the period May 8 through August 8, 1979. Although overlap is considerable, synchrony is not complete among males in an area. The duration of incubation and feeding of nestlings is approximately the same for the various pairs. The periods of mate attraction, egg laying, and feeding of fledglings vary greatly among the pairs, and are largely responsible for the existing asynchrony. The males who leave care of the first set of fledglings to the female remate sooner for the second brood (N = 4).

The date of onset of breeding activities was not known for all the males. Several pairs breeding at the fringes of the study areas were discovered after the onset of incubation. For these individuals, starting date of incubation was extrapolated after the nestlings had hatched, and no mating or egg laying period is indicated.

One male, NML of the Greenburgh site, was polygynous during the 1979 season (see Figure 7b). Although playbacks were done to this male, his results after the second female's arrival are not included in the analysis because he could not be categorized into a single breeding stage due to asynchrony between the nests of the females.

The activity of the male with regard to the nest, mate, and young is highly variable. During the mating period, the male plays an active role in courtship and nest building, but once egg laying and incubation commence, the male devotes less time and energy to the nest and female. Nevertheless, males during this period do enter the nest cavity, feed the incubating female (although she obtains the large part of her food through her own foraging efforts), call the female on and off the nest, and accompany her when she forages. The proportion of the feeding of nestlings done by the male varies individually and seasonally. During the first brood of the 1978 season, four of eight males fed, while during the second brood, none of the five did so. In 1979, two of nine males fed during the first nesting, seven of eleven during the second nesting. Undoubtably, insect abundance in the territories is a prime factor determining whether females can be successful as sole providers for the young, although empirical evidence of this is not available for the Wren. Once the young leave the nest, the females care for them with assistance from the male confined to the first few days if manifested at all.

Songs of the Male

Vocalizations of the female are limited to call notes and a courtship song heard when the female is receptive and soliciting copulations. The males are highly vocal, singing loudly and frequently throughout the day during the spring and summer. Resident males sing only from within their territories, and excursions into other areas are silent unless the resident is attempting to expand his territory to include those areas.

The test tapes which were used in the playbacks of neighbors and strangers were analyzed using a continuous spectrum analyzer, a Princeton Applied Research (PAR) unit. The song of the male averages 1.7 sec (Kroodsma 1977), and is composed of recognizable units. The terminology for these units is that proposed by Shiovitz (1975) and Greenewalt (1968). A figure (or syllable) is a sound which produces a single complete and distinct impression. A phrase is a subdivision of a song based upon recognizable groups of sequented figures, especially in terms of time or frequency. The variability and complexity of the House Wren song makes a categorization into song types difficult (Kroodsma 1977 and personal communication). I have defined song type as a unique sequencing of phrases, and a variation of a song type as a change in the number of figures within one or more of the phrases. The song types were numbered in the order in which they were categorized. The sonagrams of the song types and variations of several representative males and stages of nesting are shown in Figures 9a-k. In the sequence of singing, males exhibit what has been called "repertoire plus variations" (Hartshorne 1973), often changing the number of figures within a phrase between repetitions of the song type. There is a variability in the number and identity of the song types among residents of an area, as well as between residents of Scarsdale, NY and Greenwich, CT, which are approximately 13 km apart. Sharing of song types or variations is less common than the sharing of figures between males. The songs of each male are unique in the sequencing of these figures into phrases, and the phrases into songs. There is as much dissimilarity in the test tapes among the songs of neighbors as between neighbors and birds breeding one kilometer away and used as strangers (Table 1). Since a complete repertoire analysis was not done it is impossible to say what proportion of the total song repertoire of an individual is represented by the test tape.

As mentioned previously, the song tapes used in the playbacks were representative of the singing activities of an individual. The number of song types found on the sampling of tapes ranges from one to five. There is evidence for other species that the size of an individual's song type repertoire may affect success in territorial maintenance activities. Great Tits habituate less rapidly to test tapes with a larger number of song types (Krebs 1976). Speaker-occupied territories are maintained longer against intruders when multiple song types are broadcasted (Krebs _et al_ 1978). Red-winged Blackbirds (_Agelaius phoeniceus_) similarly show a relationship between song-repertoire size and success in territorial activities (Yasukawa _et al_. 1980; Yasukawa 1981).

The number of song types present on the test tapes, an indication of repertoire size of an "intruder" conspecific, was an uncontrolled variable in the study. In order to evaluate the effect that this variable may have had on the residents' response to the playbacks, a chi-square goodness of fit test was used. The results of the analysis are presented in Table 2. The number of songs sung by the resident (Songs Raw) during the play and post-play periods were the only measures to differ significantly with number of song types on the test-tapes. The uncontrolled variable of song repertoire size may have influenced these measures of response to the playbacks. However, further research is needed to examine the relationship of number of intruder song types and resident response.

Data Analysis

Playbacks were made to resident males at identifiable stages of nesting during the breeding seasons of 1978-1980. The sample sizes used in the data analyses are listed in Table 3, showing number of playbacks and, in parentheses, number of different males for each stage and condition. Results of playbacks were not included for analysis in cases of incorrect identification of stage, equipment malfunction, unknown shifts of boundary which resulted in improper speaker positioning, and disturbances by humans and machinery in the vicinity. These non-inclusions are responsible for the small sample sizes for some of the experimental conditions.

The data for the three years were analyzed separately due to slightly altered methodology. (The double-blind protocol was not used in 1978.) Each measure of response at each stage of the nesting cycle was analyzed separately. In all cases, the differences in the response of the resident to the test-tapes (neighbor or stranger) at two boundary locations (normal or opposite) were assessed.

The F-ratios obtained using a one-way analysis of variance for unequal sample sizes (Sokal and Rohlf 1969) on square-root transformed data are shown in Table 4 and Table 5. The ANOVA indicated overall differences among the experimental groups for several measures of response at many of the stages. In order to move beyond the question of overall effect, however, it was necessary to statistically examine specific comparisons between the groups.

I was most interested in four condition contrasts in the evaluation of the hypotheses of status, location and stage effects: a) the response to a neighbor on and away from the normal boundary (NO vs. NN), b) the response to neighbor and stranger at the opposite boundary (NO vs. SO), c) the response to neighbor and stranger at the "normal" boundary (NN vs.

SN), and d) the response to a stranger on and away from the normal boundary with the neighbor (SO vs. SN). The existence of a difference in response and the direction of such a difference are both very important. In order to evaluate these differences, the non-parametric two-tailed Mann-Whitney test was chosen as a powerful analogue of the parametric two-sample t-test without the latter's underlying assumptions of normality and homoscedasticity, and required adjustments for unequal sample sizes which decrease the power of the test. Although the analysis of variance is rather robust in spite of slight violations of these assumptions, the t-test is not (Zar 1974).

The Mann-Whitney statistic, U, has a maximum value of n_1n_2 where n_1 and n_2 are the sizes of the two samples. When $U = (n_1n_2)/2$, the two samples are equivalent. Any U greater than (or less than) this value indicates a degree of directionality. When the critical value of $U_{\alpha(2)\ n_1,n_2}$ is equaled or exceeded, the null hypothesis of equivalence of the two samples may be rejected at the α significance level.

The values obtained after analysis of the 1978-1980 data are presented in Table 6, Table 8, Table 10, and Table 12. The critical value of $U_{0.1(2)n_1,n_2}$ is included at the bottom of each column. Significance at $\alpha = 0.1$, 0.05, and 0.01 is indicated, the symbols explained in the legend preceding the tables and figures. The directionality of response was determined using the means in cases where the U value indicated nonequivalence of the samples. The directionality of response is indicated in Table 7, Table 9, Table 11, and Table 13. Boxed entries are significant at $p \leq 0.1$, double-boxed entries at $p \leq 0.05$.

Trends in all cases must be interpreted with care. The standard errors for many of the measures of response were large and, as such, samples were not clearly different although the means were not equal. Conclusions drawn from the data analyses were based upon those measures which evidenced significant difference. Consistent trends in the data are indicated as such, but await further experimentation for clarification. Evaluation of the data of the Mating I, Egg Laying, and Nestling II stages is hampered by the fact that the experiments were performed only during one season.

The Status, Location, and Stage Effects

In order to interpret the response measures, it is helpful to consider the normal behavior of a male House Wren toward a territorial challenger. An intense agonistic interaction between male conspecifics is characterized by both auditory and visual displays. Songs of both males are short in length, rapidly following one another. Countersinging, in which the song of one male elicits singing by the other, is apparent. The highest vigor may result in almost complete overlap in time of the songs of the combatants. Churrs may be uttered throughout the interaction. The countersinging bouts may occur with the males separated by as little as one meter, although five to ten meters is the most common separation. While singing, the wings are often slightly dropped, and quivered rapidly.

The resident, upon first hearing the songs of the other male in such an interaction, leaves his perch and flies closer to the singing male. Numerous short flights past one another may lead to long circling chases, and physical contact between the conspecifics.

After the conspecific has been driven beyond the borders of the territory and has ceased singing, the resident often continues singing frequently for some time.

NN vs. SN

The analyses show no difference at the $\alpha = 0.05$ level of significance in the response of residents to the songs of neighbor and stranger at the "normal" boundary (see Table 6 and Table 7). Many measures of response show no difference, or contradictory indications when year replicates are compared. When consistencies are present between year replicates, the trends are largely in the direction of a stronger response to the songs of a neighbor.

During the play period, the Songs Corrected measure reflects an increase in singing over the control period during the Inc I, Nes I, and Fl/M/E stages. In the first incubation, the trends in Flights and Approaches to 10 and 3 m also suggest a strong neighbor response although none reach significance. A shorter latency to sing in response to stranger songs is indicated for the incubation stages during both broods (Lat.Song 10 m, Inc I; Lat.Song 10 m and Lat.Song Tot, Inc II). During the four minutes after playback, the Inc I stage shows more songs (Songs Raw, Song Int.) in response to a stranger's songs, although trends for several other stages are in the direction of more songs after a neighbor playback.

Overall, the analyses indicate that at the normal boundary, neighbors and strangers are treated similarly. There is little evidence that stage of nesting influences the response of the resident. At this location, whether the conspecific is a neighbor or a stranger makes little difference in the nature of the resident's response.

NO vs. SO

On the other hand, the status of a conspecific challenger on the opposite border influences the response of the resident. A conspecific singing from this location is an unusual event since this boundary was vacant for all residents tested.

Stranger song from this boundary elicited more of an increase in song as compared to the control period (Song Cor.) during all stages but Egg Laying I and Nes II (see Table 8 and Table 9). Latency to sing is also shorter in response to stranger songs, although the trend approaches significance only during the Fl/M/E ($p \leq 0.10$) stages. During the post-play period, significant differences were found only during the Fl/M/E stage for several measures of singing activity, with stronger response following a neighbor playback (Song Raw, Song Cor., Song Intrvl., $p \leq 0.05$).

Stronger visual threat during the playback of neighbor song was seen during the Egg Laying I, Inc I, Fl/M/E and Nes II stages for the measures of approach (Ap. 10 and 3 m), latency to approach (Lat. Ap. 10 m), and latency to leave the vicinity of the speaker after playback (Lat. Lv. 10 m).

During the mid-season Fl/M/E stage, the stronger response is directed toward the neighbor with one exception (Lat. Song 10 m, 1978, $p \leq 0.10$), and includes visual display of approach and flights, quick response after onset of playback, and song activity during the period after playback.

NO vs. NN

When the responses of the resident to the songs of a neighbor at two boundary locations are contrasted, several features are apparent (see Table 10 and Table 11). Interpretation of the response differences is made difficult by the inconsistencies in the year replicates for several of the measures of response.

Where differences are significant for measures of response by song, the normal boundary playback elicits a stronger response. There are more songs sung (Song Raw, $p \leq 0.05$), a larger increase over the control period song rate (Song Cor, $p \leq 0.05$), songs are begun sooner after the playback begins (Lat. Song Tot., $p \leq 0.05$), and continued throughout the period (Song Intrvl., $p \leq 0.05$). Year replicate trends support less than half of these significant measures, and non-significant trends similarly show an inconsistency.

Few measures of visual threat have reached significance, but the consistent trends indicate a stronger response directed toward the neighbor on the opposite boundary (Flights: Fl/M/E, $p \leq 0.05$; Ap. 10 m: Egg I, Nes I, Fl/M/E, Nes II; Lat. Ap. 3 m: EggI, Nes I, Fl/M/E).

There is some indication that at the normal boundary, a neighbor's song is more likely to be responded to vocally, while at the opposite boundary, more visual threats are elicited. This characterization of response during the playback period is seen at several stages throughout the breeding season.

During the post-play period, consistencies facilitate interpretation of the results. The normal boundary neighbor's song elicits more songs (Song Raw: Mat I, Egg I, Inc I, Inc II); Song Cor.: Inc II, $p \leq 0.10$, 1979), a shorter latency to leave the vicinity of the speaker (Lat. Lv. 10 m: Egg I, Inc I, Nes I, Fl/M/E, Nes II), more time spent singing (Song Intrvl: Mat I, Inc I, Inc II). The opposite boundary situation, where the neighbor's songs are an unusual occurance, elicits a strong song response during the Fl/M/E stage (Song Raw: $p \leq 0.10$, 1978, $p \leq 0.05$, 1979; Song Cor.; Song Intrvl., $p \leq 0.10$, 1978).

The vocal response to a neighbor's song at the normal boundary persists into the post-play period, except at mid-season, when the strong response to the opposite border playback may be related to the large amount of boundary shifting that is occuring.

SO vs. SN

As in the NO-NN contrast, inconsistencies are evident for many of the measures of response and few approach significance, although replicate years support those measures that do so 6% of the time. Some patterns of response do seem clear (see Table 12 and Table 13).

A stranger on the opposite border tends to be approached sooner (Lat. Ap. 10 and 3 m) and throughout more of the playback period (Ap. 10 and 3 m). Response by song is not consistent although the Fl/M/E stage shows an increase in songs at the normal boundary during the playback (Song Cor., $p \leq 0.10$) and the Inc I stage after playback (Song Raw, $p \leq 0.10$, Song Intrvl., $p \leq 0.10$). Churrs during the post-play period, although not significant, are more frequent at the opposite boundary. Trends in the data during the post-play period suggest that stranger songs at the "normal" boundary are more likely to elicit visual threat display during the play period.

There may be a stage effect in the response of the resident during the post-play period. During the first brood (with the exception of Mat I), singing response is stronger to a stranger's songs at the "normal" boundary, although differences are not significant.

Stage Effects

The overall effect of stage is difficult to assess from the results of the analyses. Small sample sizes in some cases precluded statistical analysis, and experimental data for some stages lacked replication in another season. Directionality of response was not always consistent in season replicates, suggesting that chance factors may be operational. The uncontrolled variable of song types may be a contributing factor in the inconsistencies in the Songs Raw measure of response. All factors considered, where stage effects were clearly evidenced in the results, these effects were noted in the contrasts presented above.

Further research which addresses the stage effect should examine the early and late stages of nesting in particular. The direction of many measures of response reversed between the Mat I and Egg I and between Inc II and Nes II. The size of the sample renders it impossible to rule out chance factors as responsible for this effect, but the data suggest that these early and late stages may differ from the rest of the breeding season. Since the majority of the neighbor/stranger discrimination work in other species has been done very early in the breeding season, examination of a stage effect at this time is especially important.

DISCUSSION

Natural selection has shaped avian behaviors that act to safeguard the integrity of the male's territory during the breeding season. Efficient allocation of time and energy resources is served when the defender grades the intensity of the defense to the magnitude of the threat posed by a challenger. In the House Wren, the response of a resident to conspecific threat posed by a neighbor or a stranger has been shown to be influenced by the location of the challenger and, to some degree, by the stage of the nesting cycle.

As previously discussed, the territories of adjacent House Wrens are not contiguous, but rather a "border area" exists which neither male uses. The existence of such a "border area" in other species has not been widely noted, although it has been observed that neighboring conspecific Chaffinch (Marler 1956a) and Twite, *Acanthus flavirostris* (Marler and Mundinger 1975) territories may not abut. A male House Wren other than the resident singing from the border of the territory is thus an unusual event, and one that might elicit an agonistic response by the resident. A neighboring conspecific male singing from the border may imply a threat which differs from that of a strange male under the same circumstances.

When a neighbor's song is heard by a resident under normal conditions, the neighbor is usually singing from within the border of his own territory. A prolonged bout of neighbor's song from the boundary of the resident's territory is less common, and might precede or follow a tresspass. A stranger singing from the same location might likewise indicate a strong challenge to that part of the territory. In both cases, a resident defending his territory responds quickly with visual and auditory displays. Where there is a difference in the response to playbacks of neighbor and stranger at the normal boundary, the trend is often in the direction of a stronger response to the neighbor's song, but the difference is never statistically significant. At that position along the territorial border, the resident's response is similar to neighbor and to stranger.

