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BEHAVIORAL ASPECTS OF THE BREEDING BIOLOGY OF THE BLUE JAY
CYANOCITTA CRISTATA

City University of New York PH.D. 1983

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BEHAVIORAL ASPECTS OF THE BREEDING BIOLOGY OF THE BLUE JAY
CYANOCITTA CRISTATA

by

HARRIET LAINE

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.

1983

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

Mating systems have been defined as those aspects of a population's social organization that determine the ways in which females and males come together for breeding purposes (Brown 1975). Typically, these systems have been divided into 3 major categories: monogamy, polygamy and promiscuity. While it is clear that these systems may show considerable plasticity with different individuals or different populations within a species showing different mating patterns, there are, nonetheless, general criteria under which any mating system may be defined. Thus monogamy is a system where each breeding adult has only one mate at any time, polygamy is a system where an individual of either sex has two or more mates and promiscuity is a system in which no pair bonds are present at all.

Several theories have been put forth to account for this variation in mating strategies. These include the work of Lack (1968), Verner and Willson (1966), Orians (1969), Selander (1972), Trivers (1972) and Emlen and Oring (1977). Essentially these investigators have argued that mating systems are ecological adaptations, that factors affecting the reproductive success of the female as well as male are important in determining the system, and that the degree of parental investment by both the female and the male is another crucial element influencing the mating system. Brown (1964) introduced the concept of economic defendability to this discussion. Although initially concerned with territoriality, this idea has been extended, especially by Emlen and Oring (1977) to include defendability of mates. They have suggested that certain environmental factors, especially the spatial distribution of key resources and the temporal availability of mates will be the critical determinants of mating systems. Thus the prerequisite for a monogamous mating system is the 'economic defendability of a mate'. They go on to propose that monogamy is expected to occur when 'neither sex has the opportunity to monopolize additional members of the opposite sex, directly or through 'resource control'. Weatherhead (1979), in support of this model, found that in tundra-breeding Savannah Sparrows, Passerculus sandwichensis, monogamy is maintained as a consequence of the limited temporal availability of mates.

Over 90% of all bird species show some form of monogamy (Lack 1968), either serial, in which the pair mates for a breeding season or some part of it but separates during the non-breeding season, or continuous (often called permanent), in which the pair mates for life, or at least for several seasons. Partners tend to remain together during the non-breeding season as well (Skutch 1979). In serial monogamy switching of mates for the next season is typical. Lack (1968), who does not distinguish between the two types, suggests that the reason for this high percentage of monogamous species is due to the fact that in most cases two parents can better feed and therefore raise more young than can the female feeding (the young) alone. Monogamy occurs typically in those species with altricial rather than precocial young although there certainly are exceptions (Orians 1969). Other generalized features of monogamy include increased male participation in care and feeding of young, strong site tenacity from one breeding season to the next, and the tendency to sexual monomorphism

(Orians 1969; Selander 1972; Skutch 1979). Those species showing continuous monogamy tend, in addition, to remain on or closely associated with the nesting territory throughout the year, although, again, there are exceptions. Some continuously monogamous species migrate in which case the pair tends to remain together on the winter grounds. And although not necessarily gregarious, some of them associate in flocks and are colonial nesters (Skutch 1979).

Despite the awareness of these generalized attributes, more progress has been made in explaining polygamous mating systems, especially in clarifying the particular environmental factors involved. Wittenberger and Tilson (1980) suggest that the development of a comprehensive theory of monogamy has been hindered by 'the great diversity of environmental conditions and social behaviors associated with its evolution. No single hypothesis is sufficient to explain all known instances of monogamy'. They view monogamy as 'the logical product of selection when conditions favoring alternative mating systems are not met'. Based on previous work with non-monogamous systems, they have developed 5 criteria for the evolution of monogamy: (1) when male parental care is nonshareable and indispensable to female reproductive success, (2) in a territorial species if a female benefits more from mating with an unmated than mated male, (3) in non-territorial species when the majority of males can reproduce most successfully by defending exclusive access to a single female, (4) if aggression by females prevents a male from acquiring 2 mates, and (5) when males are less successful with 2 mates than with one. Altricial birds tend to follow the patterns suggested in hypotheses one and two, although there are exceptions.

As stated above, parental care plays a crucial role in the maintenance of a species' mating strategy. Young, especially those of altricial species, place high demands on their parents, requiring food, warmth, protection from the elements and protection from predators. Exactly how these responsibilities are divided may vary between the sexes. Trivers (1972) was one of the first to suggest this idea. He argued that since females produced the eggs (which are much larger than the male sperm) they are more likely to invest further in the nest and eggs, whereas the males, which have invested so little in the eggs, are more likely to increase their own fitness by copulating with more females. Thus Trivers predicted that parental responsibilities will be divided unequally. Males, moreover, may 'cheat'; monogamy would be favored by females, males would show some form of polygyny or at least promiscuity. (This prediction would not necessarily apply in harsh environments where males are more likely to remain with their mates.) Alternatives to this model have been suggested by both Howe (1979) and Gladstone (1979) who propose that, for monogamous species, especially those in which the male does not invest time and/or energy in defending a territory, one would expect a more equivalent pattern. Howe (1979), for example, found (in the Common Grackle) that, contrary to Trivers' predictions, males do not desert and that both parents bring food of similar quality and quantity to the nestlings. More recently Burger (1981) has proposed that in monogamous birds males would be expected to invest more, not less, in reproductive effort, because of the potential threat of insemination by another male. While females invest in the young (in the form of both eggs and nestlings) males would be expected to invest in both offspring and the female in order to avoid insemination by another male. Moreover, as Burger (1981) also points out, elements such as courtship feeding and/or nest building can also be viewed as components of male parental care.

Just as overall mating strategies are affected by environmental considerations, so too, are the specifics of parental care patterns. For example, Wittenberger (1982) found that both female and male Bobolinks (*Dolichonyx oryzivorus*) adjust their parental activities from season to season to changes in food availability and weather conditions. And Pierotti's (1981)comparison of parental roles in two different island populations of the typically monogamous Western Gull (*Larus occidentalis*) revealed that differing environmental conditions (such as food availability) influence the demand for male parental care, and, in this case, lead to a change in male reproductive tactics.

The Blue Jay is an ideal species in which to examine parental activities. It holds a unique place among the New World Jays, sharing some of the characteristics of the more thoroughly studied monogamous colonial and communal species in this group (see below), yet maintaining a social structure that is neither colonial nor communal. The Blue Jay, in fact, can be viewed as occupying an intermediate position in this continuum of social systems (Brown 1974). The findings of this study are important, therefore, in understanding the role(s) of monogamy and parental care patterns both for the Blue Jay and the other New World Jays as well.

Despite the fact that it is a common resident of the Northeast, little work has been done with the Blue Jay. Indeed, outside of Hardy's (1961) study, no detailed paper has been published. Thus a descriptive analysis of the breeding behavior of this species is crucial to our understanding of the above-mentioned issues.

The Blue Jay is one of 33 species of jays in North and South America (Brown 1974). The social systems of these birds run the gamut from colonial to territorial to communal. Of the species that have been studied, the Piñon Jay stands at one extreme, exhibiting a colonial system (Brown 1974; Balda and Bateman 1971, 1972), while a number of species (n=24, 67%) stand at the other extreme, displaying communal breeding patterns which involve regular help in care and feeding of the young (Brown 1978). As stated above, the Blue Jay, along with six other species (Steller's Jay, California Scrub Jay, Dwarf Jay, Black-chested Jay, Green Jay and Omilteme or White-throated Jay) occupies an intermediate position in this continuum (Brown 1974). Because of the high percentage of communal or cooperative breeders among a closely related group of birds a great deal of attention has been directed towards the jays. While the Blue Jay is not known to breed communally, it does share a number of characteristics with those that do. These include: (1) a significant contribution to feeding of young by males, (2), a long period of juvenile dependence, (3) regular exchanges of food among adults and (4) long lived species (Gutkin 1978; Brown 1974; Laskey 1958). Interestingly enough, as mentioned above, these are also some of the correlates associated with monogamy.

Goodwin (1976) suggests that almost all corvids whose behavior is reasonably well-known show some form of monogamy, either serial or continuous. For some species this evidence is circumstantial or based on captive or tame birds (Goodwin 1951). But Baeyens (1979), for example, has done a comparative study of serial and continuous monogamy in two European corvids, Jackdaws and Magpies. Her findings suggest that intense competition for both nesting sites and food favor continuous monogamy as found in the Jackdaw while the advantages of pairing to a site-experienced bird favor serial monogamy in the Magpie. Evidence for continuous monogamy is far more extensive among North and South American jays. Among those species where it is thought to occur are: Steller's Jay (Brown 1963a and pers comm), Pinon Jay (Balda and Bateman 1971), Green Jay (Alvarez 1975) and the Florida Scrub Jay (Woolfenden 1973). Again, despite the prevalence of monogamy, these species show differing social organization.

By providing a detailed description of the breeding behavior of the Blue Jay, the findings of this study will serve to elucidate the role(s) of monogamy in the social organization of this species as well as its relationship to the other New World Jays. By examining how each sex contributes to the overall effectiveness of this system, the findings of this study will help to reveal some of the relationships between parental care patterns and the breeding biology of a species.

MATERIALS AND METHODS

General

The study area included several sites 8 km E. of the village of Cold Spring, New York (Putnam County) on land adjacent to and part of Fahnestock State Park. These woods are predominantly oak/birch/ beech (Quercus, Betula and Fagus spp), the preferred nesting habitat of the Blue Jay (Anderson and Stugart 1974; Bent 1964). Sunflower seeds and cracked corn were supplied to feeding stations during the non-breeding seasons both to facilitate extended viewing of the birds and aid in trapping for banding purposes.

Birds were banded with U.S. Fish and Wildlife serialized aluminum bands and plastic color bands. By using unique combinations of two color bands on one leg and one color band and the U.S. Fish and Wildlife band on the other leg I was able to provide for individual recognition in the field. Both Potter and confusion ground traps were used for trapping; mist nets proved to be totally unsuccessful since the jays tended to fly over them. 163 birds were banded during the course of this study. Due to the inaccessibility of most nests only limited banding of nestlings took place; 14 (out of 82) in all. These were typically banded when young were 10-12 days of age; their eyes were open but they were not fully feathered. Young were lowered to the ground for banding and then replaced in the nest. All banded young, except for those from one nest, fledged successfully. The remaining nest was dislodged in a heavy storm following banding and the young were never found.