From the opposite boundary, a neighbor's song is an unusual occurance. A prolonged bout of song could indicate the attempt of the neighbor to expand his territory to include that area, and lay claim to nest boxes for future matings. During the first nesting cycle, that would not be unusual, and the resident who countered such threats would be able to maintain his own area, and minimize competition for unmated females. A stranger in the area likewise would be attempting to claim the vacant area as his own. Playbacks of neighbor and stranger songs from the opposite boundary elicit significantly different responses during the mid-season stage when remating is occurring and boundaries are unstable. A neighbor's song away from his territory at this time is a powerful stimulus, and the strong response of the resident includes persistence of the song after the songs of the challenger cease. Although other measures at other stages are not significant, trends indicate that a stranger is likely to elicit song, and that song begins sooner after the playback commences. The resident reaffirms his presence and willingness to defend the territory. A neighbor's song, however, elicits a visual threat in the form of an approach. Under normal conditions, an approach is a strong threat to a conspecific, and often acts to escalate the conflict if the challenger does not leave.

An unfamiliar conspecific implies a threat wherever he sings along the border of the territory, but when the stranger is on the usually unoccupied opposite border, the resident approaches quickly and remains in the area longer, although not significantly so. Once challenger song ceases there, however, a vocal response of the resident is less likely to continue that when the strange challenger is on the normal boundary.

Several species cited previously have demonstrated an ability to discriminate neighbor and unfamiliar conspecific on the basis of song. The White-throated Sparrow (Falls and Brooks 1975), Stripe-backed Wren (Wiley and Wiley 1977) and Common Yellowthroat (Wunderle 1977) use location as a cue in performing the discrimination. The House Wren also uses location as a cue, but differs from these other species in the directionality of the response differences between neighbor and stranger at normal and opposite boundary locations. The lowest intensity response in the species other than the House Wren has been directed toward the song of a neighbor, and in the species so tested, the neighbor was singing from the normal boundary. The decrement in response has been attrubuted to habituation (Thorpe 1956), a stimulus specific waning in responsiveness.

Individuals of the species that have deomonstrated neighbor-stranger discrimination abilities utilize a single song type with the exception of the Great Tit, House Wren, Song Sparrow, and Stripe-backed Wren. As Hartshorne (1973) and Krebs (1976,1977) have discussed, habituation is facilitated under these conditions. It is important to consider that the singing behavior of the Great Tit is very different from that of the House Wren, and the conclusions drawn from the habituation studies of Krebs (1976) may not be applicable to the wren. Songs of the Great Tit are composed of short repeated phrases of three notes. The same song is repeated many times before the male switches to another song type. Invariant repetitions of a song type may last five minutes, with songs interspersed with longer pauses. A male may possess up to seven song types, with 2.8 the average repertoire size (Krebs 1976).

The House Wren songs are much more complex than those of the Great Tit, consisting of a sequence of phrases, each phrase composed of several notes or figures. A unique sequencing of phrases is considered as one song type. Although the same sequencing of phrases and hence the song type may be utilized several times in succession, each rendition of a song varies in that the number of figures within a phrase changes. The complexity and variability of the songs doubtlessly affect habituation rates. As in other species which employ a repertoire of several song types and variations in their territorial defense, associative learning may function to link an individual with a position in space (Richards 1979).

The lack of such a decrement in response to the song of a neighbor on territory in the House Wren may be due to several factors. The position of the speaker on the border may be a prime factor, and future studies should include playbacks from within the neighbor's territorial borders as well as along the boundary. The uncontrolled variable of song types may be influencing the songs raw measure of response during the play and post-play periods. Alternatively, the

House Wren may be failing to habituate to neighbors on their territories because neighbors pose a real threat to nesting success. It is important to note that a strong response to neighbors has been reported in other species as well.

Marler (1956b:250) described the strong response a neighboring Chaffinch male sometimes elicited: "Neighboring rival males seem to be much more responsive to each other's songs than to those of strangers." Kroodsma (1976a:99) noted that "Song Sparrow...males responded strongly to songs of neighboring males." Harris and Lemon (1976) similarly noted a stronger response to neighboring Song Sparrows than predicted from other species tested, and attributed the neighbor response to the organization of the song repertoire, the breeding density of conspecifics in the area, and the early stage of the breeding season, all of which might interfere with response decrement through habituation. But even in these cases of strong neighbor response, the stronger response was evoked by the songs of an unfamiliar male.

With its repertoire size and breeding density, the House Wren is similar to the Song Sparrow. Habituation might be difficult, although Kroodsma (1976a:99) speculates that "It is entirely possible that powers of recognition (or rates of habituation) have increased proportionately with the evolution of larger repertoires." In any case, evidence from the breeding biology of the House Wren indicates that the male is behaving appropriately to a large threat from a neighboring male. Conspecific threat of this type is evidenced along three lines: 1) loss of part or all of a territory, 2) loss of mate, eggs, or young, and 3) succession of territory after removal of original resident male.

An important aspect of the species' behavior to be considered is that the matings may be polygynous. Although Kendeigh's (1941) reported incidence of such pairings as six percent is small, I think that only a scarcity of surplus breeding-condition females keeps this figure from greatly increasing. In the report based on his nineteen year study of the House Wren breeding in habitats very similar to those of my study areas, Kendeigh made numerous references to neighbor-neighbor conflicts as males sought to add additional nesting sites and attract mates throughout the breeding season. "The acquiring of nest-sites aften involved the destruction...of eggs or young of other birds already nesting there" (p.23). "Unguarded nests not infrequently have the eggs removed or even the young killed and carried out of the box by new males or males from neighboring territories" (p.28). The directing of such activities toward other cavity-nesting species as well, especially the Eastern Bluebird (Sialia sialis), the House Sparrow (Passer domesticus), and the Black-capped Chickadee (Parus atricapillus) has contributed to the reputation the House Wren has acquired as an aggressive and intolerant species (p.34).

Destructive behavior directed toward the nests of conspecific and heterospecific rivals is shared with other wren species as well. Picman and Picman (1980) report observations of nest destruction by the Short-billed Marsh Wren (Cistothorus platensis) and cite similar observations made of the Long-billed Marsh Wren (Cistothorus palustris) (Allen 1914), Cactus Wren (Campylorhynchus brunneicapillus) (Anderson and Anderson 1973), and their own of the Bewick's Wren (Thryomanes bewickii). In the Short-billed Marsh Wren, both males and females pecked and destroyed nests.

House Wrens trespass into other conspecific territories, and I have seen intruders (sex unknown) enter nest boxes containing eggs while the residents were foraging. Kendeigh (1941:39-40) has noted that, "When they are beyond the boundaries of their territories, they [the intruders] do not sing...and if seen, are chased by the owner to the limits of his possession. The invaders do not offer resistance, but as soon as they return to their own areas, they proclaim their authority there by song."

Additional nest sites are usually procured from areas adjacent to the territory, but such is not always the case. Kendeigh (1941) reports that eleven per cent of males nesting in one of his areas at one time or another established disconnected territories. This usually occurs while the female is caring for young of the first brood, and the male is advertising for a mate for the second brood. The appearance of an unmated female at any time in the season in a territory, or especially in an unclaimed area, may induce boundary conflicts and shifts.

Conspecific neighbors pose a threat after territories are established in other species as well. Marler (1956a:76), whose observations of strong neighbor responses of Chaffinches have been noted, wrote, "If a territory or part of one is vacated at any time, it is usually absorbed by neighbors." Krebs (1971:7) removed nesting male Great Tits and observed that they were replaced by strangers to the area. "Spaces not filled by newcomers were filled by expansion of residents. In some cases, residents completely left their original area to occupy one in the removal area." In prime nesting areas, such usurpations by neighbors were especially common.

In many passerine species, a large population of floaters or nonbreeding birds exists from which comes rapid movement into undefended territories (Krebs 1971). The size of the nonbreeding population in the House Wren has been estimated to be between 28 and 35 percent of the total population in an area.(Kendeigh 1941). My impression is that this figure is an overestimation of the size of the nonbreeding group in the New York area. Nonetheless, the appearance of new males in the study areas has been noted, and these are often successful in establishing territories and attracting mates. The strong response to strange male songs during the playbacks is certainly to be expected. The fact that it is exceeded under some circumstances by that to neighbor's songs is noteworthy.

The study I have reported did not, in the strictest sense of the word, determine if House Wrens are capable of individual recognition of neighbors. The male resident responds differently to a neighbor away from a normal territorial association. As Johnson (1977:419) has discussed, such a discrimination is evidence only of categorization of class, since "recognition is not based on a permanent component of that individual's phenotypic variability, but rather on an associated component such as position in space, territory, or hormonal state."

The study has indicated, however, that House Wren males may discriminate neighbors from strangers on the basis of song when such a discrimination is biologically meaningful. On the normal boundary, a conspecific song implies a threat that elicits a response that does not significantly differ with the status of the challenger. At the opposite border, a neighbor is responded to in a different manner than is a stranger, particularly during that part of the breeding season when territory shiftings are most common.

The question of changes in response through a breeding season needs further investigation before clear trends in response can be delineated. A relationship between fluctuating testosterone levels in the male and behaviors in defense of territory would be an important addition to the body of neighbor-stranger work that has already been done. Additionally, an investigation of the type reported here should be extended to include other wren species whose inter-neighbor aggressiveness has been documented and in which habituation to the songs of neighbors on territory could be a similarly maladaptive response.

SUMMARY

Territorial male House Wrens (Troglodytes aedon) have been shown to respond agonistically to playbacks of conspecific song. The intensity of response differs depending upon the boundary location and whether the conspecific song is that of an adjacent neighbor or a stranger breeding one kilometer distant.

Playbacks were divided into four minute pre-play, play, and post-play periods, and intensity of resident response assessed using sixteen measures of auditory and visual display. Four condition contrasts were statistically analyzed using the Mann-Whitney U-test: 1) the songs of neighbor vs. those of a stranger from the normal boundary between the resident and neighbor; 2) the songs of neighbor vs. those of a stranger from the opposite boundary; 3) the songs of neighbor from the normal vs. the opposite boundary; and 4) the songs of strangers from the normal vs. the opposite boundary.

House Wrens do not exhibit the response decrement to the songs of neighbors on territory that has been reported for numerous other passerine species. Indeed, for several measures of response at various stages of the nesting cycle, the response to the songs of neighbors exceeds that to the songs of strange conspecifics.

Observations indicate that the resident male House Wren is responding to a real threat posed by neighbors to the integrity of his territory. Suitable nesting cavities are a crucial resource for successful breeding, since such cavities are acquired rather than excavated, and multiple nesting sites within a territory increase the

liklihood of attracting one or more female to nest. Acquisition of nest sites may occur at any time in the season, but is most prevalent at mid-season when much shifting of territorial boundaries occurs. Under such circumstances, a waning of response to the activities of neighbors could prove disadvantageous to the resident, and a strong response to the challenges of neighbor and stranger is to be expected.

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Legend for Symbols Used in the Tables and Figures

Stages:

Mat I, M I = Mating I

Egg I, E I = Egg Laying I

Inc I = Incubation I

Nes I - Nestling I

Fl I/M/Egg II, F I/MII/E II, F/M/E = Fledgling I / Mating II / Egg Laying II

Inc II = Incubation II

Nes II = Nestling II

Fl II, F II = Fledgling II

Conditions:

NO = Neighbor, Opposite boundary

NN = Neighbor, Normal boundary

SO = Stranger, "Opposite" boundary

SN = Stranger, "Normal" boundary

Measures of Response: (See also Materials and Methods Section)

Song Raw = Songs Raw

Song Cor. = Songs Corrected

Churr = Churr

Flights = Flights

Ap. 10 m = Approach 10

Ap. 3 m = Approach 3

Lat. Ap. 10 m = Latency 10

Lat. Ap. 3 m = Latency 3

Lat. Song 10 m = Latency Song 10

Legend (cont'd)

Lat. Song Tot. = Latency Song Total

Lat. Lv. 10 m = Latency to Leave 10

Song Intvl. = Song Intervals

Statistical Significance:

d.f. = Degrees of Freedom

n_1, n_2 = Sample Sizes

= $0.05 \leq p \leq 0.10$

* = $0.01 \leq p \leq 0.05$

** = $p \leq 0.01$

Status, Location:

N = Neighbor

S = Stranger

Nr, N = Normal Boundary

Op, O = Opposite Boundary

Maps:

〰 = Territorial Boundary

X = Utilized Nesting Cavity

Table 1. Composition of Representative Test Tapes
(From Figures 9a-k)

Bird	Location	Stage	Song Type No.	Number of Variations
Cnfr	NY	Inc II	1	4
			2	1
Ochd	NY	Inc II	3	4
Ochd	NY	F/M/E	4	3
NML	NY	Inc I	5	3
			6	1
			7	1
NML	NY	F/M/E	6	4
			8	1
BeHv	NY	F/M/E	1	3
			9	2
			10	4
			11	1
BeHv	NY	Inc I	10	1
			11	2
Dgwd	NY	Inc I	1	8
			11	1
Dgwd	NY	F/M/E	12	4
Str 1	NY	Inc I	13	1
			14	1
Str 2	NY	Nes II	1	2
			10	1
			12	3
			15	1
			16	3
Str 1	CT	Nes I	17	3
Str 2	CT	Inc II	5	4
			18	1
Appl	CT	Inc II	19	1
			20	2
			21	2
Grdn	CT	Nes I	22	3
Grdn	CT	Nes II	23	7
Barn	CT	Inc I	24	8

Table 2. The Effect of Number of Song Types on Test-Tape on Resident Response

Measure		# of Song Types				Chi-square, p
		1	2	3	4	(d.f.=3)
Song Raw	obs.	24	20	9	12	$X^2=8.908$
	exp.	16.25	16.25	16.25	16.25	$.05 \geq p \geq .025$
Ch + Fl	obs.	6	1	6	7	$X^2=4.40$
	exp.	5	5	5	5	$.5 \geq p \geq .1$
Ap. 10 m, Ap. 3 m	obs.	6	4	6	7	$X^2=0.91$
	exp.	5.75	5.75	5.75	5.75	$.9 \geq p \geq .5$
Lat. Ap. 10 m	obs.	9	12	10	9	$X^2=0.60$
	exp.	10	10	10	10	$.9 \geq p \geq .5$
Lat. Ap. 3 m	obs.	12	15	12	13	$X^2=0.46$
	exp.	13	13	13	13	$.975 \geq p \geq .9$
Lat. Song Tot.	obs.	7	11	8	4	$X^2=3.33$
	exp.	7.5	7.5	7.5	7.5	$.5 \geq p \geq .1$
Lat. Song 10 m	obs.	4	4	7	5	$X^2=1.2$
	exp.	5	5	5	5	$.9 \geq p \geq .5$
Song Intrvl.	obs.	10	10	5	7	$X^2=2.25$
	exp.	8	8	8	8	$.9 \geq p \geq .5$
Song Raw Post	obs.	22	23	12	34	$X^2=10.67$
	exp.	22.75	22.75	22.75	22.75	$.025 \geq p \geq .01$
Song Cor.	obs.	5	4	3	8	$X^2=2.8$
	exp.	5	5	5	5	$.5 \geq p \geq .1$
Ch + LLv + SI	obs.	13	12	8	20	$X^2=5.64$
	exp.	13.25	13.25	13.25	13.25	$.5 \geq p \geq .1$

Table 3. Sample Sizes 1978-1980

(Number of individuals in parentheses)

		Mat I	Egg I	Inc I	Nes I	Fl I/M/Egg II	Inc II	Nes II
1978	NO			2(2)	5(4)	4(3)	5(5)	
	NN			3(3)	5(4)	3(3)	3(3)	
	SO			1(1)	3(3)	5(3)	4(4)	
	SN			1(1)	4(4)	2(2)	3(3)	
1979	NO			2(1)	4(3)	8(4)	3(3)	2(1)
	NN			10(4)	2(1)	6(4)	5(3)	6(3)
	SO			9(6)	1(1)	10(7)	2(1)	1(1)
	SN			8(6)	3(1)	5(5)	5(3)	1(1)
1980	NO	2(2)	3(3)					
	NN	4(4)	3(3)					
	SO	3(2)	3(3)					
	SN	1(1)	4(4)					

Table 4.

F-Ratios, One-way Analysis of Variance For Unequal Sample Sizes. 1978 Data.

Stage:	Mat I	Egg I	Inc I	Nes I	Fl I/M/Egg II	Inc II	Nes II
d.f.:			3,3	3,13	3,10	3,11	
Response							
Play: Song Raw			0.451	0.686	0.228	0.254	
Song Cor.			0.222	1.484	0.655	0.171	
Churr			72.000**	0.591	0.353	0.274	
Flights			2.037	2.460	1.130	1.343	
Ap. 10 m			1.106	2.036	1.232	0.925	
Ap. 3 m			1.106	0.708	1.085	1.737	
Lat. Ap. 10 m			1.077	0.111	0.303	3.164#	
Lat. Ap. 3 m			1.077	0.995	0.783	3.900*	
Lat. Song 10 m			0.286	0.390	2.712	0.227	
Lat. Song. Tot.			0.502	0.228	0.689	0.350	
Song Intrvl.			0.779	0.416	0.223	0.195	
Post: Song Raw			11.789*	0.089	1.369	0.651	
Song Cor.			1.208	0.826	0.952	0.833	
Churr			36.094**	0.199	0.325	0.896	
Lat. Lv. 10 m			4.715	0.765	2.288	0.538	
Song Intrvl.			1.815	0.182	1.531	0.481	

Table 5.

F-Ratios, One-way Analysis of Variance For Unequal Sample Sizes. 1979-80 Data

Stage:	Mat I	Egg I	Inc I	Nes I	Fl I/M/Egg II	Inc II	Nes II
d.f.:	3,6	3,9	3,25	3,6	3,25	3,11	3,6
Response							
Play: Song Raw	0.054	0.533	3.970*	0.901	1.147	0.893	1.241
Song Cor.	0.765	0.824	1.124	1.641	2.777#	0.901	1.264
Churr	0.508	0.281	1.718	0.259	0.972	1.324	1.600
Flights	0.384	1.981	1.157	6.605*	2.434#	0.293	1.872
Ap. 10 m	0.497	3.719#	0.831	2.692	1.475	0.841	1.221
Ap. 3 m	0.259	2.769	0.573	1.344	1.688	2.462	0.160
Lat. Ap. 10 m	0.527	0.811	0.914	5.098*	1.993	0.472	1.554
Lat. Ap. 3 m	0.548	3.271#	0.788	1.693	0.954	0.616	0.160
Lat. Song 10 m	0.077	1.049	0.269	0.936	0.936	0.733	1.600
Lat. Song Tot.	0.931	3.917*	3.349*	1.637	0.622	0.380	6.706*
Song Intrvl.	0.106	0.672	3.586*	0.750	1.052	0.818	1.446
Post: Song Raw	0.234	0.582	1.705	0.897	4.031*	0.492	0.971
Song Cor.	1.354	0.566	0.866	0.903	3.683*	1.694	0.834
Churr	1.491	0.828	1.847	0.000	0.837	0.517	2.041
Lat. Lv. 10 m	0.688	3.681#	0.502	0.682	1.449	0.611	0.790
Song Intrvl.	0.139	0.346	1.384	2.602	3.721*	0.425	1.270

Table 6.

Mann-Whitney Test. NN-SN Contrast

Stage:	Mat I	Egg I	Inc I		Nes I		Fl I/ M/Egg II		Inc II		Nes II
Year:	'80	'80	'78	'79	'78	'79	'78	'79	'78	'79	'79
n_1, n_2	1,4	3,4	1,3	8,10	4,5	2,3	2,3	5,6	3,3	5,5	1,6
Play: Song Raw	--	9.0	--	43.0	11.0	4.5	6.0	18.0	6.0	17.0	--
Song Cor.	--	8.0	--	59.5	12.0	5.5	4.0	16.0	6.0	17.0	--
Churr	--	7.0	--	52.0	14.0	4.0	3.0	15.5	6.0	16.5	--
Flights	--	7.0	--	45.0	11.0	5.5	3.0	22.5	6.5	13.0	--
Ap. 10 m	--	6.0	--	44.0	12.0	4.0	3.0	17.0	6.0	15.5	--
Ap. 3 m	--	6.0	--	54.0	11.0	4.5	4.0	15.0	5.0	16.5	--
Lat. Ap. 10 m	--	6.0	--	41.5	11.5	4.0	3.5	17.0	5.0	16.0	--
Lat. Ap. 3 m	--	6.0	--	43.5	13.0	4.5	4.0	16.0	5.0	15.0	--
Lat. Song 10 m	--	6.5	--	42.0	10.5	3.5	4.0	16.0	6.0	15.5	--
Lat. Song Tot.	--	7.0	--	42.0	12.5	5.0	5.5	21.5	6.0	14.5	--
Song Intrvl.	--	8.0	--	44.0	11.0	5.0	4.0	19.5	5.0	17.0	--
Post: Song Raw	--	8.5	--	59.5	12.5	3.0	3.0	15.5	5.0	13.0	--
Song Cor.	--	8.0	--	42.5	11.0	4.0	3.0	19.0	6.5	18.5	--
Churr	--	8.0	--	52.0	10.5	3.0	4.0	17.5	4.5	15.0	--
Lat. Lv. 10 m	--	6.0	--	43.5	10.0	4.5	3.0	18.0	4.5	15.0	--
Song Intrvl.	--	7.5	--	58.0	11.5	3.0	5.0	18.0	5.5	13.0	--
$U_{0.1(2)n_1,n_2}$	--	12.0	--	60.0	18.0			25.0	9.0	21.0	--

Table 7.

Directionality of Response Difference, Mann-Whitney Test, $p \leq 0.1$, NN-SN Contrast

Stage:	Mat I	Egg I	Inc I		Nes I		Fl I/ M/Egg II		Inc II		Nes II
Year:	'80	'80	'78	'79	'78	'79	'78	'79	'78	'79	'79
<u>Play</u>: Song Raw	N<S	S<N	N<S	S<N	S<N	S<N	N<S	N<S	N<S	N<S	N<S
Song Cor.	N<S	N<S	N<S	S<N	S<N	S<N	S<N	S<N	S<N	N<S	N<S
Churr	N<S	S<N		S<N	S<N	N<S			S<N	S<N	
Flights	S<N	S<N	S<N	S<N	N<S	S<N		N<S	S<N		
Ap. 10 m	S<N		S<N	S<N	N<S	S<N		N<S	S<N	N<S	S<N
Ap. 3 m	S<N		S<N	S<N	N<S	S<N	S<N		S<N	N<S	S<N
Lat. Ap. 10 m	N<S		S<N		S<N	N<S		S<N	N<S	S<N	N<S
Lat. Ap. 3 m	N<S		S<N	N<S	S<N	N<S	N<S	S<N	S<N	S<N	N<S
Lat. Song 10 m	N<S		S<N	S<N			N<S	S<N	S<N	S<N	
Lat. Song Tot.	N<S	N<S	S<N	N<S	N<S	N<S	S<N	N<S	S<N	S<N	S<N
Song Intrvl.	N<S	S<N	N<S	S<N	S<N	S<N	N<S	S<N	N<S	N<S	N<S
<u>Post</u>: Song Raw	S<N	S<N	N<S	N<S	S<N				S<N		N<S
Song Cor.	S<N	N<S	S<N	N<S	S<N	S<N		S<N	S<N	S<N	N<S
Churr	S<N	S<N		N<S			S<N	S<N		S<N	S<N
Lat. Lv. 10 m	S<N			S<N		S<N		N<S		N<S	S<N
Song Intrvl.	S<N	S<N	S<N	N<S	S<N		N<S	S<N	N<S		N<S

Table 8.

Mann-Whitney Test. NO-SO Contrast

Stage:	Mat I	Egg I	Inc I		Nes I		Fl I/ M/Egg II		Inc II		Nes II
Year:	'80	'80	'78	'79	'78	'79	'78	'79	'78	'79	'79
n_1,n_2	2,3	3,3	1,2	2,9	3,5	1,4	4,5	8,10	4,5	2,3	1,4
Play: Song Raw	3.5	6.0	--	14.5	10.0	--	11.5	52.5	11.5	3.5	--
Song Cor.	4.0	5.0	--	11.0	15.0*	--	15.0	44.5	12.0	4.0	--
Churr	4.0	5.0	--	10.0	8.5	--	10.5	52.0	11.0	3.0	--
Flights	4.0	7.5	--	12.0	13.0	--	14.0	57.0	15.5	3.0	--
Ap. 10 m	4.0	9.0*	--	10.5	12.5	--	16.5	58.5	15.0	3.5	--
Ap. 3 m	4.0	7.5	--	12.0	10.0	--	14.5	55.5	17.0	4.5	--
Lat. Ap. 10 m	4.0	9.0*	--	9.5	12.0	--	14.0	59.0	18.5*	3.5	--
Lat. Ap. 3 m	4.0	7.5	--	12.0	10.0	--	10.5	54.0	18.5*	4.5	--
Lat. Song 10 m	3.5	9.0*	--	11.5	8.0	--	19.5*	56.0	12.0	3.0	--
Lat. Song Tot.	4.0	9.0*	--	16.0	8.0	--	12.0	45.0	12.0	4.5	--
Song Intrvl.	3.5	5.0	--	15.5	10.0	--	12.0	49.5	11.0	3.0	--
Post: Song Raw	4.0	6.5	--	10.5	8.5	--	16.0	68.5*	14.5	4.0	--
Song Cor.	5.0	5.5	--	15.0	10.0	--	12.0	74.0*	14.0	4.0	--
Churr	5.0	6.0	--	13.0	9.0	--	12.0	48.0	12.5	4.5	--
Lat. Lv. 10 m	4.0	7.5	--	11.5	9.0	--	15.0	50.0	14.5	3.0	--
Song Intrvl	4.0	6.5	--	9.5	8.5	--	16.0	67.5*	14.5	4.0	--
$U_{0.1(2)}n_1,n_2$		9.0	--	17.0	14.0	--	18.0	60.0	18.0		--

Table 9.

Directionality of Response Difference, Mann-Whitney Test, $p \leq 0.1$, NO-SO Contrast

Stage:	Mat I	Egg I	Inc I		Nes I		Fl I/ M/Egg II		Inc II		Nes II
Year:	'80	'80	'78	'79	'78	'79	'78	'79	'78	'79	'79
Play: Song Raw		S<N	N<S	N<S	N<S	S<N	N<S	S<N	N<S		S<N
Song Cor.	N<S		N<S	S<N	$\boxed{N<S}$	N<S	N<S	N<S	N<S	N<S	S<N
Churr	N<S		N<S	N<S	N<S	S<N		N<S	N<S		S<N
Flights	N<S	S<N	N<S	S<N	N<S	S<N	S<N	S<N	N<S		S<N
Ap. 10 m	N<S	$\boxed{S<N}$	S<N	S<N	N<S	N<S	S<N	S<N	N<S		S<N
Ap. 3 m	N<S	S<N	S<N	S<N	N<S	N<S	S<N	S<N	N<S	N<S	
Lat. Ap. 10 m	S<N	$\boxed{N<S}$	S<N		S<N	N<S	N<S	N<S	$\boxed{S<N}$		N<S
Lat. Ap. 3 m	S<N	N<S	S<N	N<S	S<N	N<S		N<S	$\boxed{S<N}$	S<N	
Lat. Song 10 m		$\boxed{N<S}$		S<N	S<N	S<N	$\boxed{S<N}$	N<S	N<S		N<S
Lat. Song Tot.	S<N	$\boxed{N<S}$	S<N	S<N	S<N	S<N	S<N	N<S	S<N	N<S	S<N
Song Intrvl.			N<S	N<S	N<S	N<S	N<S	S<N	N<S		S<N
Post: Song Raw	N<S	S<N	N<S	S<N	S<N	N<S	S<N	$\boxed{\boxed{S<N}}$	N<S	N<S	N<S
Song Cor.	N<S	S<N	N<S	S<N	S<N	S<N	S<N	$\boxed{\boxed{S<N}}$	N<S	N<S	N<S
Churr	N<S	S<N	N<S	S<N	N<S		S<N	N<S	N<S	N<S	S<N
Lat. Lv. 10 m	N<S	S<N	S<N	S<N	S<N	S<N	S<N	S<N			S<N
Song Intrvl.	N<S	S<N	N<S		N<S	S<N	S<N	$\boxed{\boxed{S<N}}$	N<S	N<S	N<S

Table 10.

Mann-Whitney Test. NO-NN Contrast

Stage:	Mat I	Egg I	Inc I		Nes I		Fl I/ M/Egg II		Inc II		Nes II
Year:	'80	'80	'78	'79	'78	'79	'78	'79	'78	'79	'79
n_1,n_2	2,4	3,3	2,3	2,10	5,5	2,4	3,4	6,8	3,5	3,5	2,6
<u>Play</u>: Song Raw	4.0	4.5	4.0	20.0*	14.5	8.0	8.0	27.0	9.0	11.0	8.0
Song Cor.	6.0	6.0	4.0	13.5	18.0	8.0	8.0	40.5*	8.5	7.5	9.5
Churr	6.0	5.0	3.0	14.0	15.0	5.0	7.5	28.0	8.0	12.0	9.0
Flights	5.0	7.0	3.0	11.5	18.0	5.0	10.0	40.0*	12.0	10.5	9.0
Ap. 10 m	7.0	8.0	4.5	12.0	14.0	6.0	8.0	33.0	12.0	11.0	8.5
Ap. 3 m	5.0	7.5	4.5	12.5	13.0	4.5	7.0	32.5	9.0	7.5	7.0
Lat. Ap. 10 m	7.0	6.0	4.5	12.0	14.5	7.0	7.5	34.0	11.0	11.0	8.5
Lat. Ap. 3 m	5.0	7.5	4.5	12.5	13.0	6.0	7.5	34.0	8.0	7.5	7.0
Lat. Song 10 m	4.0	6.0	4.0	11.0	15.0	4.5	10.0	30.0	9.0	12.0	9.0
Lat. Song Tot.	7.0	7.0	4.0	20.0*	13.0	5.0	8.0	31.0	9.5	9.0	8.0
Song Intrvl	5.0	5.0	4.0	20.0*	14.5	5.0	7.5	31.0	8.5	11.0	8.0
<u>Post</u>: Song Raw	6.5	6.0	6.0	12.0	14.0	6.0	12.0*	42.5*	9.5	11.0	7.5
Song Cor.	5.0	5.5	5.5	18.0	15.0	7.0	10.0	32.5	13.0	14.0*	7.5
Churr	5.0	5.0	6.0	19.0*	12.5	4.0	6.5	28.0	8.5	10.5	10.5
Lat. Lv. 10 m	6.0	7.5	6.0	13.5	15.0	5.0	9.0	33.0	9.0	7.5	8.5
Song Intrvl.	6.5	4.5	6.0	11.0	14.0	6.5	12.0*	35.5	8.0	11.0	7.5
$U_{.1(2)n_1,n_2}$		9.0		19.0	21.0		12.0	37.0	14.0	14.0	12.0

Table 11.

Directionality of Response Difference, Mann-Whitney Test, $p \leq 0.1$, NO-NN Contrast

Stage:	Mat I	Egg I	Inc I		Nes I		Fl I/ M/Egg II		Inc II		Nes II
Year:	'80	'80	'78	'79	'78	'79	'78	'79	'78	'79	'79
Play: Song Raw			Nr<Op	Op<Nr	Nr<Op	Op<Nr	Nr<Op	Op<Nr	Op<Nr	Nr<Op	Nr<Op
Song Cor.	Op<Nr	Nr<Op	Op<Nr	Op<Nr	Op<Nr	Op<Nr	Nr<Op	Op<Nr	Op<Nr		Nr<Op
Churr	Op<Nr			Op<Nr	Op<Nr	Nr<Op	Nr<Op	Op<Nr	Nr<Op	Op<Nr	Nr<Op
Flights	Op<Nr	Nr<Op		Nr<Op	Op<Nr	Nr<Op	Nr<Op	Nr<Op	Op<Nr	Nr<Op	Nr<Op
Ap. 10 m	Op<Nr	Nr<Op	Op<Nr	Nr<Op	Nr<Op	Nr<Op	Nr<Op	Nr<Op	Op<Nr	Nr<Op	Nr<Op
Ap. 3 m	Op<Nr	Nr<Op	Op<Nr	Nr<Op	Nr<Op		Nr<Op	Nr<Op	Op<Nr		Op<Nr
Lat. Ap. 10 m	Nr<Op	Op<Nr	Nr<Op	Op<Nr	Nr<Op	Op<Nr	Op<Nr	Op<Nr	Nr<Op	Op<Nr	Op<Nr
Lat. Ap. 3 m	Nr<Op	Op<Nr	Nr<Op	Op<Nr	Op<Nr	Op<Nr	Op<Nr	Op<Nr	Nr<Op		Nr<Op
Lat. Song 10 m		Op<Nr	Op<Nr	Nr<Op	Op<Nr		Nr<Op	Op<Nr	Op<Nr	Op<Nr	Op<Nr
Lat. Song Tot.	Nr<Op	Op<Nr	Op<Nr	Nr<Op	Op<Nr	Nr<Op	Nr<Op	Nr<Op	Nr<Op	Op<Nr	Op<Nr
Song Intrvl.	Nr<Op		Nr<Op	Op<Nr	Op<Nr	Op<Nr	Op<Nr	Op<Nr	Op<Nr	Nr<Op	Nr<Op
Post: Song Raw	Op<Nr	Op<Nr	Op<Nr	Op<Nr	Nr<Op	Op<Nr	Nr<Op	Nr<Op	Op<Nr	Op<Nr	Nr<Op
Song Cor.	Op<Nr	Op<Nr	Op<Nr	Nr<Op	Nr<Op	Op<Nr	Nr<Op	Nr<Op	Op<Nr	Op<Nr	Nr<Op
Churr	Op<Nr		Nr<Op	Nr<Op	Nr<Op			Op<Nr	Op<Nr	Op<Nr	Nr<Op
Lat. Lv. 10 m	Op<Nr	Nr<Op	Nr<Op	Nr<Op	Nr<Op	Nr<Op	Nr<Op	Nr<Op	Op<Nr		Nr<Op
Song Intrvl.	Op<Nr		Op<Nr	Op<Nr	Nr<Op	Op<Nr	Nr<Op	Nr<Op	Op<Nr	Op<Nr	Nr<Op

Table 12.