Blue Jays are monomophic; behavioral criteria, known to be sex-specific, were used to sex adult individuals (Woolfenden and Fitzpatrick

1977; Brown 1964). These included food begging, incubation, and brooding behavior for the female and copulatory behavior for the male. Sex determination based on behavior proved correct for all birds observed to breed.

Data were collected during the breeding seasons (April to August) of 1979-1981 as well as during the winters (December-March) of 1979 and 1981 for a total of 2160 hr of field observations (1520 during the breeding season and 640 hr during the winter). An additional 9 days (137 hr) were spent in the field during the 1982 breeding season in dusk-dawn observations.

Data Collection

During the breeding season I collected data on behavioral features of the breeding biology of the Blue Jay by observing individuals, interactions between mated pairs and interactions between parents and young.

Before nesting was completed data were collected with respect to the components of courtship behavior (listed below) and nest building activities. The latter included carrying and offering of nest building materials as well as actual building of the nest. Anti-predator behavior was also noted, as were frequencies of several specific displays and vocalizations (see below).

Once the jays began nesting, I collected data on frequencies of behaviors occurring at or near the nest; presence in the area, foraging, anti-predator behavior (active chase and/or silent perch), incubation, brooding and feeding of the young, and feeding of the female.

During the winter months data were collected primarily at feeding stations. A principal objective of these observations was to determine if mated pairs stay together during this period. I gathered information on individual birds; with whom did they associate and in what context (i.e.: feeding only, arriving/leaving a feeding station together, moving through the woods together). Frequencies of specific vocalizations and displays were also noted (see below).

Because of their potential relevance to breeding behavior, several specific vocalizations and displays were chosen for descriptive analysis. These are:

Vocalizations: (1) Soft chirp, (2) Monotone cry, (3) Short cry, (4) Food solicitation, (5) Squeaky gate, (6) Bell call and (7) Rattle. Displays: (1) Bobbing, (2) Food transfer, (3) Food beg, (4) Silent sit, (5) Sidling, and (6) Diving. (See Appendix I for a description of components.)

During the 1979 and 1980 seasons I also recorded these vocalizations using a Uher 4200 Report Stereo recorder and a Sennheiser shotgun microphone. These recordings were then compared sonographically with those of Conant (1972) to insure that, despite some differences in the terminology, the calls represent the same ones discussed in the literature.

General descriptive data included weather conditions, dates and duration of each stage of the breeding cycle, nest tree species and height, number of young and number of young fledged. It was not possible to determine the number of eggs due to the extreme height of the nests. In an effort to reduce human disturbance determination of stage in the breeding cycle was based on behavioral criteria, even for those nests whose contents could be checked, and is, therefore, only approximately correct. Thus incubation was defined as beginning when a bird increased markedly the time it sat on the nest (typically from 1-2 min-15 min). Brooding (before young were visible) was characterized by either one or both of the adults bringing food to the nest and/or the female's extreme attentiveness to the contents under her with much adjusting of her position. The number of young was determined, when possible, by counting the number of heads or beaks.

Nesting Season

I divided the nesting season into 5 stages: (1) Courtship, (2) Copulation/Egg Laying, (3) Incubation, (4) Nestling, (5) Fledgling. This covered the period from the beginning to mid-April through the end of August. Data were collected at all stages although, as can be seen in Table 1, not all birds contributed equally to data from all stages nor was the sample size the same from year to year. A total of 33 pairs are included in this analysis and while information was gathered on both banded and unbanded individuals, all information discussed below was obtained from banded birds unless otherwise stated.

Observations were made by following the birds with binoculars (7 x 35) and on foot as they moved through the woods. Once nesting began a spotting telescope (20x) was also used, placed as close to the nest as possible without disturbing the birds. The distance from which I was able to observe varied from 3-7 m from the base of the nest tree, depending on the stage of the cycle and the particular birds under observation. Camouflage mosquito netting, draped as a poncho, served as a blind. This provided for greater ease of movement than a solid structure in dense woods and proved to be an effective cover.

Sampling of individual birds was randomized for the 1980 season;

because of the small sample size this led to limited observations at some of the nests. Sampling for 1981 was therefore partially randomized; individuals to be observed were picked at random from all known individuals in the group. This was done in such a way, however, that all individuals were observed on a regular basis. The daily sequence in which nests were observed was rotated so that each nest was observed at different times on different days.

I collected data between dawn and noon (EST). Each observation period lasted 2 hr with a maximum of 3 of these periods (2 hr on each of 3 nests) per day. Spot checks of anywhere from 5 min-1 hr were made at other times of the day as well. During each observation period I recorded the frequency of occurrence of each specific behavior listed above within a 5 min period. These were then added to yield a total frequency of occurrence for each behavior for each 2 hr period. A cassette tape recorder was used to record data in the field; this was then transcribed onto data sheets for further analysis.

Winter Season

As stated above, the primary question addressed at this time was whether mated birds remained together or not. I gathered information primarily at 4 feeding stations set up within known breeding areas. When possible, I also followed the jays on foot (using a pair of 7 x 35 binoculars) as they moved through the woods.

I collected data from between ½ hr after sunrise-1100 (EST) hr with spot checks occurring throughout the day, dependent upon the arrival of jays at a feeding station.

During this period I collected information on which birds fed together, which arrived and/or departed from a feeding station together, and which were observed moving through the woods together. I noted the occurrence of any of the vocalizations and/or displays listed above. Data were recorded onto a cassette tape recorder and transcribed for further analysis.

Data Analysis

Sexual differences in parental activities during the breeding season were analyzed using a 2-tailed binomial probability test (Sokal and Rohlf 1969). Year comparisons both within each sex and between the sexes were analyzed using t-tests (Sokal and Rohlf 1969). To determine how consistent each sex is from year to year, data were first converted to rates of behavior (frequency of occurrence divided by total observation hours) before performing the t-tests. To determine if behavioral shifts occurred between the sexes from year to year, I divided the female frequency by the male frequency for each category (see p. 30) before performing the t-tests. Since all tests were repeated many times, the significance level was set at $P = .02$ so as to avoid the chance of spurious significance.

The heterogeneity (or interaction) X^2 test was used to analyze sexual differences in feeding of the young (Sokal and Rohlf, 1969). This test is a method of determining whether the outcomes of all the replicates are homogeneous, that is, whether separate samples are uniform enough to be added together. They are said to be heterogeneous if they are not. The expected frequencies are based on an extrinsic hypothesis, one external to the data, where there is a prior concept of expected values. In the data to be presented below, the null hypothesis was that there is a 1:1 ratio between the sexes in feeding of the young. The expected values were therefore derived by dividing the total frequency in half.

RESULTS

Courtship

The first noticeable shift to this stage in the breeding cycle occurs in late February or early March and is characterized by (1) a general increase in activity levels as represented by the bobbing display (Fig 1); an increase in the frequency of several vocalizations, specifically the pumphandle (or bell call) and the squeaky gate (Fig 2) and the formation of small groups. (All terminology is after Hardy 1961, unless otherwise stated.) Both Hardy (1961) and Conant (1972) have described in detail the characteristics of these vocalizations and displays. I would like to emphasize the marked increase in frequency for both vocalizations and the rather sudden appearance of bobbing as indicative of early courtship in the Blue Jay. Early in the season bobbing is performed between birds of the same, as well as between those of the opposite sex, and by birds familiar to one another as well as strangers. It also appears to be elicited by a human as well as a 'blue jay' stimulus, for it occurred at my approach. At this point in the cycle, bobbing is probably more associated with states of excitement rather than actual courtship. The associated vocalizations, the pumphandle and squeaky gate, are also most likely indicative of the transitional nature of this early time and excited state of the birds, since they too, occur in a variety of contexts (from feeding to moving through the woods) between members of the same as well as opposite sex.

The small groups, composed typically of 3-6 birds, are also essentially transitional in nature (Fig 3). They consist of individuals who have spent the winter in the same area but not necessarily in association with one another. Membership changes over time, frequently with little or no further association among previous members as the season progresses. Nor is membership divided along sexual lines; since there is much shifting of individuals there is considerable variation in the sexual composition of the groups. For example, observations recorded on 20 February 1981 show 3 groups: one composed of 2 females and 1 male, one composed of 3 females, 1 male and 1 unknown bird, and one composed of 2 females and 4 males. The composition of 3 different groups 10 days later (2 March 1981) showed 3 females and 3 males, 1 female and 4 males, and one composed of 4 females.

The following specific account (10 March 1981; 07:15 (EST), is illustrative of the interactions seen among members of these early Spring groups. A single male flew in uttering the squeaky gate call. He was joined almost immediately by 2 other birds, both males, and all 3 began bobbing and giving the pumphandle call. There was a distinct lack of synchrony in the interaction; bobbing motions were irregular, sometimes one bird bobbed while the others were motionless. The overall sense was of a unit lacking in cohesion and coordination, quite erratic in its movements. The bobbing lasted 4-5 sec. The birds perched silently for about 10 sec and then repeated the bobbing four more times. They then flew out of the area. I have also observed groups to fly to other trees and repeat the above, with individuals joining and leaving at various points along the way. Again, there is an apparent lack of organization in form, content and group membership suggestive of this transitional phase and in marked contrast to similar displays occurring later in the season to be described below.

By late March it is not unusual to see, along with these early Spring groups, single birds perched high in tree tops, sitting for as long as 20 minutes without moving except for an occasional head turn. Sometimes 2 or 3 will sit this way in one tree, each on a different limb. There is no obvious interaction amongst these birds, but when one flies off (typically giving the jaay call) the others follow.

The beginning of April marks a shift to the courtship stage proper and is characterized by the inclusion of several new elements: (1) diving, (2) sidling, (3) silent sitting, (4) food transfers, and (5) food begging or solicitation (Fig 4). A description of these activities, except for diving and silent sitting, can be found in Appendix I. Neither diving nor silent sitting has been described for the Blue Jay before and are as follows: Diving typically occurred as a single bird was flying through the trees. It would suddenly and silently perform a very steep and erratic dive complete with sharp turns and lasting about 1 min. Because of the height of the dive (often above 18 m) I was not able to determine the sex of the diver. Balda and Bateman (1972) in describing a similar display for the Piñon Jay suggest that divers are unmated males pursuing unmated females. This is certainly a plausible hypothesis; the few (6) times that I was actually able to see a bird land, it landed in a tree where several birds were perched. Immediately the other birds began bobbing and giving both bell and squeaky gate calls. After about 45 sec all birds flew off with much jaay calling.