Mann-Whitney Test. SO-SN Contrast

Stage:	Mat I	Egg I	Inc I		Nes I		Fl I/ M/Egg II		Inc II		Nes II
Year:	'80	'80	'78	'79	'78	'79	'78	'79	'78	'79	'79
n_1,n_2:	1,3	3,4	1,1	8,9	3,4	1,3	2,5	5,10	3,4	2,5	1,1
<u>Play</u>: Song Raw	--	8.0	--	45.0	10.0	--	7.0	36.5	6.5	6.0	--
Song Cor.	--	10.5	--	37.0	10.0	--	8.5	39.0*	9.0	5.0	--
Churr	--	9.5	--	36.5	8.0	--	6.0	28.0	7.5	6.0	--
Flights	--	7.5	--	42.5	10.5	--	8.5	30.5	8.5	6.0	--
Ap. 10 m	--	6.0	--	48.5	11.0	--	5.5	30.0	7.0	6.5	--
Ap. 3 m	--	8.0	--	39.0	8.5	--	9.0	27.0	10.0	7.0	--
Lat. Ap. 10 m	--	9.0	--	47.0	11.0	--	6.0	30.0	10.0	5.5	--
Lat. Ap. 3 m	--	6.0	--	41.0	9.5	--	9.0	27.0	10.0	6.0	--
Lat. Song 10 m	--	9.0	--	38.0	9.5	--	7.0	30.0	8.0	6.0	--
Lat. Song Tot.	--	7.5	--	45.0	9.5	--	7.0	26.0	7.5	7.0	--
Song Intrvl	--	8.0	--	41.0	10.0	--	6.0	33.5	7.0	6.0	--
<u>Post</u>: Song Raw	--	8.5	--	55.5*	6.5	--	7.0	31.5	8.0	5.0	--
Song Cor.	--	7.0	--	47.0	6.5	--	5.0	36.0	8.0	6.5	--
Churr	--	6.0	--	37.5	7.0	--	6.0	30.0	7.5	6.0	--
Lat. Lv. 10 m	--	6.0	--	39.5	6.0	--	5.0	27.0	7.0	6.0	--
Song Intrvl.	--	8.0	--	60.5*	8.0	--	6.0	30.5	8.0	5.0	--
$U_{.1(2)n_1,n_2}$	--	12.0	--	54.0	12.0	--	10.0	39.0	12.0	10.0	--

Table 13.

Directionality of Response Difference, Mann-Whitney Test, $p \leq 0.1$, SO-SN Contrast

Stage:	Mat I	Egg I	Inc I		Nes I		Fl I/ M/ Egg II		Inc II		Nes II
Year:	'80	'80	'78	'79	'78	'79	'78	'79	'78	'79	'79
Play: Song Raw	Op<Nr	Nr<Op	Nr<Op	Op<Nr	Nr<Op	Op<Nr	Nr<Op	Op<Nr		Op<Nr	Nr<Op
Song Cor.	Nr<Op	Op<Nr	Nr<Op		Nr<Op	Op<Nr	Nr<Op	$\boxed{\text{Op<Nr}}$	Nr<Op		Op<Nr
Churr		Op<Nr	Nr<Op		Nr<Op	Op<Nr	Nr<Op	Nr<Op	Nr<Op	Op<Nr	
Flights	Nr<Op	Op<Nr	Nr<Op	Op<Nr	Nr<Op	Nr<Op	Nr<Op	Op<Nr	Nr<Op		Nr<Op
Ap. 10 m	Nr<Op		Nr<Op	Nr<Op	Nr<Op	Nr<Op		Op<Nr	Nr<Op	Nr<Op	
Ap. 3 m	Nr<Op			Nr<Op	Nr<Op	Nr<Op	Nr<Op	Nr<Op	Nr<Op	Nr<Op	
Lat. Ap. 10 m	Op<Nr	Nr<Op		Op<Nr	Op<Nr	Op<Nr	Nr<Op	Nr<Op	Op<Nr		
Lat. Ap. 3 m	Op<Nr			Op<Nr	Op<Nr	Op<Nr	Op<Nr	Nr<Op	Op<Nr	Op<Nr	
Lat. Song 10 m	Op<Nr	Nr<Op		Nr<Op	Op<Nr	Op<Nr	Op<Nr	Nr<Op	Nr<Op	Op<Nr	
Lat. Song Tot.	Op<Nr	Nr<Op	Op<Nr	Nr<Op	Op<Nr	Op<Nr	Nr<Op		Nr<Op	Nr<Op	Op<Nr
Song Intrvl.	Nr<Op	Nr<Op	Nr<Op	Op<Nr	Nr<Op	Op<Nr	Op<Nr	Op<Nr	Op<Nr	Op<Nr	Nr<Op
Post: Song Raw	Nr<Op	Op<Nr	Op<Nr	$\boxed{\text{Op<Nr}}$		Op<Nr	Op<Nr	Op<Nr	Nr<Op		Nr<Op
Song Cor.	Nr<Op	Op<Nr	Nr<Op	Op<Nr		Op<Nr		Op<Nr	Nr<Op	Nr<Op	Op<Nr
Churr	Nr<Op		Nr<Op		Nr<Op		Nr<Op	Nr<Op	Nr<Op	Nr<Op	
Lat. Lv. 10 m	Nr<Op			Nr<Op		Nr<Op		Nr<Op	Op<Nr	Op<Nr	
Song Intrvl.	Nr<Op	Op<Nr	Nr<Op	$\boxed{\boxed{\text{Op<Nr}}}$	Nr<Op	Op<Nr	Op<Nr	Op<Nr	Nr<Op		Nr<Op

Figure 1.

Hypothetical Territory of Bird I

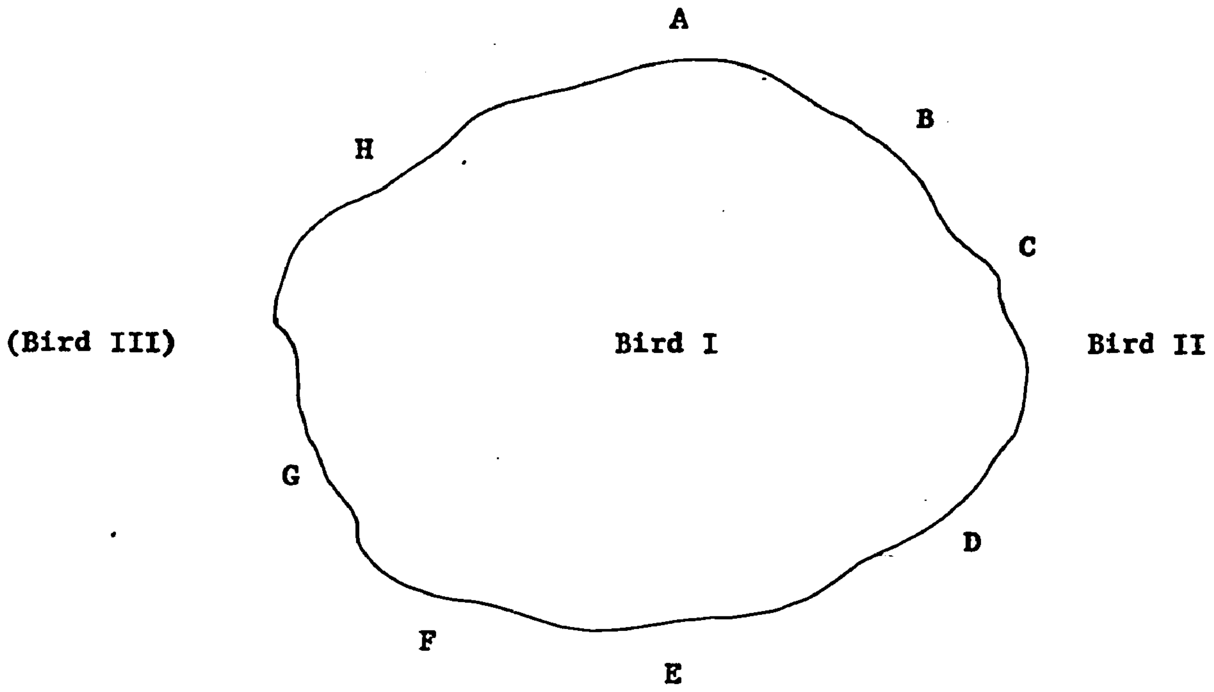

A
B
H
C
(Bird III)
Bird I
Bird II
G
D
F
E

Figure 2.

Overview of Experimental Design

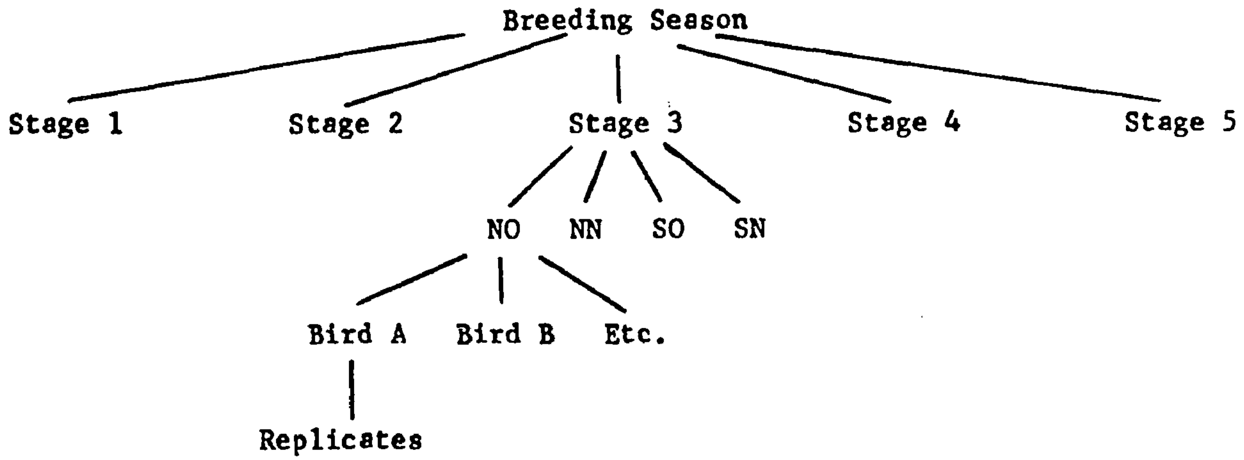

Breeding Season
Stage 1
Stage 2
Stage 3
Stage 4
Stage 5
NO
NN
SO
SN
Bird A
Bird B
Etc.
Replicates

Figure 3.

Territorial Boundaries During Incubation I 1979 at the Greenburgh Nature Center, Scarsdale, NY

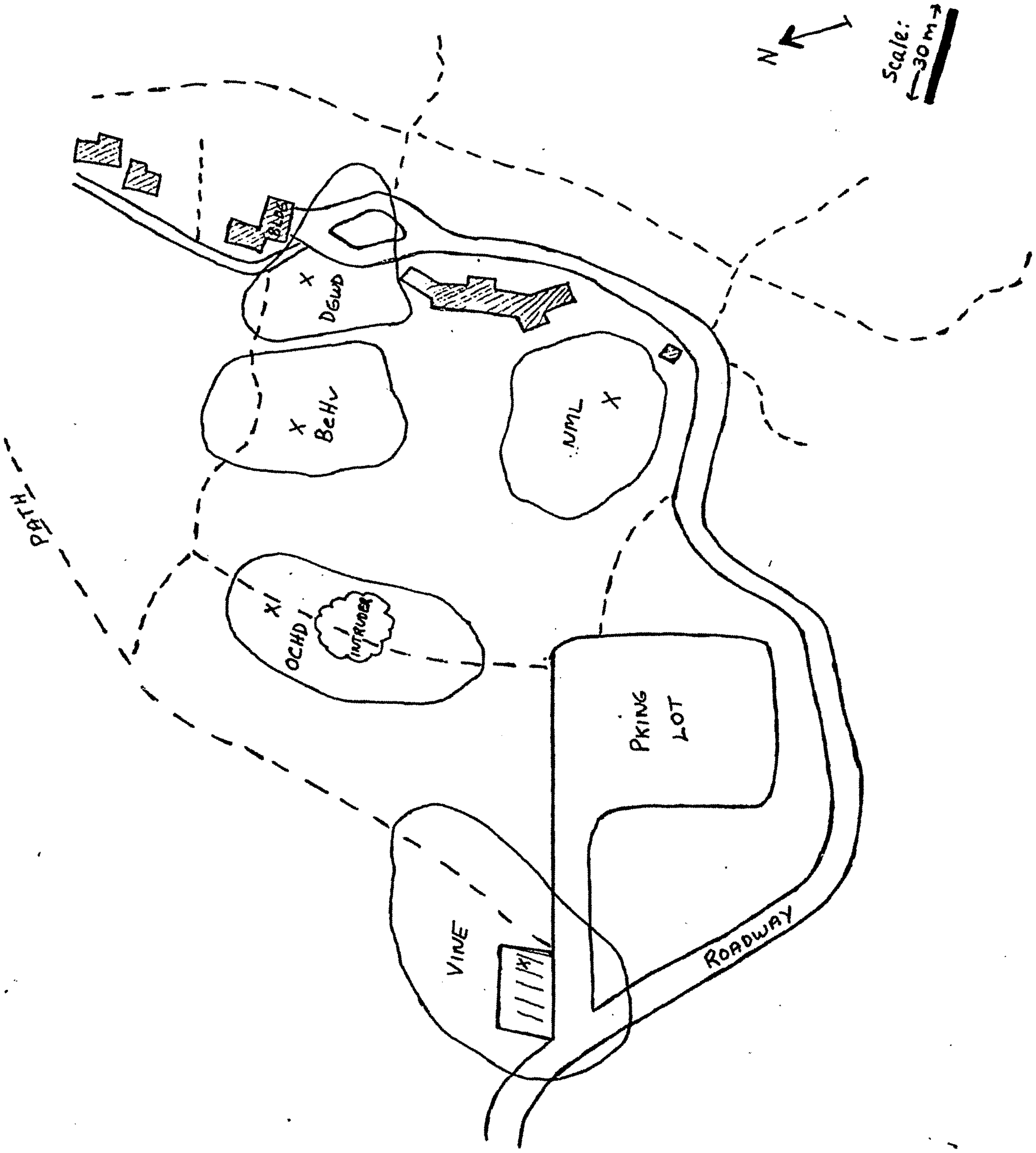

N
Scale: ←30m→
BLDG
DGWD
BeHv
NML
PATH
OCHD
INTRUDER
PKING LOT
VINE
ROADWAY

Figure 4.