Silent sitting has also been described by Balda and Bateman (1972) as occurring between pairs of Piñon Jays during the courtship period. In my study population it involved 2 birds sitting silently next to one another on a limb for a period of about 5 min. This might have followed a food transfer or a joint foraging expedition and was often terminated by the female flying off with the monotone cry. Although quantitatively impossible to distinguish from resting behavior, I have included it because it occurred frequently (19% of the activity for each sex during observation period, 1980 season; Fig 4) and it is in marked contrast to the heightened activity typically observed during this period. Moreover, unlike resting behavior, silent sitting occurred only between pairs, suggesting, perhaps, that it is a form of contact behavior before actual nesting has begun.

As shown in Fig 4 food transfers are the dominant activity during the courtship period. By definition this activity involves male offering and female accepting of food. I have never observed a known female to offer food to another bird with the following puzzling exception: On 4 May, 1980, I observed a known pair eating at a feeding station. They were joined by a 3rd, unbanded bird which both members of the pair fed. The 3rd bird at no time solicited food, nor did it refuse any offerings. Feeding of this bird continued on and off throughout that day, with sometimes the male and sometimes the female feeding this individual. The male also fed the female throughout that day and the pair nested successfully that season. Unfortunately, I have never observed this event again.

As mentioned above, the flock displays of this later period are more structured than those observed at an earlier time. On 11 May, 1980 I observed the following interaction typical of this time in a group that consisted of at least 1 female, and 2 males. (Two unbanded birds completed the group.) The female flew to a branch of a tree with a monotone cry. On alighting she gave 1 very slow bob. Two birds (at least 1 of which was a male) flew in after her and perched on the same limb. With each bob and cry she gave, they responded with a series of silent rapid bobs. This pattern was repeated for about 3 min after which another bird (male) flew in with a bell call and began to join the silent bobbing. The female gave a rattle call at this point. One of the 5 birds moved to another limb. The female continued to slowly bob and vocalize; the others continued to bob rapidly and silently. After 6 min all flew to another tree and continued to repeat the display for two more min. Again the female's slow single bobs were in contrast to the very rapid and silent bobbing response of the other birds. After this 2 min period she flew off giving soft chirps. The others followed. This female subsequently mated with one of the males from this group. Regardless of when during courtship they occur, however, apparently only inexperienced (first-time breeders) birds participate in flock displays. I have never observed a previously paired individual to join in.

Not all the birds observed to perform these displays actually bred, however. In 1981 of the 14 pr observed during this stage only 9 pair were known to have nested although it is certainly possible that at least some of the other nested out of the study area. (None remained without nesting.) Thus despite the fact that they have participated in much of the activity described above, by the end of April many of the winter residents have dispersed (Table 2). Shortly after these winter birds left, other individuals moved in (Table 2). There are, in fact, 2 groups of breeding jays in the area: those that spend the winter and those that migrate, returning in the spring. Returning birds pair rapidly, typically within 10-14 days, and may renest with mates from previous years (Table 3). In fact, 46.6% of birds with known history repaired with the same mate. Although the group display described above does occur, it is more typical to see these birds involved in food transfers or other interactions involving only 2 birds. During the 1981 season none (n = 7 pair) of the previously paired birds participated in group bobbing displays, while all newly paired individuals (n = 8 pr) did.

Copulation/Egg Laying

This stage is characterized by nest building, copulation and egg-laying in that order.

Hardy (1961) has suggested that, prior to building a nest, Blue Jays build what he has called a 'false nest', that is, a nest that lacks the solidity of a 'true nest' and that rarely, if ever, is used by its builder for nesting. It precedes the building of a true nest and is 'symbolic in nature'. In Hardy's population all pairs that built true nests first built false ones. I did not find this to be the case, but rather, a 'rare' event. Only once in 3 seasons (n = 33 pr) did I observe a pair to build a false nest. This pair built 3 nests in 3 different locations so may not, in fact, be representative of this phenomenon. However, at 10 (out of these 33) nests I did find remnants or suggestions of previous Blue Jay nests quite near active nests (average distance between the two was 5.46 m; range 1.9 - 10 m). These may have been false nests, although it is equally possible that they were nests of previous years since jays tend to nest in the same area. In 1981 six pairs (out of 15) used trees within 3 - 4 m of where a pair had nested in previous years and where the old nest could still be seen. Given damage over time and/or lack of history on banded birds these might appear as false nests.

It has been suggested (Bendire in Bent 1964; Anderson and Shugart 1974) that Blue Jays prefer oaks and birch (Quercus and Betula spp) for nesting. As shown in Table 4 my data support this hypothesis. Of 33 nests, 27 (81.8%) were found in these species; these represent moreover, more successful (defined as number of young successfully fledged) nests (Table 4). It is, however, rather curious that oaks are one of the preferred trees since they tend to be one of the last trees to leaf out; nests, therefore, while more exposed to solar radiation are also more exposed to possible predators for longer periods.

If the following observation is typical there might be some 'trying out' of nest sites once the pair focuses in on an area and a tree: A single female flew in to a maple (Acer sp) and began to give the food begging vocalization. She was joined almost immediately by a male who fed her and then flew off. The female continued to vocalize, now crouching and wing quivering, for about 15 sec. The male was not in sight. She then silently squatted down in a crook of this tree, one near the main trunk, as though she was sitting on a nest. Almost immediately she flew off. About 15 min later both birds returned, one with a thin twig, which it placed in the crook where the female had been squatting. Again the female squatted in this crook and again both moved off very rapidly. Twenty min later they both returned, carrying twigs. Both flew to the crook and began to arrange the twigs; the male making several trips and offering material to the female who continued to organize the twigs in the crook. After 10 min all work on the nest stopped and the pair left to forage. (They bred successfully at this nest.)

Blue Jays build a fairly typical corvid nest (Bendire in Bent 1964), large, bulky, somewhat 'scruffy' in appearance. The outer platform is composed of large twigs, either picked up from the ground, or more typically, pulled from nearby trees. American Beech (_Fagus grandifolia_) appears to be a preferred species for this platform; 70% (n = 10) of pairs observed to build used it, perhaps because it is rather flexible and can be easily molded. The inner cup consists of fine twiglets, shredded grasses and, occasionally, moss.

The nest itself is typically placed either in the crotch or close to the main trunk and sometimes on the extremity of a horizontal limb-but this only at a height of above 15 m.

The time spent in nest construction was not easy to measure, partially because the birds appeared to either reduce or stop altogether any nest building activity on cold, rainy days. Data from two nests in 1980 and four in 1981 show an average construction time of five-six days.

Although both members of the pair contribute to nest building there is a clear division of chores with males doing most of the carrying and offering of this material to the female who does most of the actual building, especially of the inner lining (Table 5). It is not unusual, however, for males to do more on the outer portion of the nest. Birds work the nest as a pair, typically using soft chirps and other buzzing sounds to maintain contact when not actually at the nest together. It was rare to see a single bird at the nest during this stage in the cycle. Often this meant that while one bird, typically the female, was actually working on the nest, the other, the male, remained silently perched in a nearby tree.

It is most likely that the silently perched bird takes on the role of sentinel, or nest-watcher during this time. While there were not sufficient data to quantify in any meaningful way, the trend appears clear: the silently perched bird, regardless of its sex, was the first to respond to the approach of a possible predator, typically with alarm or jaay call, followed by an active pursuit (*n* = 9 obs). This was especially true when the intruder was a chipmunk (Tamias striatus), which, as will be brought out below, is a serious predator of Blue Jay eggs. In all cases the bird on the nest followed its mate, both in giving vocalizations and in active pursuit.

Although stealing of nesting material has been reported for both the Mexican Jay (Brown 1963b) and the Piñon Jay (Balda and Bateman 1972), I observed it only rarely in my population (3 times in 3 seasons) and in each case, the nest was unattended at the time. More typically, birds use material from abandoned nests.

Copulation was difficult to observe in the field, although I did witness it twice, with each being totally different. According to Hardy (1961), Blue Jays copulate almost exclusively in trees, typically near the nest, on a large horizontal limb. The first copulation I observed (1979) conformed to this description with the pair copulating in the nest tree itself. They had been quietly foraging, both birds uttering soft chirps. The female flew up to the nest tree and assumed the begging posture or crouch associated with food solicitation and began to utter food begging calls interspersed with soft chirps. Almost immediately the male flew up to her and mounted her. Copulation lasted 3-4 sec after which the male flew off.

The second copulation (1981) was unusual in a number of respects including that it took place, not in or near the nest tree of this pair, but in the home range of another pair who were present throughout (although neither one gave any apparent response). This copulation was preceded by the following: while the female remained perched on a limb the male circled her, hopping. This was repeated several times. As the male circled, the female occasionally opened her mouth but gave no sound. After 20 sec she flew to another tree; the male, after first bill wiping, followed her at which point copulation occurred. Unlike the previous observation, this was totally silent.

Neither sex spends a great deal of actual time at the nest during the period of egg laying. During the 1980 season (n = 10 pr, 26 hr obs) the average female time at the nest was 7 min/hr (range 4-10 min); the male average was less than 1 min/hr (range approximately 10 sec-2 min). During the 1981 season (n = 11 pr, 30 hr obs) female averages were 10 min/hr (range 3-12 min), males 2 min/hr (range 0-3 min). More typically, they forage quietly in the area or silently perch in a nearby tree as during nest building. It is common to see either one or both of the birds during this period fly to the nest, almost grazing it, in what appears to be a 'nest check'. If a bird does alight at the nest it will remain there for no longer than 5 sec before flying off again.

Incubation

As is typical of this species (Arnold in Bent 1964) incubation lasted 17-19 days in my population, although there was one instance of a female sitting for 22 days before the young hatched (Table 6).

The female is the primary incubator, although I have observed males to sit on the nest (n = 9). Whether or not a brood patch is present on the male was not ascertained.

I have never observed a non-pair member to participate in incubation duties, or engage in any activity at a nest not its own. I report the following, therefore, because of its unusual nature.

On 17 May 1981 (0700) four birds approached a nest, the two pair members (both banded) and two unbanded individuals. This approach was silent. All four alighted on the same branch of a tree about ½ m from the nest and all four remained there for approximately 3½ min. The male then flew off with one of the unknown birds, both of them giving bell calls. The female then gave one rattle call and both she and the other bird moved to another branch of this tree, where they sat, silently, for 3 min. Then the female flew to her nest and began incubating; the other bird remained where it was. After 4 min the male returned, presumably with the same unbanded bird with whom he left. Again both gave bell calls. These two flew to the tree with the unknown bird where they were now joined by the female. Again all four sat silently for 3½ min and then all flew off with both jaay and bell calls. The pair continued to incubate and subsequently brood young, but the 'strangers' were not seen again.

The female spends more and more time on the nest as this stage progresses (Fig 5). At the start of incubation she may spend only 15 min (per observation hour) sitting, whereas by the last week she is off the nest only infrequently and rarely for more than 1-2 min per observation hour. Her time off the nest is not spent in foraging, but rather in preening and stretching activities (see below). This is true regardless of whether the male is present or not. That is, even if the male (who provides the female with almost all of her food both during this and the next stage--see below) is absent, the female is more likely to stretch or preen rather than forage when she is off the nest.

The male begins feeding the female during courtship; the importance of his feeding of her is reflected in the finding that food transfers make up 75% of all courtship activities (Fig 4). Indeed, I have observed females (n = 7) to sit and wait to be fed rather than take food on their own (These observations occurred at feeding stations, where food was readily available.) By the time of incubation, the male is providing all of the female's food. In 2 seasons of observations, I never observed a female to take food on her own at this stage (1980, 10 females, 59 hr obs; 1981, 12 females, 66 hr obs), except for an occasional removal of an insect on the nest while she was sitting. Obviously the female's ability to take food on her own is limited by her role as primary incubator. 55.9% of her feeding took place while on the nest, with the remaining 44.1% occurring off the nest.

The female shows at least 2 different responses to predators during this period, one of which, has not, to my knowledge, been described for the Blue Jay before. The first is an active chase, given especially in response to small mammals such as chipmunks, which are probably the

the largest predator of Blue Jay eggs in the area) and red squirrels (Tamiasciurus hudsonicus). The chase is extremely vocal; jaay cries are given almost continuously as the female chases the predator. Frequently she is joined by the male and the two are rather relentless in their pursuit. I am not sure how effective this response is, however, since I have observed the predator to return the next day. An active chase can also be initiated by the male and apparently depends, as it did during the previous stage (egg laying), on which bird is aware of the predator first. I have observed neighboring jays (n = 14 obs) to join in a chase, but this is more typically a response to aerial rather than ground predators. In this situation the predator (typically low flying crows, Corvus brachyrhynchos, or hawks, Accipiter and Buteo spp) are chased and mobbed until they are out of the area.

The second response appears to be specific to hawks (Accipiter and Buteo spp). I have observed females (n = 14 obs) jump off the nest rather suddenly and perch in a very upright posture a few branches away in a nearby tree (never the nest tree itself) and remain there until the hawk has flown off. This response is in marked contrast to one given to humans (or other unusual activity near a nest) by either sex during this stage which typically involves sitting very still on the nest, until the danger is apparently past.

Despite suggestions to the contrary (Bent, 1964; Hardy 1961) the Blue Jays in my study population were not necessarily quiet around the nest. Indeed, as shown in Fig 6, individuals of both sexes gave several vocalizations while at the nest. Some birds, females and males alike, announced their approach to the nest with loud repeated monotone cries and/or squeaky gates. Others approached silently, but gave these same vocalizations, as well as bell calls, on reaching the nest. If, in 3 out of 4 approaches, either or both pair members gave one of these loud vocalizations, I have categorized the nest as 'noisy'. If the approach was silent and/or only soft chirps or other low contact sounds were heard at the nest, I have categorized the nest as 'quiet'. Eighteen (out of 32) or 56.25% were noisy nests; 14 or 43.75% were quiet nests. A X^2 test of independence revealed no significant difference between the two for reproductive success (number of young successfully fledged).

Nestling

This stage, of 16-20 days length (Table 6) is characterized by the care and feeding of the developing young. Feeding of the young is principally done by the male. I have also observed males to brood young; this has been described elsewhere (Laine 1982). As with male incubation, this is not a widespread phenomenon (n = 2).

As shown in Table 8, Heterogeneity X^2 analysis reveals a significant difference between the sexes in feeding of young. The insignificant heterogeneity component illustrates that there is no difference among nests in feeding of young. Because this value is insignificant the pooled component can be examined and interpreted as showing a highly significant ($P < .005$) effect; males are the primary providers of food. The fact that some of the individual X^2 are not significant is most likely due to limited sampling (under 10 hr/nest) at these nests. Nonetheless, there is a clear lack of equivalence of roles, with males favored, even for these.

This difference in feeding of young remains constant over the nestling stage; that is, males continue to be the primary feeders of the young as they develop (Table 9). Only during the first seven days post-hatch is there no significant difference between the sexes, but this result may be confounded by the fact that young simply do not require as many separate feedings as later on in development. Again, there is a highly significant difference ($P \leq .005$) between the sexes, consistent over time, in feeding of the young.

As in earlier stages, the female does not feed herself and feeds young only infrequently (1980, 11 females, 60 hr obs; 1981, 9 females, 66 hr obs). I did observe (1981) 2 females, on 2 separate occasions, taking food on their own while off the nest. The males, on both occasions, were not visible in the area. More typically, however, the female is joined by the male when she leaves the nest. It is not uncommon, however, to see during this stage, neighboring jays foraging in the same, apparently shared, areas, often at the same time (14 out of 21 nests; 66.6%). In fact, unlike Hardy's 1961 population, these jays do not appear to be territorial in the least respect. Neither pair member spends any time defending an area (either actively or with vocalization) against conspecifics. Jays that enter the home range of others tend to be ignored regardless of the stage in the breeding cycle.

As during incubation, the jays were quite vocal either approaching and/or at the nest (Fig 7). Four loud calls, the monotone cry, short cry, bell call and squeaky gate, comprised 69.04% of all vocalizations given by females and 71.43% of those given by males (1980). For 1981 the figures are 48.75% for females and 69.8% for males.

Relative Behavioral Allocations

It is especially critical in monogamous species to look at the relative contributions of each sex at each stage of the breeding cycle. How are the 'chores' or parental activities divided? The trends are summarized in Table 10. One of the questions that arises out of looking at these trends is how are the sexes able to partition their chores? To what extent does one sex do more than the other? Does the relative allocation of time (frequency of occurrence) of a particular category of behavior remain constant? If, for example, male jays feed females and young, do they "steal time" from other categories or give something up in order to fulfill their breeding obligations?

To explore these questions, the concept of a 'sampling window' was developed. That is, based on the assumption that what is important is the relative relationship among a set of behaviors and not absolute time, I organized the data (frequency of occurrence) into several behavioral categories which I assumed to be biologically reasonable. These categories are:

<u>In Area</u> for either sex, indicates the bird is in the area of the nest, either foraging, stretching or preening;

<u>Feed Female</u> for males only, as described above, the offering of food items to a female;

<u>Solicit</u> for females only, as described above, the active begging/solicitation of food from the male;

<u>Alert</u> for either sex, sitting silently in the vicinity of the nest, described above in discussion of anti-predator behavior;

<u>Nest Care</u> for either sex, composed of events assumed to be of primary importance during the stage being analyzed, for example, incubation, brooding, feeding of young. Since this

category is composed of the most biologically meaningful events during the stage in question, the data were originally analyzed without this category in order to obtain perspective on the relative distribution of other acts. Except for one situation involving one pair (who were subsequently removed from the analysis) there were no differences in the results obtained either with or without this category. I have included it to provide a fuller perspective on the relative distribution of behavioral acts.

Sex Differences

Tables 11a & 11b show the results of a comparison of the sexes in the distribution of parental behaviors for two breeding seasons. The results of a binomial probability test (2-tailed) reveal definite sex differences. These differences, however, show no consistent patterns; sometimes females are more active in a particular category, sometimes males are more active. Each sex does, however, change its strategy as the season progresses. These changes appear more pronounced in 1980, where the distribution of chores alters as the season progresses with males doing more in the categories on In Area and Alert. These trends, although not statistically significant, are repeated in 1981.

Year Differences for Each Sex and Between the Sexes

In a monogamous species like the Blue Jay, where the male is an active participant in breeding/parental activites, the changing strategies pointed out above are to be expected for both sexes over the breeding season. But how consistent is each sex in its patterns from season to season? Tables 12 and 13 summarize the results of t-test comparisons and show that not only are there differences between the sexes but between years as well. Males (Table 12) show significant differences ($P < .001$) in rates of behavior between years for all categories. But no changes occur during the Incubation Stage for either year. In all cases where a rate difference in behaviors exists, 1980 is higher than 1981. Females (Table 13), on the other hand, show significant differences in the categories of In Area ($P < .02$), Solicit ($P < .001$) and Alert ($P < .001$) but not in Nest Care. All these differences occur only during the Nestling Stage.

If behavioral rate changes exist between years for either sex it might be due to a shift in the relative behavior allocations between the sexes. T-test comparisons, summarized in Table 14, show shifts for some categories at some stages and none for others. With the exception of In Area/Nestling Stage there are overall sex differences for all categories at all stages (Tables 11a and 11b). Yet there are no clear patterns associated with these differences. For example, females and males both show behavioral differences in the category of In Area during Egg Laying; while females do not change rates between years (Table 13) males did less in 1981 (Table 12). Yet during this same stage (Egg Laying) no differences in rates of behavior (Tables 12 & 13) or relative allocations (Table 14) occurred between the sexes for the category Alert.

In general, males seem to show more yearly variation and in more categories than females which show relatively little change in rate from year to year. Males also show changes in all categories; females do not.

Fledgling

Because of the difficulty of observing the events associated with this stage (movement of the young out of the nest and through the woods) what follows is a composite based on observations of fledging (leaving the nest) of 6 broods (n = 1, 1979 season; n = 2, 1980 season; n = 3, 1981 season) as well as days 1-5 post-fledge on 3 broods (1981 season, 42 hr observations).