Territorial Boundaries During Incubation I 1979

at the Audubon Center, Greenwich, CT

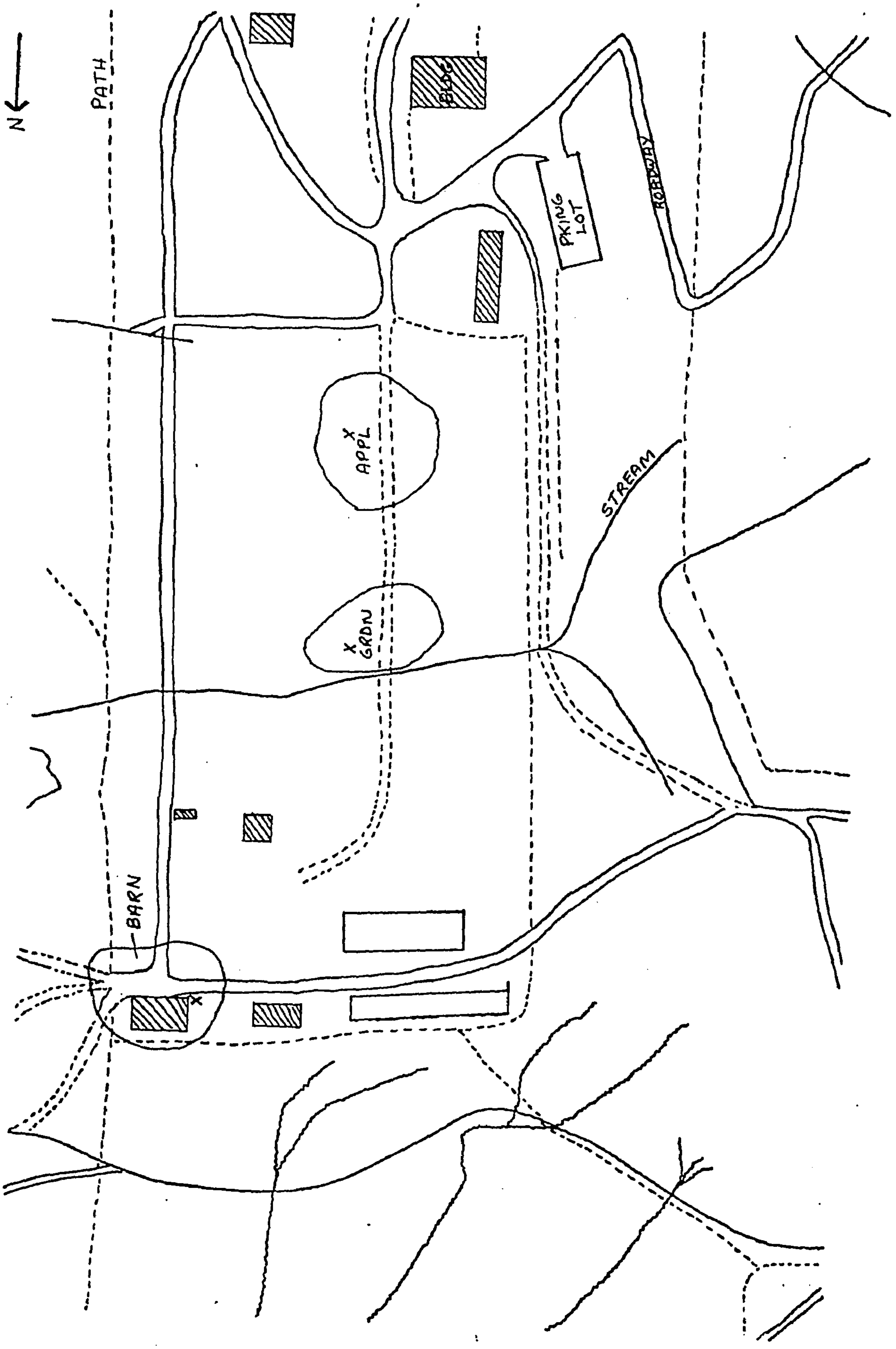

40m
N
PATH
BLDG
PKING LOT
ROADWAY
X APPL
X GRDN
STREAM
BARN
X

Figure 5.

Territorial Boundaries During Incubation II 1979 at the Greenburgh Nature Center, Scarsdale, NY

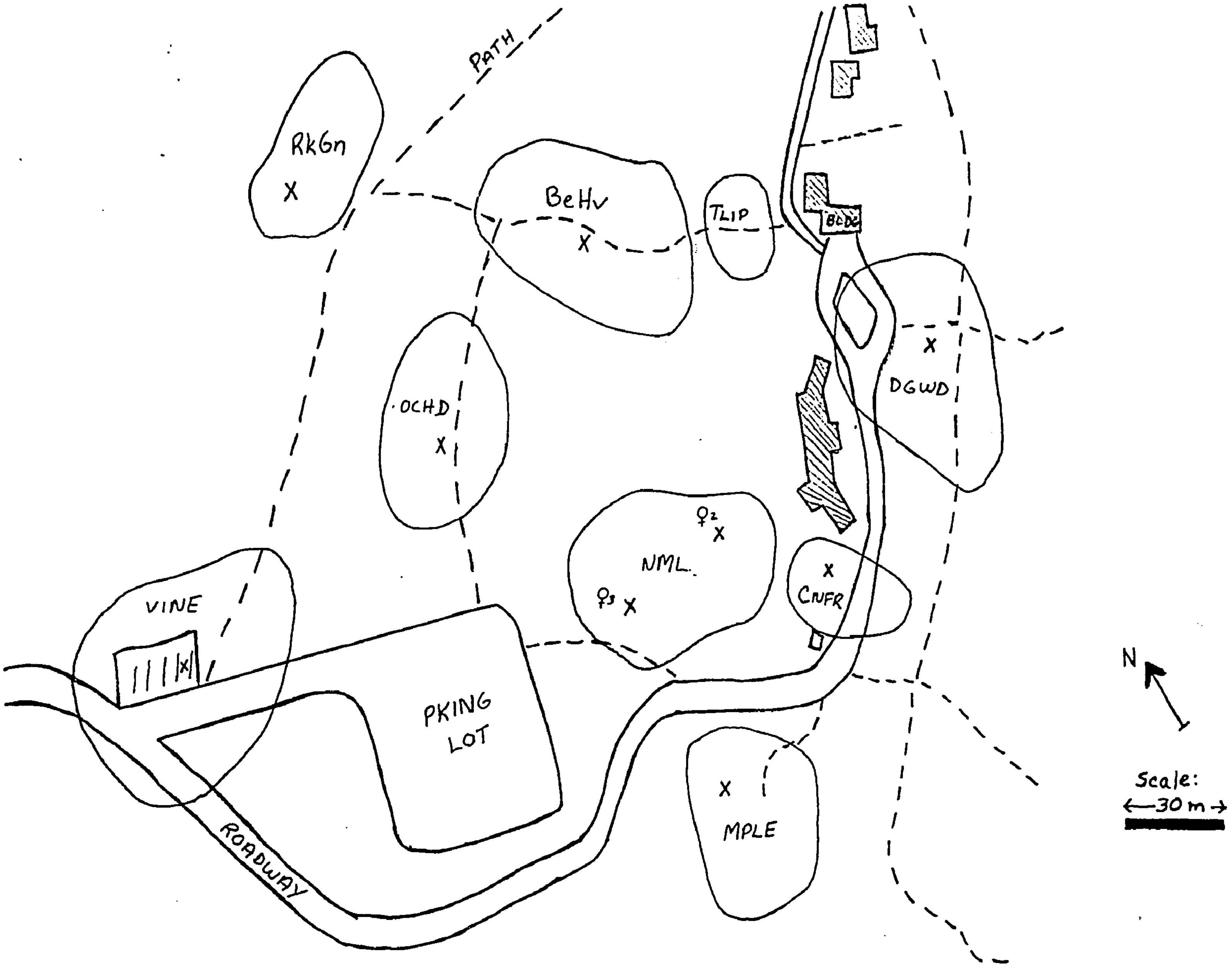

PATH
RkGn
BeHv
TLIP
BLDG
DGWD
OCHD
VINE
♀2
NML
♀3
CNFR
PKING LOT
ROADWAY
MPLE
N
Scale:
←30 m→

Figure 6.

Territorial Boundaries During Incubation II 1979

at the Audubon Center, Greenwich, CT

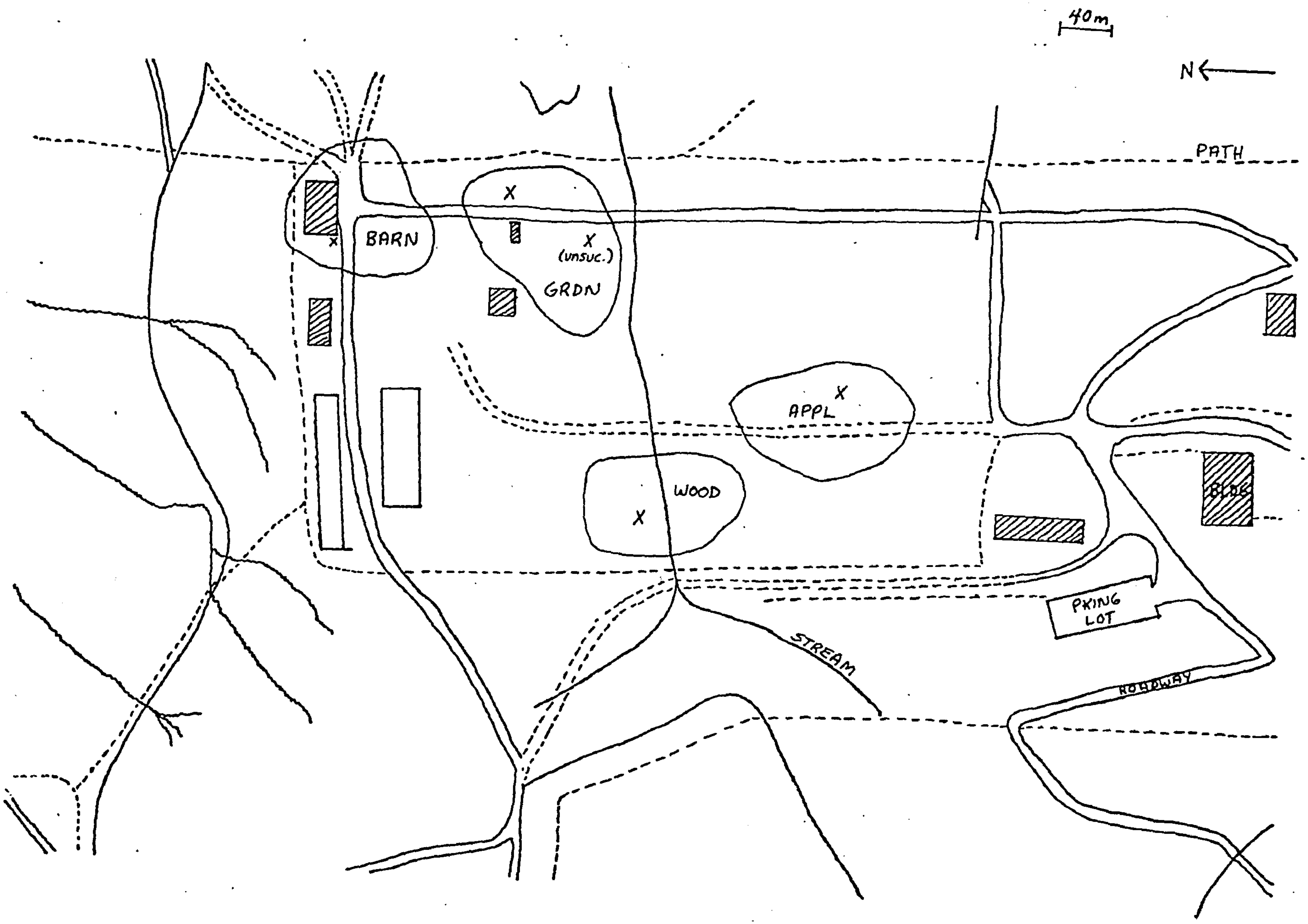

40m
N
PATH
X
BARN
X
X
(unsuc.)
GRDN
APPL
X
WOOD
X
BLDG
PKING LOT
STREAM
ROADWAY

Figure 7a.

Stages of Nesting, 1979,

Greenburgh Nature Center, Scarsdale, NY

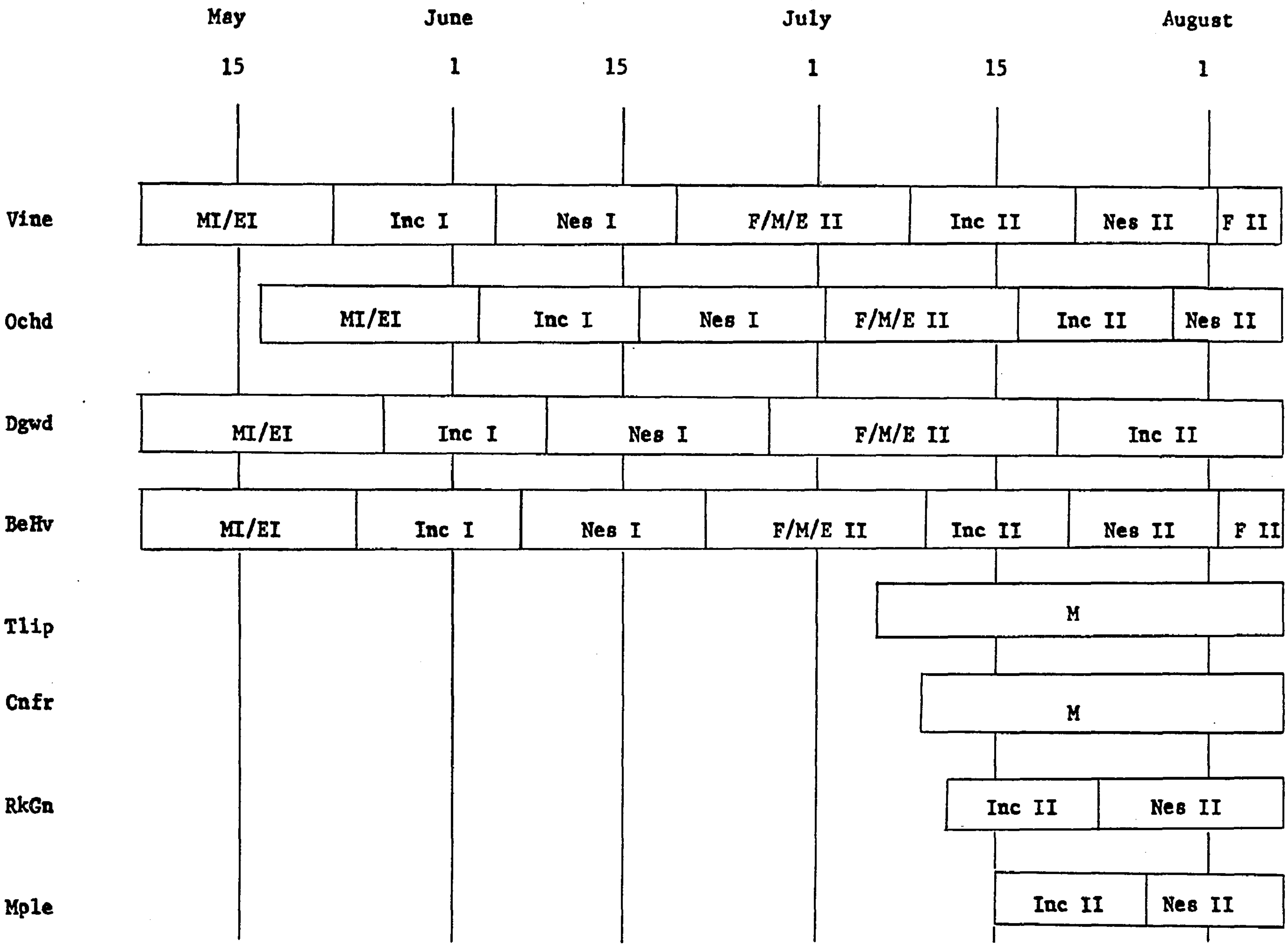

May
June
July
August
15
1
15
1
15
1
Vine
MI/EI
Inc I
Nes I
F/M/E II
Inc II
Nes II
F II
Ochd
MI/EI
Inc I
Nes I
F/M/E II
Inc II
Nes II
Dgwd
MI/EI
Inc I
Nes I
F/M/E II
Inc II
BeHv
MI/EI
Inc I
Nes I
F/M/E II
Inc II
Nes II
F II
Tlip
M
Cnfr
M
RkGn
Inc II
Nes II
Mple
Inc II
Nes II

Figure 7b.