Young (6 out of 6 broods) leave the nest in the early morning hours, separately, but in close temporal proximity to one another, fledging to nearby bushes and trees rather than the ground. Those that do fledge to the ground usually do not survive since they are easily found by predators or lost from the unit and starve (n = 2). Young leave the nest several times, returning and leaving again and again, before the final departure. This can take up to 2 hr and since each bird is moving independently, the overall effect appears quite chaotic. Both adults remain very close by throughout giving either bell calls or the whistle. The male, especially, is extremely attentive to the whereabouts of each young, frequently flying to it with either a bell call or very soft chattering. After leaving the nest for the final time young remain silently perched, almost frozen, until an adult, typically the male, approaches. They then beg for food quite loudly until either the adult flies off and/or they are fed. Young move several times within the first hour after leaving the nest, uttering, from time to time a juvenile monotone cry, which apparently serves to maintain contact among nest mates since young attempt to flock after one of them has given this vocalization. Except for food begging, young give no other vocalizations during this time and again, appear frozen in the trees. (Adults, however, appear to have no difficulty finding and feeding silently perched young.) Occasionally (12 out of 43 observations) young would fly to an adult and beg for food, but it is more typical to observe adults going to young. After the initial confusion (lasting another 2-3 hr) the birds begin to move through the woods as a unit, or family group. These family groups fill the woods from July through September at which point the young leave the area. As mentioned above, the adults leave in some years and not in others.

Based on the data collected on days 1-5 post-fledge on 3 broods (8 young) I can make the following general statements about this stage:

The male continues to be the primary feeder of the young, averaging 9 feedings/hr as compared with the female's 2/hr.

The male also continues to feed the begging female; she does, however, take food on her own during this period.

Adults are heard to give the soft chirp and other very low contact sounds when in the immediate vicinity of the young; bell calls and the whistle are given when approaching from a distance.

According to Laskey (1958) young are dependent on adults for food for up to 2 mos after leaving the nest; while not necessarily a sign of total dependence, I have observed young (14 obs on 4 young) to beg 7 weeks post fledging. At 8 weeks a begging juvenile refused food by an adult snatched it out of the adult's mouth!

Winter Organization

Blue Jays are not present in this area every winter. During the 1979-80 season, for example, there were no birds present; during the 1980-81 season 20-25 individuals remained while only 4 were present throughout the 1981-82 winter season. Thus, as stated above, data were collected primarily during the 1980-81 winter season.

These data (on both banded and unbanded birds) showed that there was a population that fluctuated from about 20-25 individuals to a core of 16-18. The birds traveled in loose groups of 4-6 with shifting membership over the season similar to that described for early spring (see Fig. 3). Based on banding history these are primarily adult birds, although there was one instance of a juvenile which did not migrate and was seen periodically over the winter season. It always traveled alone, never as a group member, and did not stay in the area past the month of March. Of 19 birds of known sex, 9 were females and 10 were males.

Table 15 shows the fate of these individuals. Two were pairs known to have bred together for the first time in 1979 (making 1981 their 3rd season together), one pair bred together initially during 1980 and 4 were pairs that bred subsequently during 1981. Two males wintered without their mates, but these females returned in March to breed with their previous partners. The female of one pair disappeared in April; this male paired with a new mate only after her disappearance. And the one female which spent the winter without her mate (having bred successfully the season before) disappeared too, in early spring.

DISCUSSION

Monogamy, as exemplified by the Blue Jay, is a mating system showing a strong division of labor between the sexes. Each sex has the potential to benefit from the 'work' of the other, while simultaneously contributing to the overall reproductive success of the pair. An examination of parental activities suggests that the relative contribution of each sex (toward reproductive success) is fairly equivalent. By providing an overall description of the breeding behavior of the Blue Jay, the findings of this study reveal the ways in which the Blue Jay is representative of monogamous species with altricial young as well as raising questions concerning the complexities of parental care patterns for each sex. In this section I will discuss the ways in which each sex carries out its breeding obligations and how these might affect overall reproductive strategy. I will then compare some aspects of the Blue Jay's breeding behavior with other New World Jays.

Mating Strategy

This study reveals the clear trend toward continuous monogamy in the Blue Jay. Although other investigators have come to similar conclusions (Gutkin 1978; Hardy 1961; Laskey 1958) this is the first study of banded birds over more than one season. While the sample size is small, there is, nonetheless, a consistent pattern of pair members associating in winter; also pair members which have not wintered together tended to remate with each other the following spring.

There is, moreover, a marked difference in behavior during the courtship period between those birds which have been previously paired ('old') and those which have not ('new'). Only 'new' birds, apparently first-time breeders, participate in flock displays. In fact, even 'old' birds pairing with a different mate (due to the absence of a previous partner) do not participate in flock displays. In other words, only new pairs, composed of birds which have not previously bred, are formed out of these flocks. Wittenberger (1979) and Wittenberger and Tilson (1980) have argued that for a monogamous system to evolve there must be a means whereby a female can determine the availability of potential mates. A male's participation (or lack thereof) in these spring flocks might serve as a signal to a female; in fact, the bobbing display, which occurs frequently during this time (Fig 1) might be used by the male for just this purpose.

"Old" Blue Jay pairs do not participate in flock displays, they spend little time in courtship behavior and tend to begin nesting earlier than 'new' pairs. Early nesting may lead to greater reproductive success (number of young successfully fledged). Of the 21 successful nests observed during the course of this study, 12 (57%) were early. While the length of this study precludes drawing any conclusions on this point, the trend appears similar to that found for other species (see, for example, Coulson 1966, 1972; Brooke 1978): early nesting, facilitated by long-term pair bonds, leads to greater reproductive success.

Despite the presence of the original pair member mate changes are known to occur in other continuously monogamous species (Coulson 1966, 1972; Cooke et al, 1981). There is no evidence for this phenomenon in my study population; no bird of either sex was ever observed to breed with a new mate if the previous partner was present, nor were there any cases of desertion once actual nesting had begun. However, since not all breeding pairs were successful, and since at least in other species (Coulson 1972) mate changes are more likely to occur after a season of reduced breeding success, it is probable that a study of greater length would reveal similar trends in the Blue Jay.

How does each sex contribute to the effectiveness of this system? Young must be warmed (or protected from the extremes of temperature), fed, and protected from predators; a division of labor is fairly crucial during the nesting season for a monogamous species with altricial young. Exactly how these chores are divided will have effects on the survival of the young, the general well-being of the adults, and, indeed, the entire social system. (See, for example, Brown (1963a) on the Stellar's Jay, Woolfenden (1973) on the Florida Scrub Jay and Balda and Bateman (1972) on the Piñon Jay - 3 monogamouns species with very different social systems.) The Blue Jay fits into the general pattern attributed to continuously monogamous species with altricial young. The female is the primary builder of the nest, the primary incubator and the primary brooder of the young. The male is responsible for providing both the female and the young with most of their food. An examination of the interactions between the sexes in carrying out their respective breeding obligations reveals some of the complexities and constraints on the system.

The Male

Feeding of the Female

The male is the primary provider of food for the female. This provisioning begins during courtship and continues at least through the nestling stage. Lack (1940) was one of the first to point out the widespread phenomenon of 'courtship feeding' throughout many orders of birds, which he stated might continue at least through incubation. (I have chosen to refer to food transfers rather than the more commonly used term of courtship feeding because of its occurrence throughout the nesting period.) It is apparently, limited to monogamous species (Smith 1980).

In the Blue Jay, feeding of the female can start as far as 6 weeks before actual nesting begins; some mechanism is needed both to bring the pairs together and keep them together, especially for previously paired birds which do not participate in the flock displays. (I do not mean to suggest that 'new' pairs do not engage in food transfers, they do. But the behavioral mechanism for bringing the pairs together is probably different for the two groups.) Indeed, it is possible that the early food transfers facilitate the early nesting of 'old' pairs, as Perrins (1970) has suggested. It is possible, moreover, that food transfers are used by female Blue Jays to somehow assess the ability of the male to feed young; a good provider in one situation will be a good provider in another, perhaps, simply because he is already primed to do so. This idea was initially put forth by Nisbet (1973) who was the first to also point out the difficulty of defending such a theory. (Nonetheless, there must be a way for a monogamous female to assess both the availability and the quality of a potential mate.)

It is also probable that food transfers provide the female with an extra source of energy, especially during egg production which is rather costly for the female. King (1973) has estimated energy costs for egg production to be roughly 13-16% above the daily requirement for small passerines and slightly more for larger species such as the Blue Jay (Nice 1943). If the male is able to obtain enough food for both, as he is apparently able to do in this species, it seems reasonable for the female to conserve her energy for reproduction. Moreover, this 'frees' the female to devote her energy toward incubation and subsequent brooding of the young.

Feeding of young

Unlike Hardy (1961) I found that males fed young far more than females did throughout the nesting period. In Hardy's population, females fed young more for the first three days after hatching, by day 4 the males fed more, and by day 17 the contribution was about equal. Although the quantitative details of our results do not agree, they both suggest a division of this chore between the sexes. In my study population the fact that males provide so much of the food for the young coupled with their extensive feeding of the female indicates that they are responsible for the bulk of their offsprings' nutritional requirements.

Incubation and brooding

Although it is rare amongst corvids for males to incubate and/or brood young (Goodwin 1976) cases have been reported (Goodwin 1976) of males standing over eggs for brief periods. And, as Skutch (1957) has stated, the heat generated in this fashion will keep eggs warm for a brief time. It is generally assumed that males do not incubate because they lack brood patches; indeed, brood patches are not thought to be present at all amongst male passerines (Bailey 1952). Yet they have been found by Mewalt (1952) on a number of Clark

Nutcrackers (Nucifraga columbiana) and by Amadon and Eckelberry (1955) on a male Magpie Jay (Calocitta formosa). I was not able to confirm the presence (or absence) of a brood patch on males in my study population of Blue Jays but I did find male incubation and brooding (Laine 1981). My study area in the Hudson River Valley is one where late snowfalls are not that unusual (1979 season - last snow 9 May) and where spring tends to be generally cold and wet. Under these conditions it is likely that male participation may be necessary to ensure the survival of the young. Other instances of male incubation and/or brooding amongst the jays have all been from northern populations where nesting tends to be early and often amidst snow and ice: Thayer (1901) reported male incubation in the Blue Jay nesting in Minnesota, Gabrielsen and Lincoln (in Goodwin 1976) reported male incubation in an Alaskan population of the Steller's Jay.

Changes within the breeding season

As the breeding season progresses, the distribution of chores changes significantly for each sex. This certainly makes intuitive biological sense, since the demands placed on each sex change with the breeding season, as, for example, eggs are laid and young are hatched, requiring feeding and protection, etc. Males increase their participation in the categories of In Area and Alert once Incubation has begun. As the female spends more time on the nest, the male must be available both to take on the role of predator protector and forage for himself and the sitting female. Emlen and Oring (1977) have suggested that a male should be responsible for a major portion of parental care only when this increases his individual fitness. This is possible when energy costs are not severe and future 'health' of the female is of value to the male. This is apparently the case for the continuously monogamous Blue Jay. The male, in order to safeguard his reproductive expenditure, must be able to respond to the changing needs of the nest and the female as the season progresses. However, since significant differences in the above-mentioned categories were found for the 1980 season only (although the trend was repeated in 1981), the pattern of male changes over the breeding season may reflect the importance of variability rather than constancy of response. For the male what may be important is that he be able to adjust his 'work load' in any one category and shift it to another should the demands of the female and the nest so require. In that way he may be able to better ensure the survival of the female and the young.

Differences between years

The data show a clear division of labor; each sex is primarily responsible for specific tasks, all of which, taken as a whole, aid in nest success. Each sex, however, fulfills its breeding obligations in a different manner. Male behavioral rates show considerable yearly variation with little, if any, associated patterns. The only consistency is in the lack of significant change in rates between years during Incubation for any category. While during other stages males tended to do less in 1981 (see Table 12), behavioral rates in all categories showed no changes between years for this stage. Since females also show no significant differences in behavioral rates for any category during Incubation, it is possible that males are responding to females (as primary incubators) as they do during the season. Alternatively, both sexes may be responding to some unknown constraint imposed on them by the requirements of incubation, one that calls for behavioral consistency rather than flexibility. That all rates were higher in 1980 than 1981 is puzzling; one obvious difference between the 1980 and 1981 seasons in my study area was the infestation of the gypsy moth in 1981. This infestation was severe enough to completely defoliate the woods, creating, in all probability, an extremely stressful environment. Since environmental factors were beyond the scope of this study, no data currently exist that might help explain environmental influences on behavioral strategy. However, several other studies (Wittenberger 1982; Pierotti 1981; Maxson and Oring 1980) have found that differences in parental care patterns for both sexes between years could be explained by changes in food abundance and/or weather conditions.

The Female

Nest Building

Although the female is the primary nest builder, the male probably contributes as much material; he simply offers it to the female rather than place it in position himself. The fact that both sexes contribute to nest building not only helps complete the nest more rapidly but may reinforce the pair bond. Given that the female is the primary user of the nest (as primary incubator and brooder) it is appropriate that she is the one who does most of the actual building, especially of the cup and the inner lining. This, moreover, frees the male to forage (both for the female and for himself) as well as take on the role of predator protector (nest watcher) at this time.

Nest protection

The Blue Jay shows some flexibility in designating which bird is to carry out this task. Apparently the major responsibility of carrying out this job is alternated, dependent on what other major biological events are taking place at the time as well as, obviously, which bird is present. While early in the season (during nest building, for example) it is the male who is primarily on the alert for possible predators, after nesting has begun the task is rotated. While in other areas of parental responsibility there is a clear delineation between the sexes, nest protection is shared. Since both birds are present at the nest (or very nearby) throughout the nesting period, this may be an effective means of ensuring protection for the young. While the data from this study are limited, predation appears to be a major cause of nest failure in this population. Eggs and newly hatched young are especially vulnerable. A system that allows for some flexibility between the sexes might mean that more young survive.

Changes within the breeding season

For the female (as for the male) the distribution of parental behaviors observed in each category changed significantly among the stages of the breeding cycle. Apparently early in the season the female is more active than the male in all categories (Tables 11a & 11b), while later on she shifts all of her attentions to the category of Nest Care. For the monogamous Blue Jay female these shifts were a result (in part, at any rate) in the changes of incubation and brooding of the female. As time spent on the nest increased, the female was simply less available to participate in the other categories. Hrdy (1981) has suggested that it is the behavior of the female that determines how much care the male must provide. "Although many ecological factors channel males and females among monogamous species toward greater interdependence and cooperation, we should not ignore the ways in which monogamy is imposed on males by females...Monogamy is maintained by ...female reproductive strategies which make male assistance imperative." Female Blue Jays are essentially unavailable to feed young or forage for themselves; if they and the young are to survive males must provide food. As suggested above, it is obviously an advantage to the male to have them both survive. While this study did not directly test this idea, the overall patterns of biparental care were extremely consistent both from nest to nest as well as from season to season.

Differences between years

While male rates show variability from year to year, females are fairly consistent, with the few significant changes occurring only during the Nestling stage (and no changes occurring at any stage in the category of Nest Care). Since two out of the three significant differences show 1981 to be the year with higher rates, it is tempting to suggest that this was due to the defoliation caused by the gypsy moths, especially since one of the categories affected is one concerned with anti-predator behavior (Alert). However, I must emphasize the speculative nature of this argument; the data do not show clear year differences in reproductive success (which one might expect if nests were more visible to predators). Moreover, the 1981 defoliation does not explain why, for the category of In Area

(Nestling stage) 1980 was the year with higher rates for both sexes.

Relative behavioral allocations between the sexes

Parental care patterns in the Blue Jay are both flexible and constrained. This is possible because each sex performs different chores at different times; the division of labor is one which, while organizing parental activities differently for each sex, ultimately contributes to reproductive success. That there are behavioral differences between the sexes in parental activities is certainly not unusual. What is unusual, especially for a monogamous species with altricial young, is the degree to which male priorities appear to be directed toward the female, while those of the female are directed toward the nest and the young. And even this, at first viewing, appears to be according to Trivers' (1972) model for a monogamous system; the female's investment appears greater than the male's throughout the season. But there is a strict constraint placed on the male; he is the primary provider of food for the young and the female.

The question of why the male is allotted the role of 'family feeder' to the degree that he is is a puzzling one. One explanation may lie in the area of anti-predator behavior. Although this study did not directly address this issue, predation appears to be a major cause of nest failure, especially early in the season during Egg Laying, when neither parent is in attendance. As the female increases her time at the nest, predation risks may drop. But she is now essentially unavailable to forage for herself or provide food for the young. As suggested above, the male, in order to 'protect his investment' must now provide food for the young and the female.

The male role in provisioning both the young and the female with food argues against Trivers' (1972) suggestion that male investment in a monogamous species is less than that of the female. The male Blue Jay has few constraints placed upon him and is potentially in a position to reduce his energy output, or direct it elsewhere. Yet the findings of this study suggest that his contribution is equal to that of the female and are in agreement with those of Burger (1981) who argued that male investment may, in fact, be greater than the female's in a monogamous bird. This view is further supported by the frequent lack of difference between the sexes in relative behavioral allocations (Table 14).

Since all female relative allocations are higher in 1981, it is, once again, plausible to suggest a response to the environment. That environmental variables will change the contribution of each sex has been shown for at least one other monogamous species, the Western Gull (Pierotti 1981). It may be to the female's advantage to be able to adjust her behavior in response to environmental changes. Were she to adopt a fixed strategy, which would, therefore, represent the best strategy under 'average' conditions, she might be at an extreme disadvantage when conditions were not 'average'. Not only might her nest success in the non-average year be poor, but future survivorship might also be affected. Blue Jays are long lived, 8-10 years on the average (Middleton 1974); one brood represents, therefore, only a portion of a female's total reproductive effort. A female may, in the long run, be more productive by remaining somewhat flexible.

Thus it would seem that males, in the long run, maximize fitness by adjusting their behavior to females. Females, in turn, adjust their behavior to the environment.

Unfortunately, aside from the few studies already cited, no relevant data are currently available for evaluating the division of labor between the sexes in monogamous birds. Thus while the patterns described for the Blue Jay suggest a system with differing but perhaps equally important allocations between the sexes, it is important to study other species to understand how constant this strategy is for monogamous birds in general.

Comparisons with other jays

Despite differences in overall social systems the Blue Jay shares several features of breeding behavior with the other monogamous New World Jays. These include the importance of food transfers, and a division of labor with the female doing most of the incubation and brooding and the male providing food for the female and sometimes, for the young as well (Goodwin 1976).

Food transfers appear early in the season and are an important source of energy for the female in all the monogamous New World Jays whose breeding behavior is known. They are the earliest courtship motivated behavior to be observed in the Piñon Jay, occurring (as with the Blue Jay), typically only between previously paired birds (Balda and Bateman 1971). In fact, Brown (1963b) concluded that the pair bond in the Mexican Jay was weak due to a reduced number of food transfers. As with the Blue Jay, food transfers provide the bulk of the female Green Jay's diet during incubation (Alvarez 1975); Balda and Bateman (1972) found that more than 80% of the female Piñon Jay's food was provided by the male during this same period.

Another similarity is found in the area of nest building. Both sexes contribute about equally in the Blue Jay; this pattern is found in the Piñon Jay (Balda and Bateman 1972), the Green Jay (Alvarez 1975), and the Florida Scrub Jay (Woolfenden 1973). Amongst New World Jays the exception is found in the Mexican Jay (Brown 1963b) where the female probably contributes more to nest building than the male. The Mexican Jay is not considered to be monogamous (Brown 1963b); participation of the sexes in each chore is apt to reflect this difference.

It is typical amongst New World Jays, taken as a whole, for females to feed young less than males (Goodwin 1976). The Blue Jay certainly fits this pattern. Woolfenden (1973, 1975) has suggested, that for the Florida Scrub Jay at least, the differences between the sexes in feeding of young might be due to the female's role in nest protection at this time. There is some indication that the female Blue Jay takes on a similar 'job' although, as discussed above, there appears to be a bit more flexibility in the Blue Jay.