Stages of Nesting, Polygynous Mating, 1979,

Greenburgh Nature Center, Scarsdale, NY

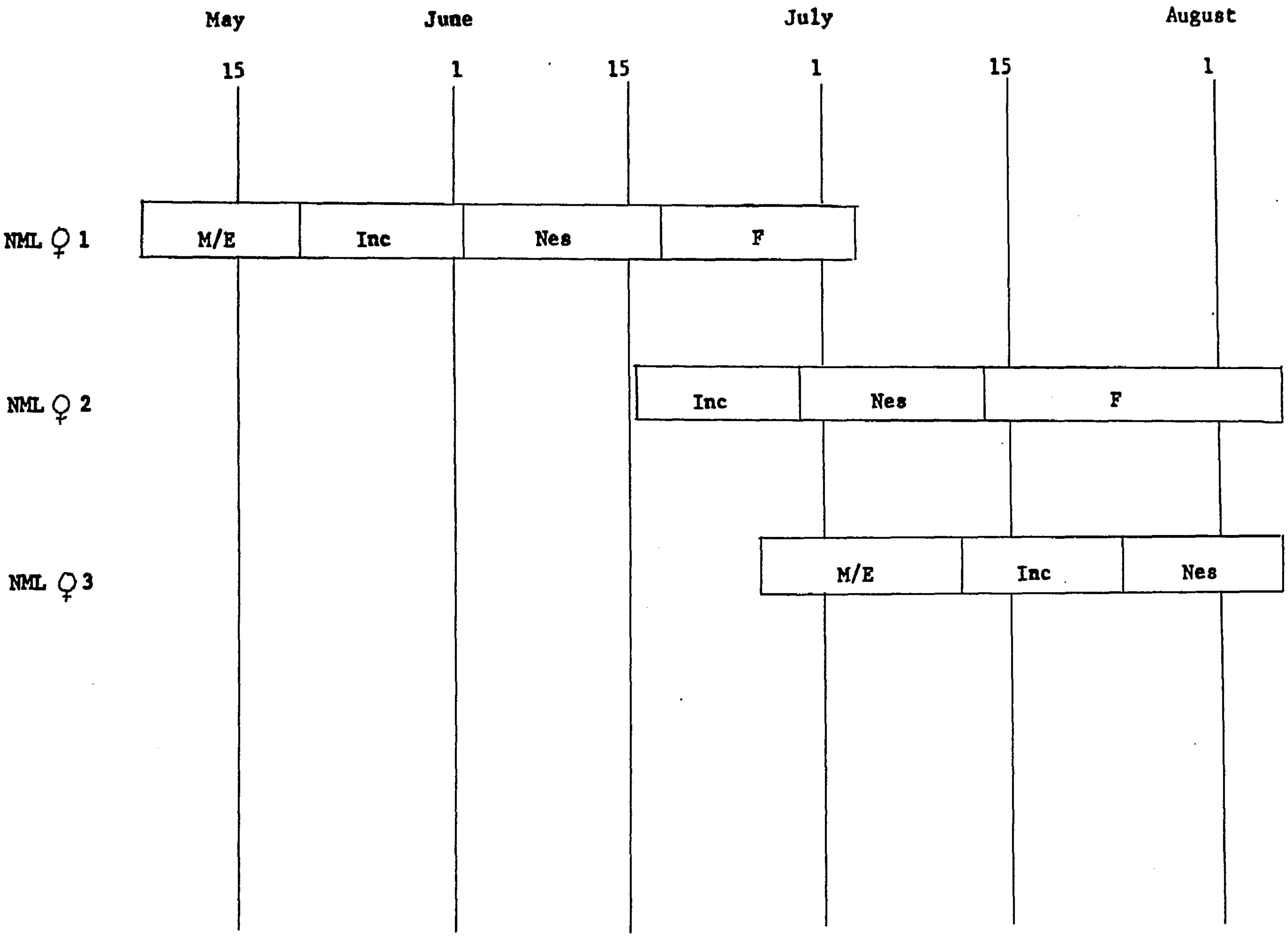
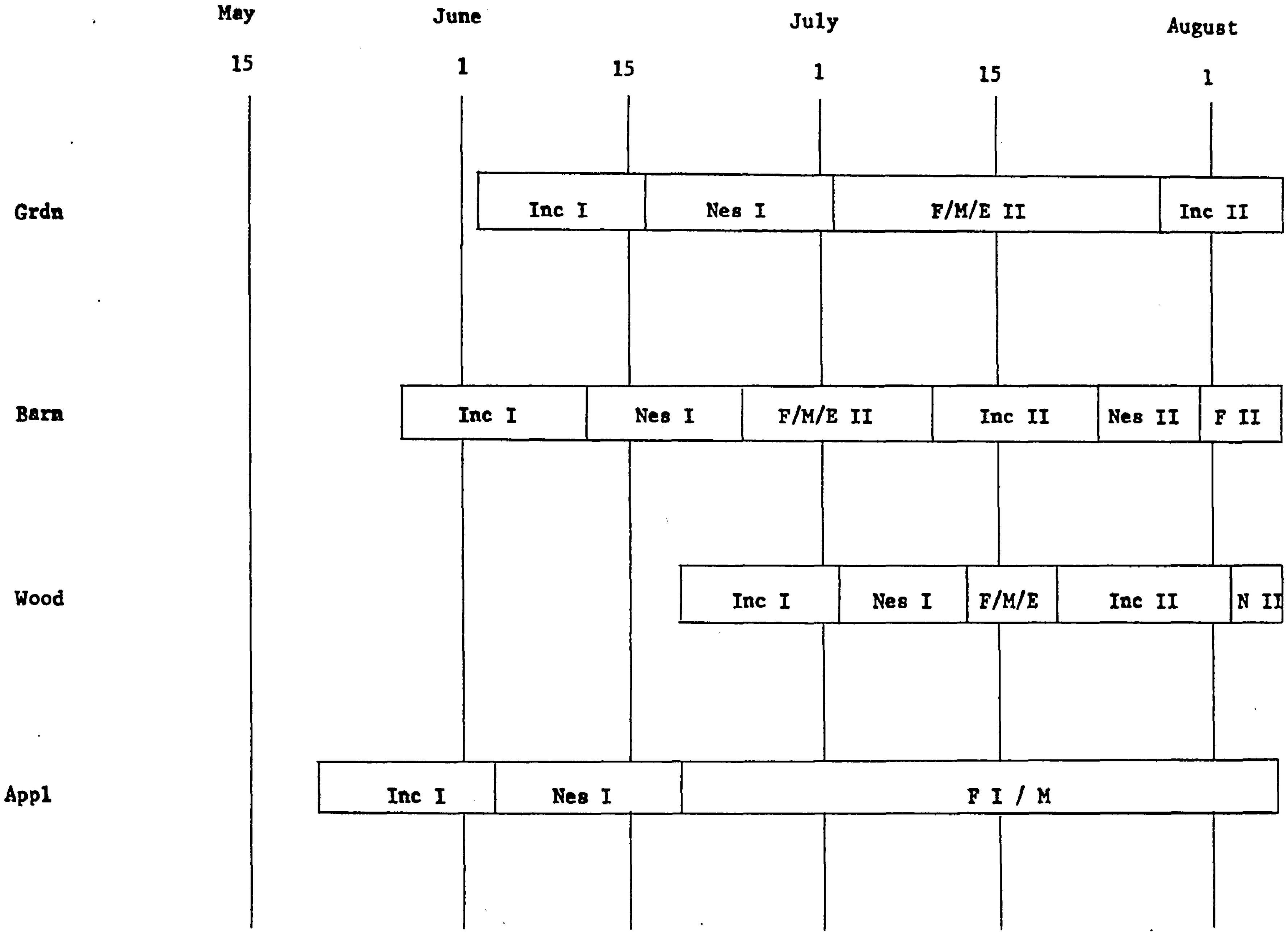

May
June
July
August
15
1
15
1
15
1
NML ♀ 1
M/E
Inc
Nes
F
NML ♀ 2
Inc
Nes
F
NML ♀ 3
M/E
Inc
Nes

Figure 8.

Stages of Nesting, 1979,

Audubon Center, Greenwich, CT



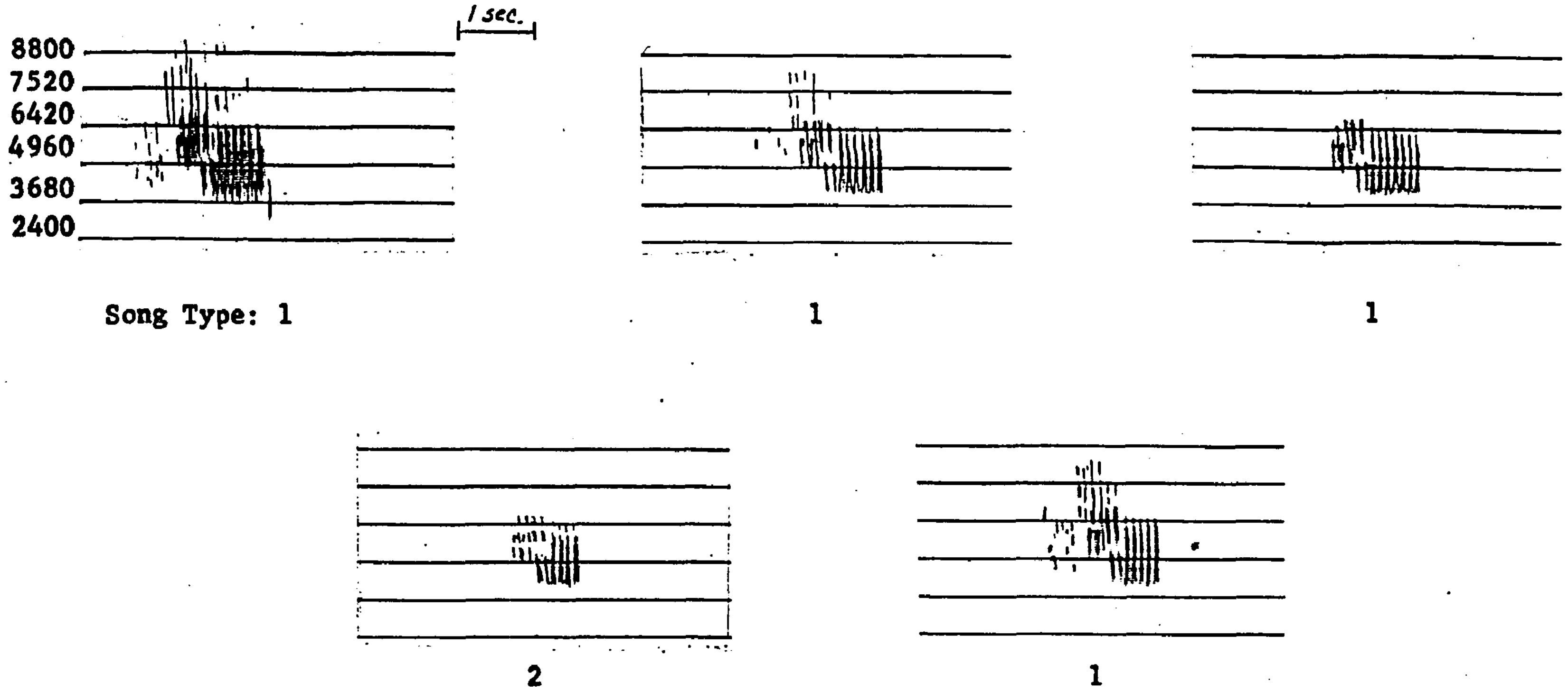
May
June
July
August
15
1
15
1
15
1
Grdn
Inc I
Nes I
F/M/E II
Inc II
Barn
Inc I
Nes I
F/M/E II
Inc II
Nes II
F II
Wood
Inc I
Nes I
F/M/E
Inc II
N II
Appl
Inc I
Nes I
F I / M

Figures 9a-k.

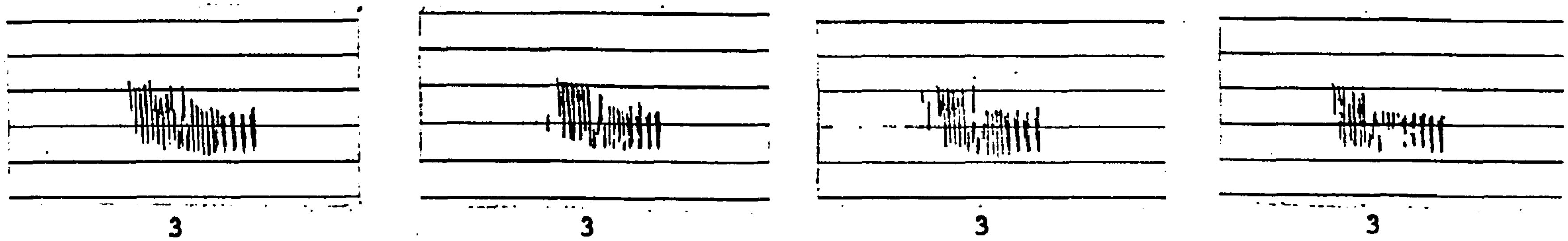
Sonagrams of Song Types and Variations Contained in Representative Test Tapes

Fig. 9a : Sonagrams

Bird: Cnfr (NY); Inc II



Bird: Ochd (NY); Inc II



Bird: Ochd (NY); Fl I/M/Egg II

Fig. 9b. <u>Sonagrams</u>

Bird: NML (NY); Inc I

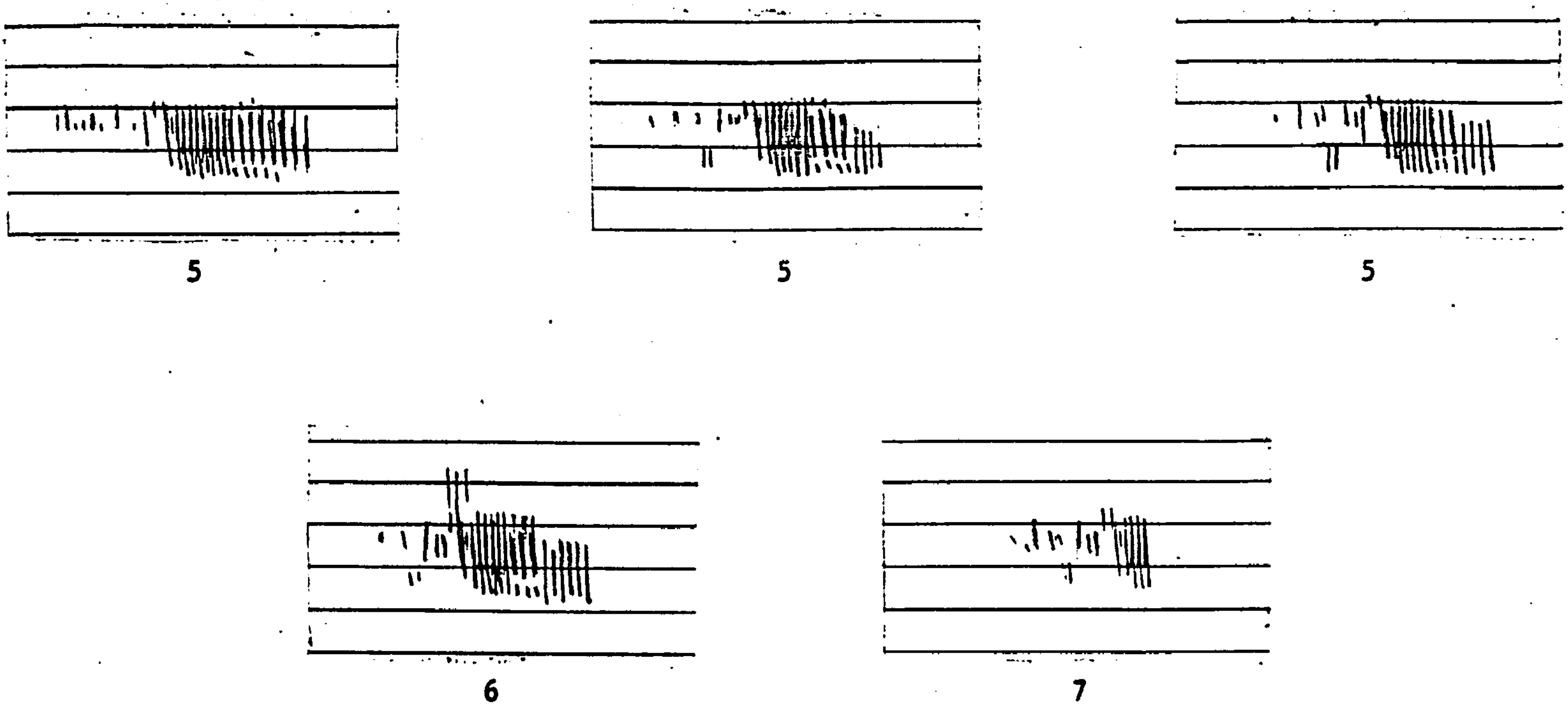
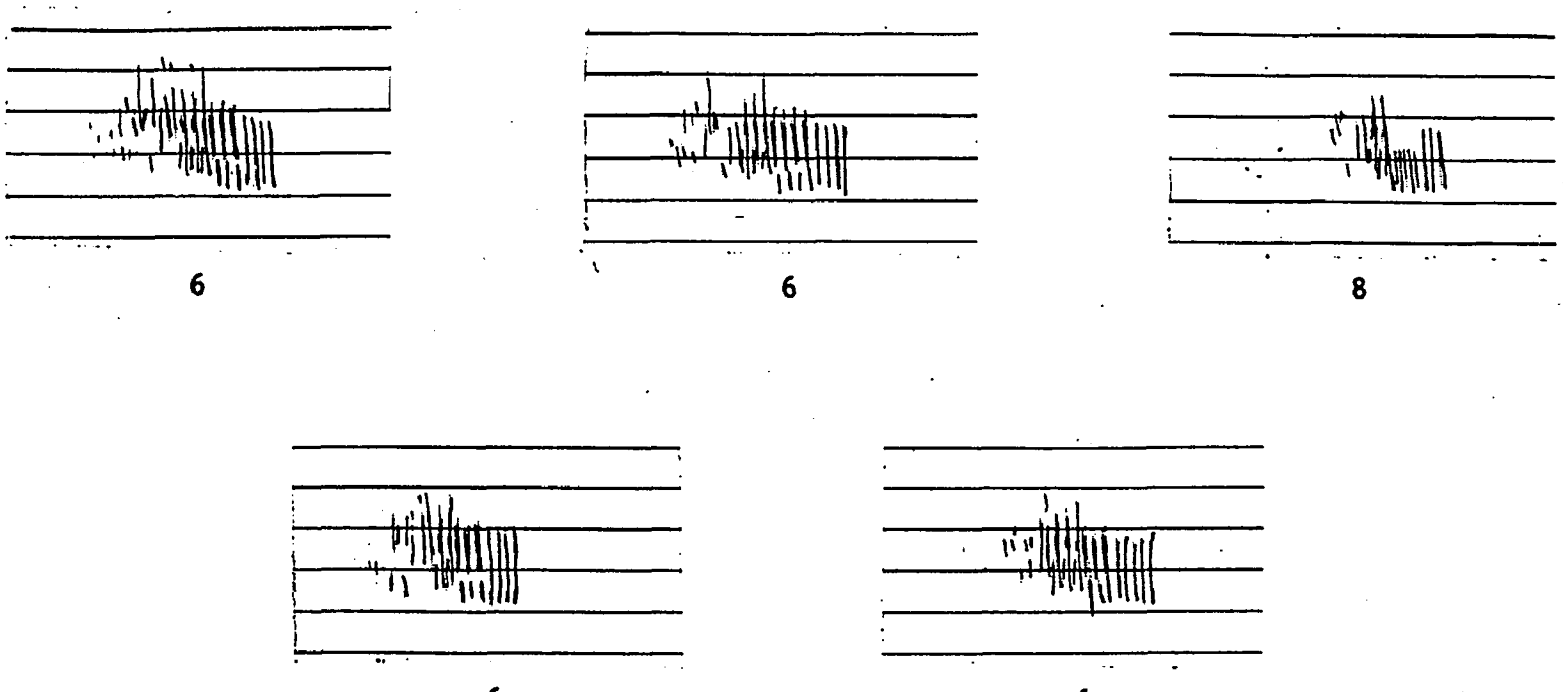