In this regard, the Blue Jay seems to differ from some of the other New World Jays where roles for this behavior are more clearly defined. In the Piñon Jay, for example, sentries are present around the periphery of the creche (where nestlings aggregate). While these birds may be parents of young in the creche, they may also be non-breeding yearlings (Balda and Bateman 1971; Balda and Balda 1978). Alvarez (1975) has described 'guards' in the Green Jay. These too, are non-breeding individuals, and the first to respond to a possible predator at the nest. That these highly social species show a degree of organization not possible in the Blue Jay is not surprising. What is interesting is how, in an otherwise fairly structured system, Blue Jays rotate the role of predator protector.

As mentioned above, 16 of the 24 species of New World Jays are communal breeders while one is colonial. In 1974 Brown postulated several reasons for the evolution of sociality amongst the New World Jays and suggested that the Blue Jay held an intermediate position in the continuum from communal to colonial species.

According to Brown (1974, 1978) communal breeding is characterized by the regular retention and delayed dispersal of young, delayed reproduction and nonmigratory habits. The findings of this study lend substantive support to his work. Only once did I observe a hatch-year bird to stay through the winter; this individual did not, to my knowledge, remain to breed. Thus it would appear that the general strategy is for young to leave the area at the end of the summer. (That they may return after a few years time to breed is possible but beyond the scope of this study.)

Moreover, migration of adult birds appears to be a regular occurrence in this population, although the patterns are irregular. Known individuals pass through both in the spring and the fall, others remain throughout the winter. The lack of consistency from year to year (a bird might leave for the winter in one year and not the next) suggests an environmental factor such as food availability, may regulate individual patterns. Indeed, permanent residency apparently does occur further south, in South Carolina, (Gutkin 1978) where food supplies might be more predictable and/or more abundant.

On the other hand, there is at least one aspect of this pop -

ulation's behavior that suggests, perhaps, a move towards coloniality. The Blue Jays of my study population are non-territorial. They do not defend an area; birds of either sex spend no time patrolling and/or singing (given the demands of parental activities described above, there would seem to be little time for such behaviors). Non-pair members (typically neighbors) are tolerated even in the nest tree. Indeed, I have observed neighbors to forage with one another in what appears to be an overlapping home range throughout the nesting period. The lack of territorial behavior does not, by itself, make the Blue Jay a colonial species. It does reveal another complexity in this species and points to the need for futher long term, in-depth studies.

Appendix I. Descriptions of Displays and Vocalizations

Displays (after Hardy 1961; Conant 1972)

Bobbing At the beginning of this display, the bird is in a neutral body position. Bobbing begins as the bird starts to crouch and lower its head; the bird next returns through the original starting position and then standing on its toes, raises its head above the body. The display gives the appearance of a curtsey. The event is concluded with a return to a neutral position.

Food Transfer ('Courtship feeding' in Hardy 1961 and Conant 1972). The offering and acceptance of food from one adult jay to another; typically the male offers and the female accepts. At the moment of exchange both birds may give soft chirps and/or the food solicitation vocalization.

Food Beg ('Courtship feeding solicitation' in Conant 1972) Characteristically a female display occurring when the female solicits food. She crouches slightly and flutters her partially fanned wings and tail. The display is typically accompanied by the food solicitation call.

Sidling A display occurring between mated pairs frequently on an exposed limb, during Courtship. The birds sit parallel to each other on this limb, about 1 m apart, either facing the same or opposite directions. The display involves one bird slowly approaching the other giving soft chirps as it does so.

Vocalizations (all physical characteristics after Conant 1972)

Food Solicitation (Begging keu in Conant 1972): Characteristically accompanies food transfers. The call is inflected downward in the first 100 ms 0.10 kHz and then remains at that frequency for the rest of that call. Its duration is approximately 158 ms.

Soft Chirp (Soft keu in Conant 1972): This is the contact note between members of a pair or family groups when birds are relatively close (less than 10 m) to one another. This is a simple short call with no inflection of the fundamental frequency. Frequency ranges from 0.60 - 2.00 kHz; its average length is 193 ms.

Short Cry (Loud keu in Conant 1972): Most often heard between pair members which are more than 10 m apart. The frequency of this call varies from 1.20 - 1.50 kHz: its average length is 486 ms.

Monotone Cry (Flock contact in Conant 1972): This call is frequently associated with bobbing especially during the non-breeding season. There are always two harmonics, either of which may be dominant. The fundamental frequency is rarely more intense than any of the harmonics; it is warbled over a range of 0.50 - 1.50 kHz above and below the initial value throughout the duration of the call. The duration averages 432 ms.

Rattle (rolling click in Conant 1972): Always accompanied by the bobbing display, this call is apparently female-exclusive. It is composed of a series of clicks. The frequency of this sound ranges from 1.70 - 2.00 kHz.

Bell (Bell Song in Conant 1972; Pumphandle in Hardy 1961): Usually 2 clear notes, the first of which has a frequency of 2.30 - 2.90 kHz with an average duration of 267 ms. The second begins 175 - 225 ms after the first at a frequency of 1.50 - 1.70 kHz. Its duration averages 113 ms. This call may be accompanied by Bobbing.

Squeaky Gate (Wheedle Bell in COnant 1972); Although similar in sound to the Bell Call, the Squeaky Gate has a very different structure. The fundamental frequency ranges from 3.30 - 3.80 kHz with an average duration of 341 ms.

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Table 1. Contribution to Data Analysis of Banded Birds by Year and Stage

Stage	Courtship	Egg Laying	Incubation	Nestling	Fledgling
Year					
1979	? (mostly unbanded)	4 pr	5 pr	3 pr	1 yg
		(5 pr overall)			
1980	17 birds (9 females; 8 males)	12 pr	13 pr	11 pr	5 yg
		(13 pr overall)			
1981	19 birds (10 females; 9 males)	13 pr	14 pr	10 pr	8 yg
		(15 pr overall)			

Table 2. Seasonal Changes in the Cold Spring Blue Jay Population. Numbers refer to those birds which remained in the area only, not to those passing through.

Total #			
Year	Winter Only	*Spring Only	*Year Round
1980	0	26	3
1981	27	30	6

*breeding birds only

Table 3. History of Returning Spring Birds.

Year	Total # Birds	Same Mate	New Mate	Unknown
1980	26	6	0	20
1981	30	14	2	14

Table 4. Blue Jay Preference: Nest Tree (1979-1981 Seasons).

Tree Species	N (of total)	% (of total)	Successful*		Unsuccessful	
			N	%	N	%
Oak (*Quercus*)	17	51.5	11	64.7	6	35.3
Birch (*Betula*)	10	30.3	8	80.	2	20.
Other**	6	18.1	2	33.3	4	66.6
	33		21		12	

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* Defined as # of young successfully fledged

** Included are: maple (*Acer*), beech (*Fagus*), Hemlock (*Tsuga*), cherry (*Prunus*) and Mt. Laurel (*Kalmia*)

Table 5. Division of Chores: Nest Building.
a. 1980 Season (n = 4 pr)
b. 1981 Season (n = 7 pr)

a: 1980 season	FEMALE		MALE	
	N	% (of total)	N	% (of total)
carry nest material	80	34.6	151	65.4
offer to another bird	11	14.4	65	85.6
build nest	233	65.4	123	34.6
perch silently	35	33.6	69	66.4

b: 1981 season	FEMALE		MALE	
	N	% (of total)	N	% (of total)
carry nest material	129	31.1	285	68.9
offer to another bird	9	8.7	95	91.3
build nest	313	60.3	206	39.7
perch silently	54	40.6	79	59.4

Table 6. Length of Nesting Period and Fate of Young for Successful Blue Jay Nests.

Nest*	Incubation (days)	Brooding (days)	# Nestlings	# Fledglings
1/79	18	19	5	5
2/79	17	18	4	4
3/79	?	16	4	3
2/80	17	17	4	4
3/80	18	20	5	4
5/80	16	18	3	3
6/80	?	18	3	3
7/80	17	17	3	3
9/80	16	17	4	4
10/80	18	18	5	4
11/80	17	18	5	4
12/80	17	16	5	5
13/80	?	?	5	4
5/81	22	17	3	3
8/81	19	18	4	3
10/81	17	19	5	?
11/81	18	20	3	3
12/81	19	19	4	2
13/81	17	17	3	3
14/81	?	19	2	1
15/81	?	16	3	3
$\bar{x}$	19.95	17.85	3.9	3.5

*numerical prefix represents nest number, suffix represents season

Table 7. Fate of 'Noisy' vs 'Quiet' Nests.

			*Successful		Unsuccessful	
	N	%	N	%	N	%
Noisy	18	56.25	12	66.66	6	33.33
Quiet	14	43.75	9	64.28	5	35.71

* Defined as number of young successfully fledged

Table 8. Sexual Differences in Feeding of Young Over Nests As Measured by Heterogeneity X^2 (1980 Season).

Nest	Female	Male	n	df	X^2
	freq. of feeding young				
2	1	10	11	1	7.36
3	2	13	15	1	8.06
5	2	3	5	1	.2
6	2	12	14	1	7.14
7	1	12	13	1	9.31
8	0	3	3	1	3.0
9	4	8	12	1	1.33
10	6	22	28	1	9.14
11	4	11	15	1	3.26
12	9	17	26	1	2.46
			Total	11	52.92 $P < .005$
			Pooled	1	46.00 $P < .005$
			Heterogeneity	10	6.92 ns

Table 9. Sexual Differences in Feeding of Young Over Time as Measured by Heterogeneity X^2.

Days post-hatch	Female	Male	n	df	X^2
	freq. of feeding				
1 - 7	7	16	23	1	3.52
8 - 14	8	25	33	1	8.76
15 - 20	28	81	109	1	25.77
			Total	3	38.05 $P \leq .005$
			Pooled	1	37.82 $P \leq .005$
			Heterogeneity	2	.23 ns

Table 10. Blue Jay Parental Activities: A Summary of the Main Features.

Stage	Female	Male
Nest Building	Builds	Watches
Incubation	Sits	Watches Feeds female
Nestling	Broods Watches	Feeds Young and Female
Fledgling	?	Feeds Young

Table 11a. Comparison of the Sexes in the Distribution of Parental Behaviors for the 1980 Season, n = 10 pr.