Fig. 9c. Sonagrams

Bird: NML (NY); Fl I/M/Egg II

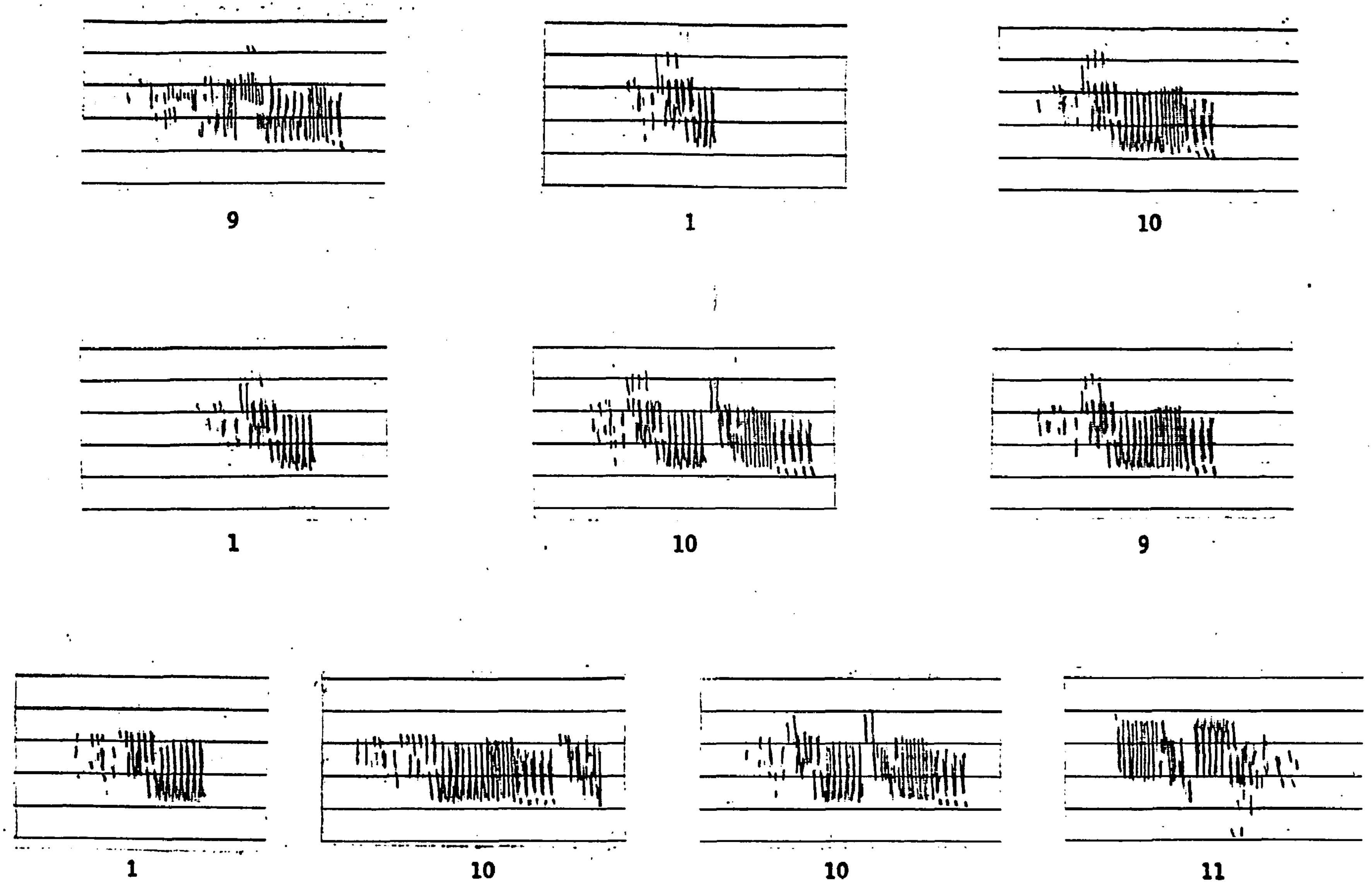


6 6 8

6 6

Fig. 9d. <u>Sonagrams</u>

Bird: BeHv (NY); Fl I/M/Egg II



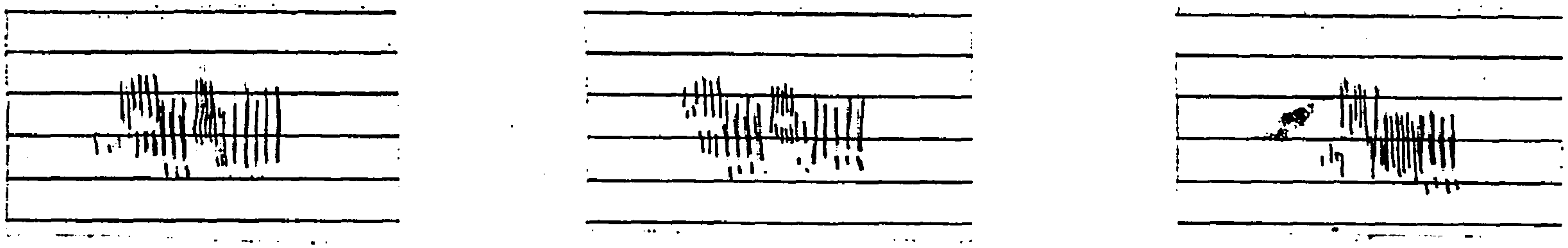
9 1 10

1 10 9

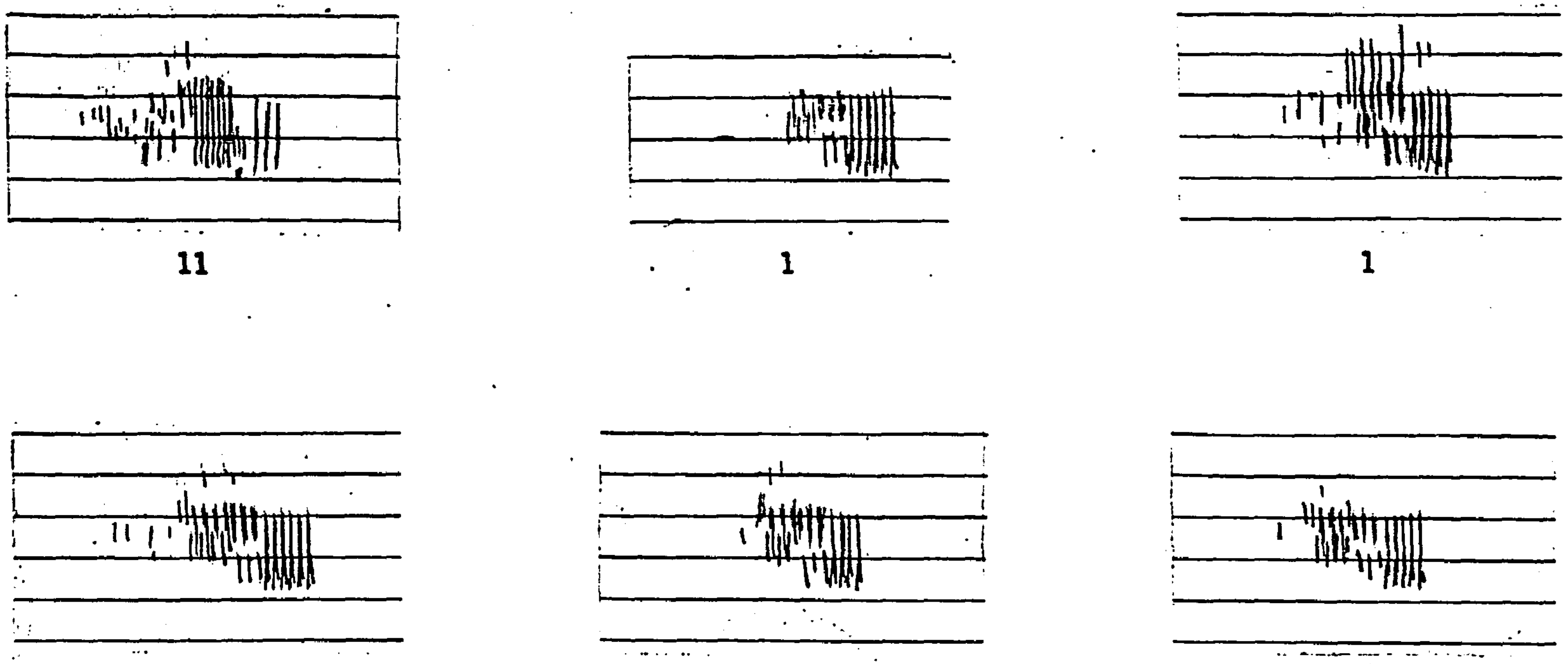
1 10 10 11

Fig. 9e. Sonagrams

Bird: BeHv (NY); Inc I

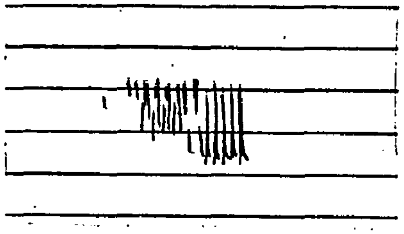

11 11 10

Bird: Dgwd (NY); Inc I


11 1 1

1 1 1

Fig. 9f. Sonagrams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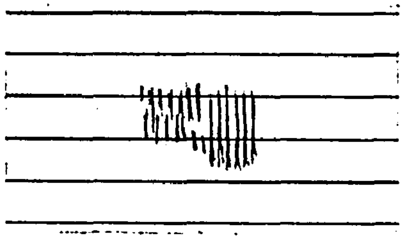
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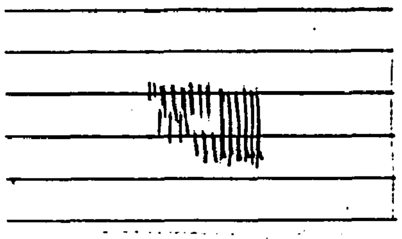
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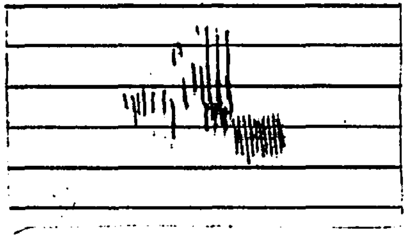
Bird: Dgwd (NY); Fl I/M/Egg II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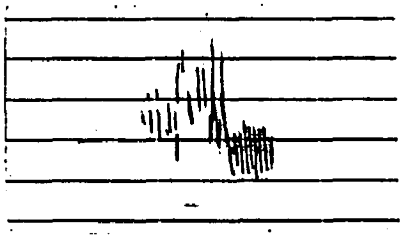
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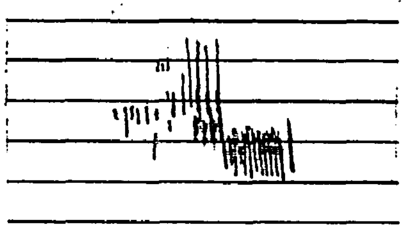
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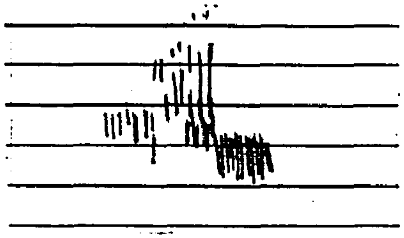
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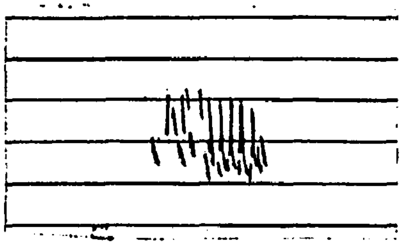
Bird: Stranger (NY); Inc I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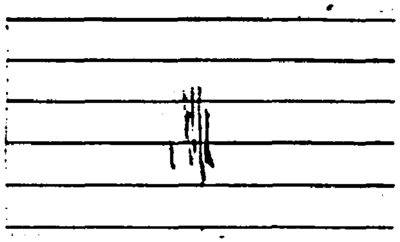
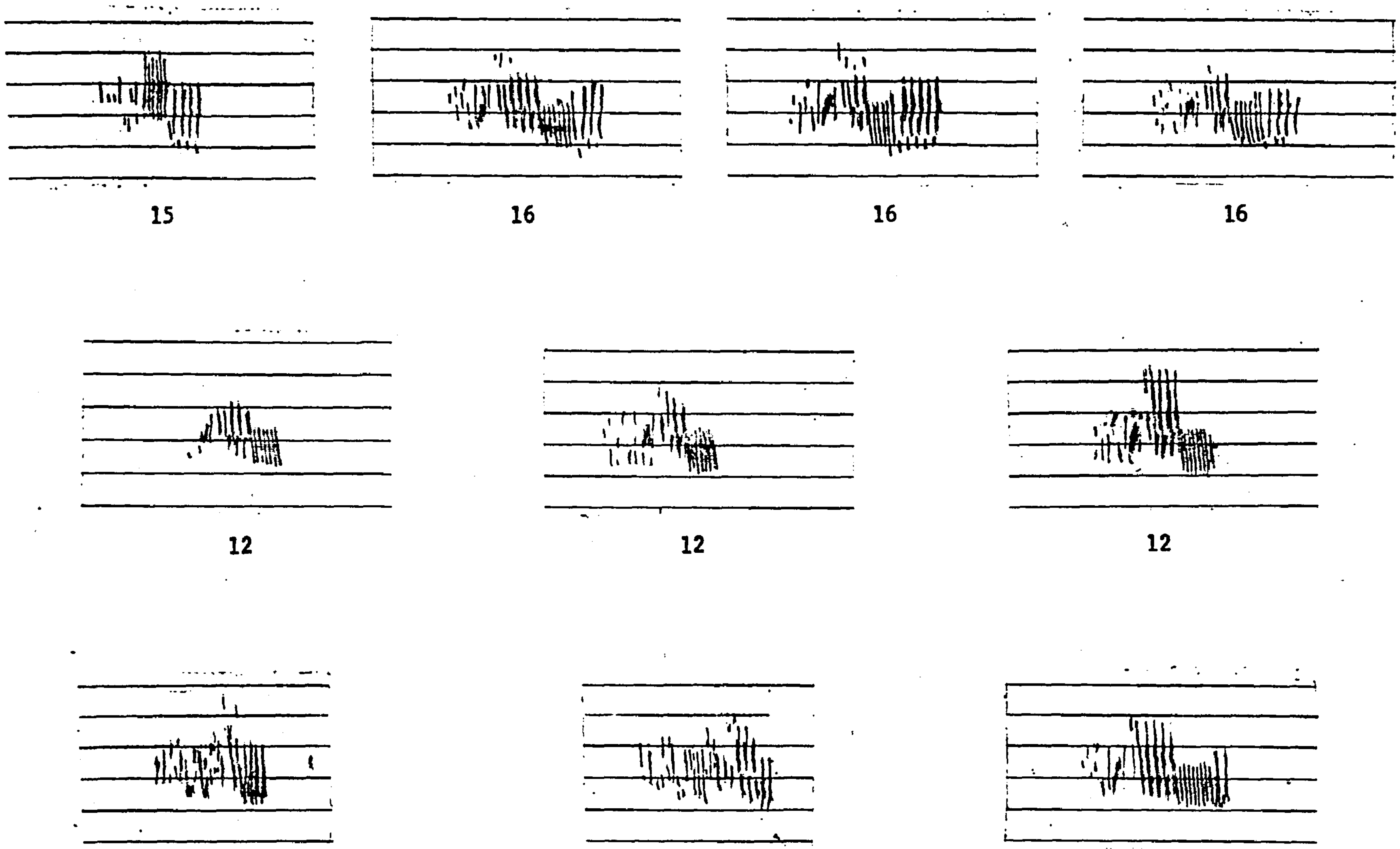

14

Fig. 9g. Sonagrams

Bird: Stranger (NY); Nes II



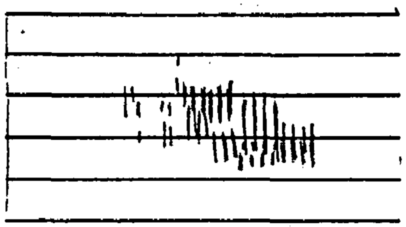
15 16 16 16

12 12 12

1 1 10

Fig. 9h. Sonagrams

Bird: Stranger (CT); Nes I



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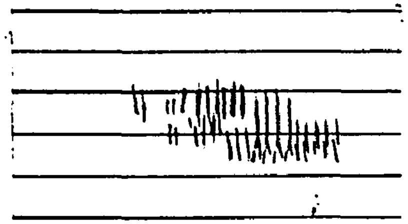

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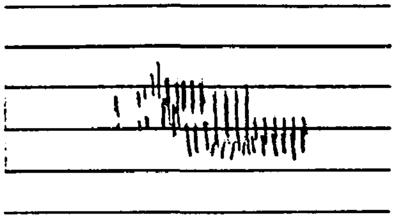
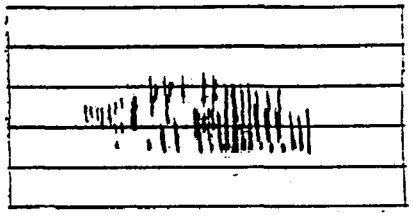


17

Bird: Stranger (CT); Inc II



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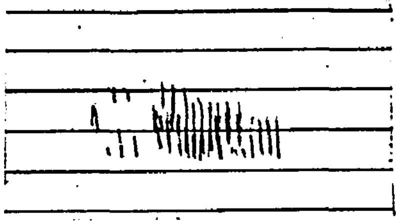

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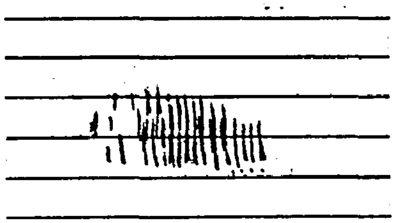

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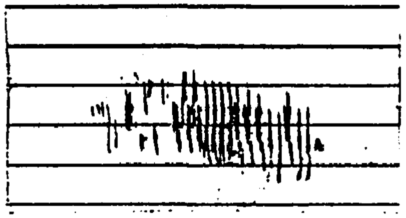

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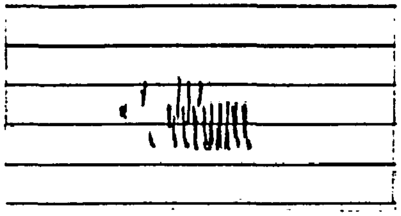
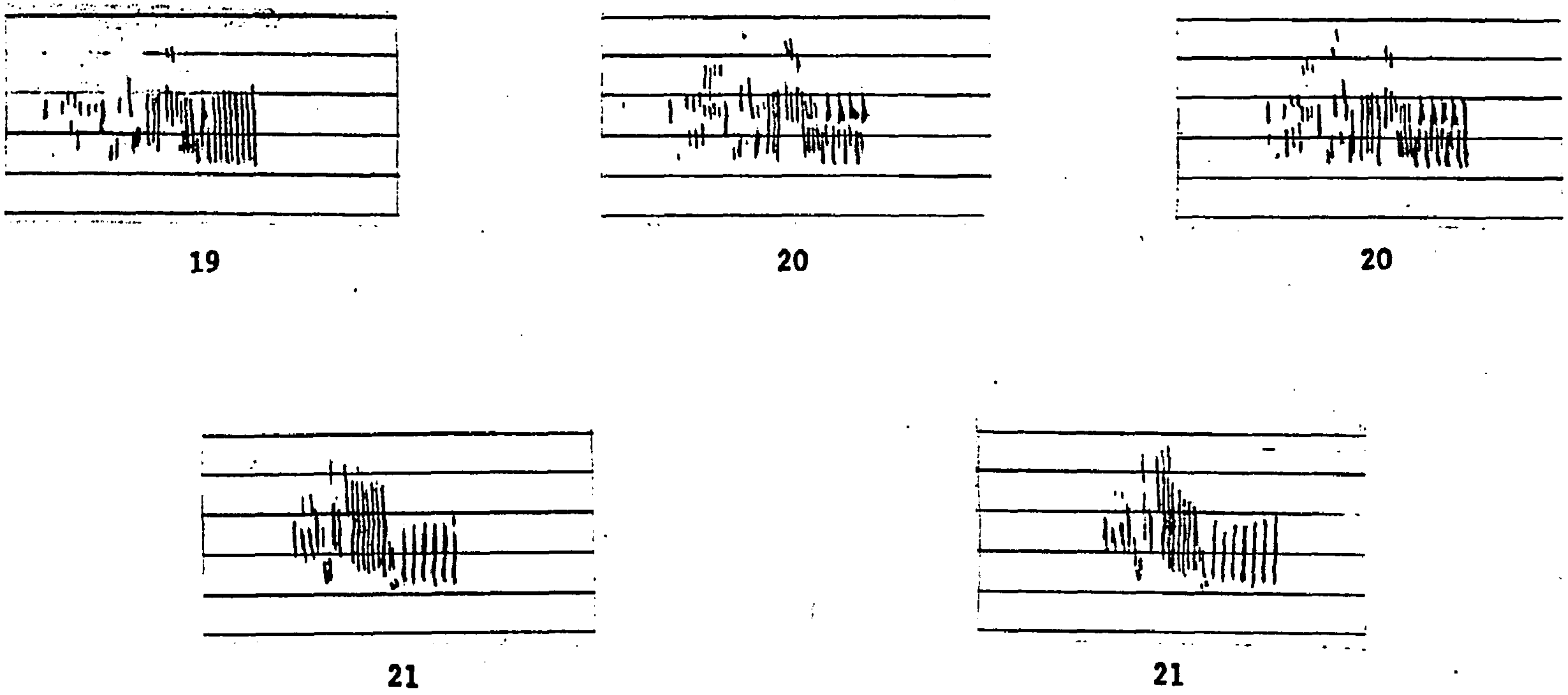


5

Fig. 9i. Sonograms

Bird: Appl (CT); Inc II



Bird: Grdn (CT); Nes I

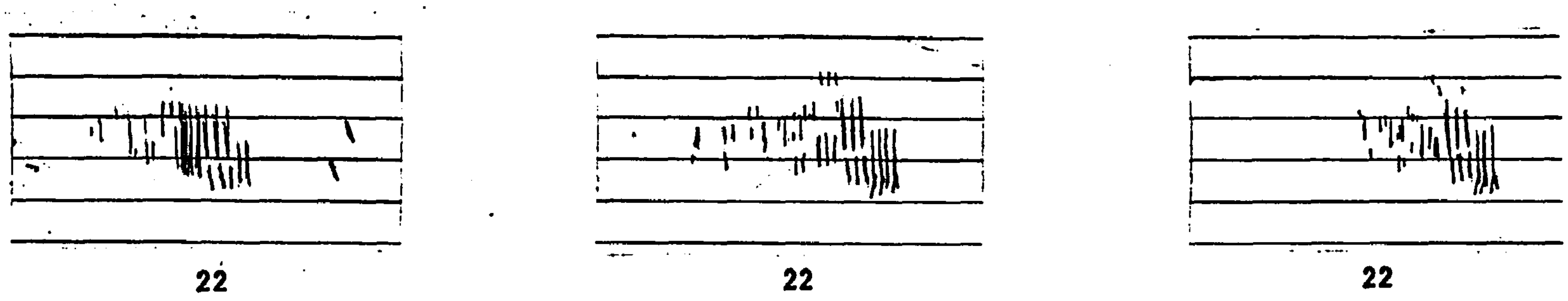


Fig. 9j. <u>Sonagrams</u>

Bird: Grdn (CT); Nes II

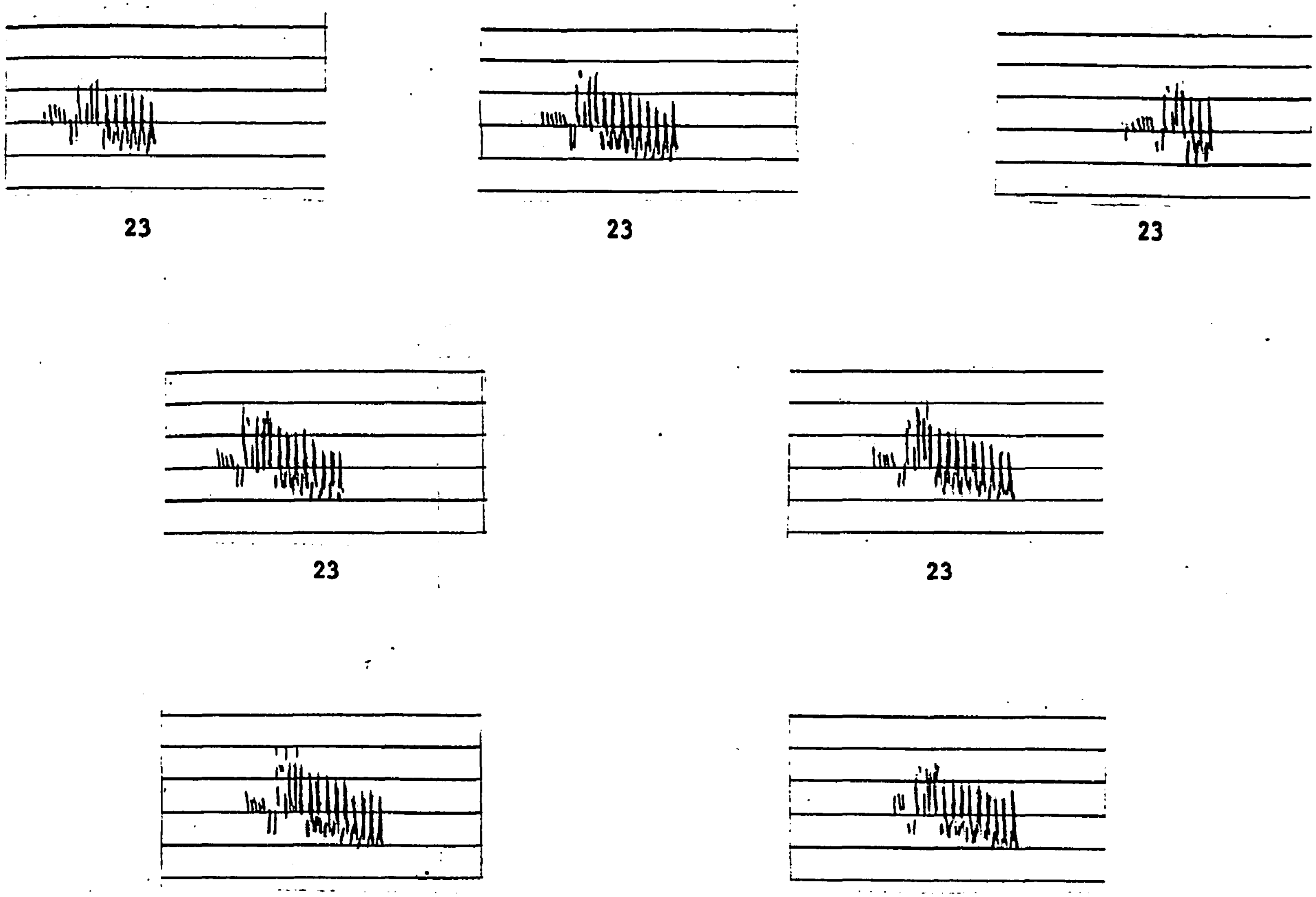


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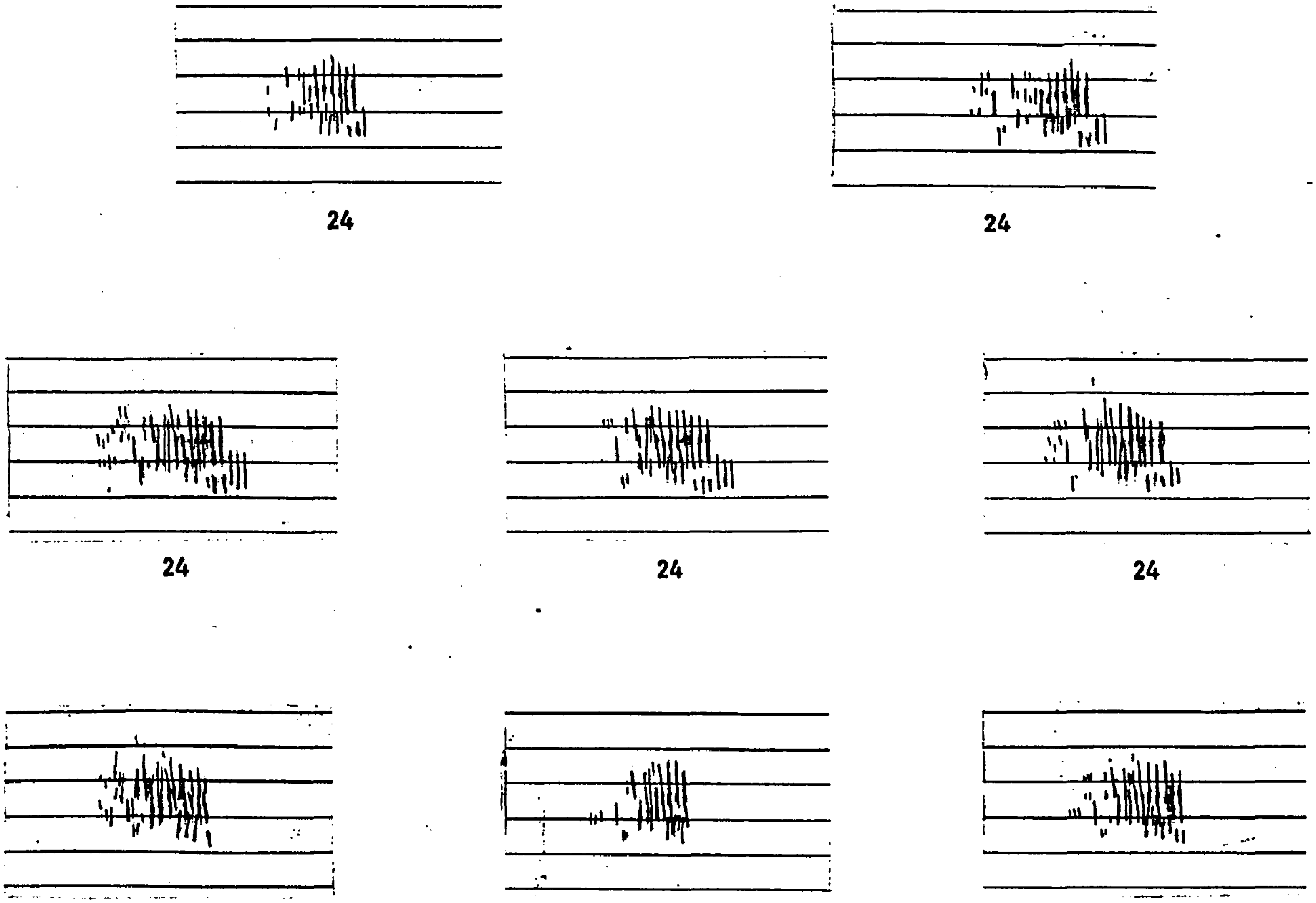
Fig. 9k. <u>Sonagrams</u>

Bird: Barn (CT); Inc I



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