Category	Stage	Outcome	Binomial Probability (2-tailed)
In Area	Egg Laying	Female > Male	P = .02
	Incubation	Male > Female	P = .002
	Nestling	ns	
Alert	Egg Laying	ns	
	Incubation	Male > Female	P = .02
	Nestling	Male > Female	P = .002
Nest Care	Egg Laying	Female > Male	P = .02
	Incubation	Female > Male	P = .0005
	Nestling	Female > Male	P = .002

Table 11b. Comparison of the Sexes in the Distribution of Parental Behaviors for the 1981 Season; n = 11 pr Egg Laying, 12 pr Incubation, 9 pr Nestling.

Category	Stage	Outcome	Binomial Probability (2-tailed)
In Area	Egg Laying	Female > Male	P = .001
	Incubation	ns	
	Nestling	ns	
Alert	Egg Laying	Female > Male	P = .001
	Incubation	ns	
	Nestling	ns	
Nest Care	Egg Laying	Female > Male	P = .001
	Incubation	Female > Male	P = .002
	Nestling	ns	

Table 12. Comparison of Behavioral Rates for Male Blue Jays for 1980 - 1981.

Category	Stage	Year Differences?		
In Area	Egg Laying	yes	1980 > 1981	$P < .001$
	Incubation	no		
	Nestling	yes	1980 > 1981	$P < .001$
Feed Female	Egg Laying	yes	1980 > 1981	$P < .001$
	Incubation	no		
	Nestling	yes	1980 > 1981	$P < .001$
Alert	Egg Laying	no		
	Incubation	no		
	Nestling	yes	1980 > 1981	$P < .001$
Nest Care	Egg Laying	yes	1980 > 1981	$P < .001$
	Incubation	no		
	Nestling	yes	1980 > 1981	$P < .02$

* The significance levels are according to t-test comparisons.

Table 13. Comparison of Behavioral Rates for Female Blue Jays for 1980 - 1981.

Category	Stage	Year Differences?		
In Area	Egg Laying	No		
	Incubation	No		
	Nestling	Yes	$1980 > 1981$	$P < .02$
Solicit	Egg Laying	No		
	Incubation	No		
	Nestling	Yes	$1981 > 1980$	$P < .001$
Alert	Egg Laying	No		
	Incubation	No		
	Nestling	Yes	$1981 > 1980$	$P < .001$
Nest Care	Egg Laying	No		
	Incubation	No		
	Nestling	No		

* The significance levels are according to t-test comparisons.

Table 14. Relative Behavioral Allocations Between the Sexes.

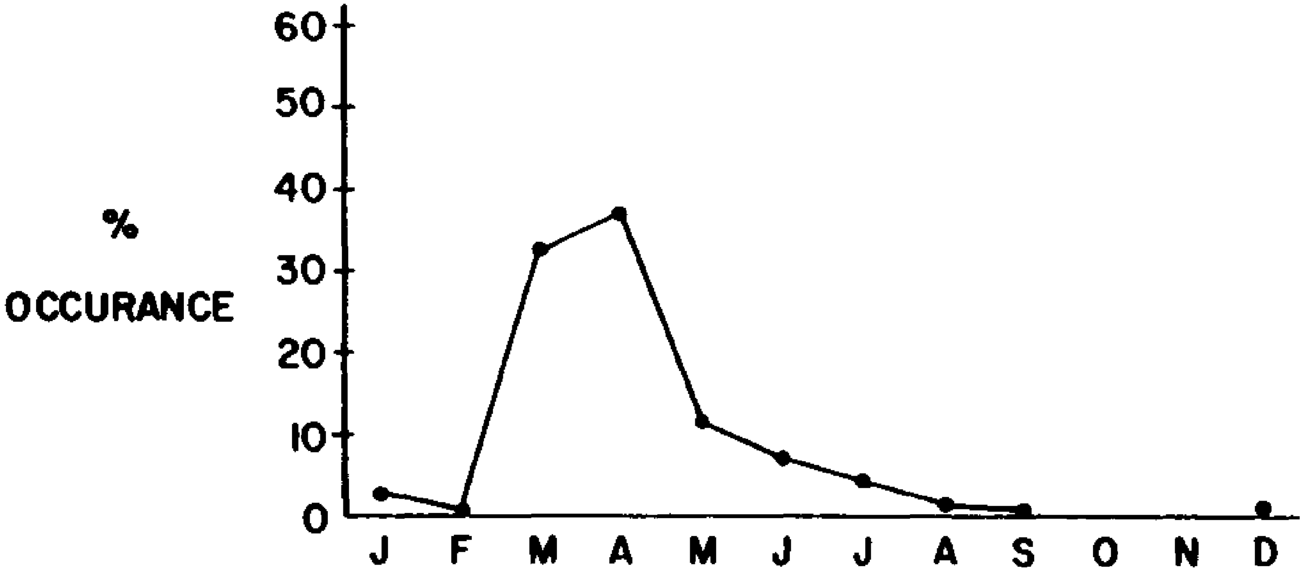
Category	Stage	Sex with Greater Relative Behavior Allocation	Year	
In Area	Egg Laying	Female	1981	*$P < .001$
	Incubation	Male	1981	$P < .001$
	Nestling	No Difference		
Alert	Egg Laying	No Difference		
	Incubation	No Difference		
	Nestling	Female	1981	$P < .001$
Nest Care	Egg Laying	Female	1981	$P < .001$
	Incubation	No Difference		
	Nestling	No Difference		

* The significance levels are according to t-test comparisons.

Table 15. Fate of Wintering Birds of Known Sex (1980 - 1981 Season).

	Remained with mate	Mates returned in Spring	New mate	Fate unknown
Females	7			2
Males		2	1	

Figure 1. Annual variation in bobbing in a population of Blue Jays for 1981.

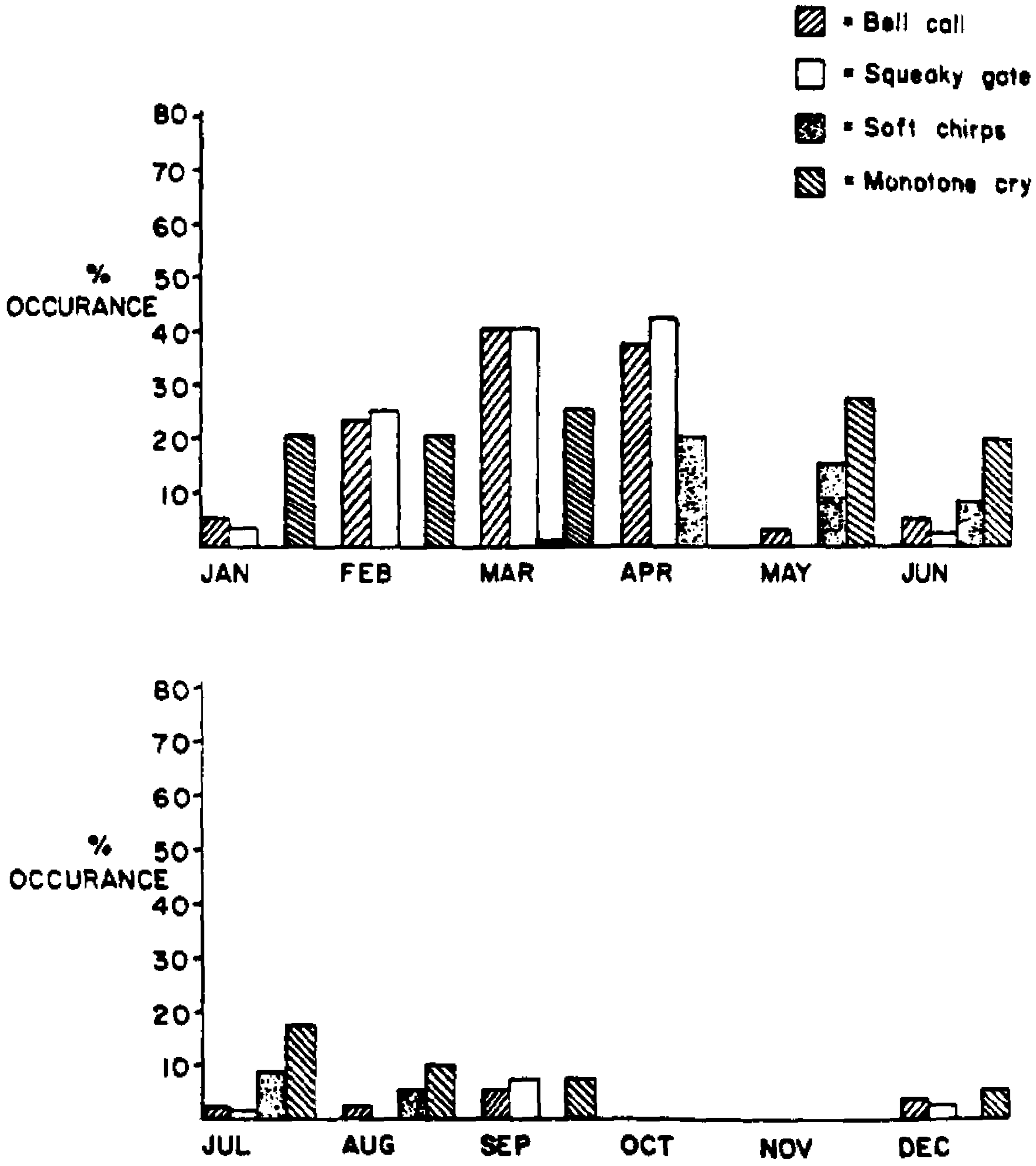


Total number of observation periods for each month:

January - 38 hours
February - 42 hours
March - 60 hours
April - 82 hours
May - 90 hours

June - 88 hours
July - 72 hours
August - 12 hours
September - 16 hours
December - 30 hours

Figure 2. Annual variation in 4 vocalizations in a population of Blue Jays for 1981.



Total number of observation periods for each month:

January	- 38 hours	June	- 88 hours
February	- 42 hours	July	- 72 hours
March	- 60 hours	August	- 12 hours
April	- 82 hours	September	- 16 hours
May	- 90 hours	December	- 30 hours

Figure 3. Compositional changes in Blue Jay spring groups (criteria for group membership: consistent movement with other bird(s) for observation period including arriving and/or departing from feeding area together, feeding together, moving through woods together).

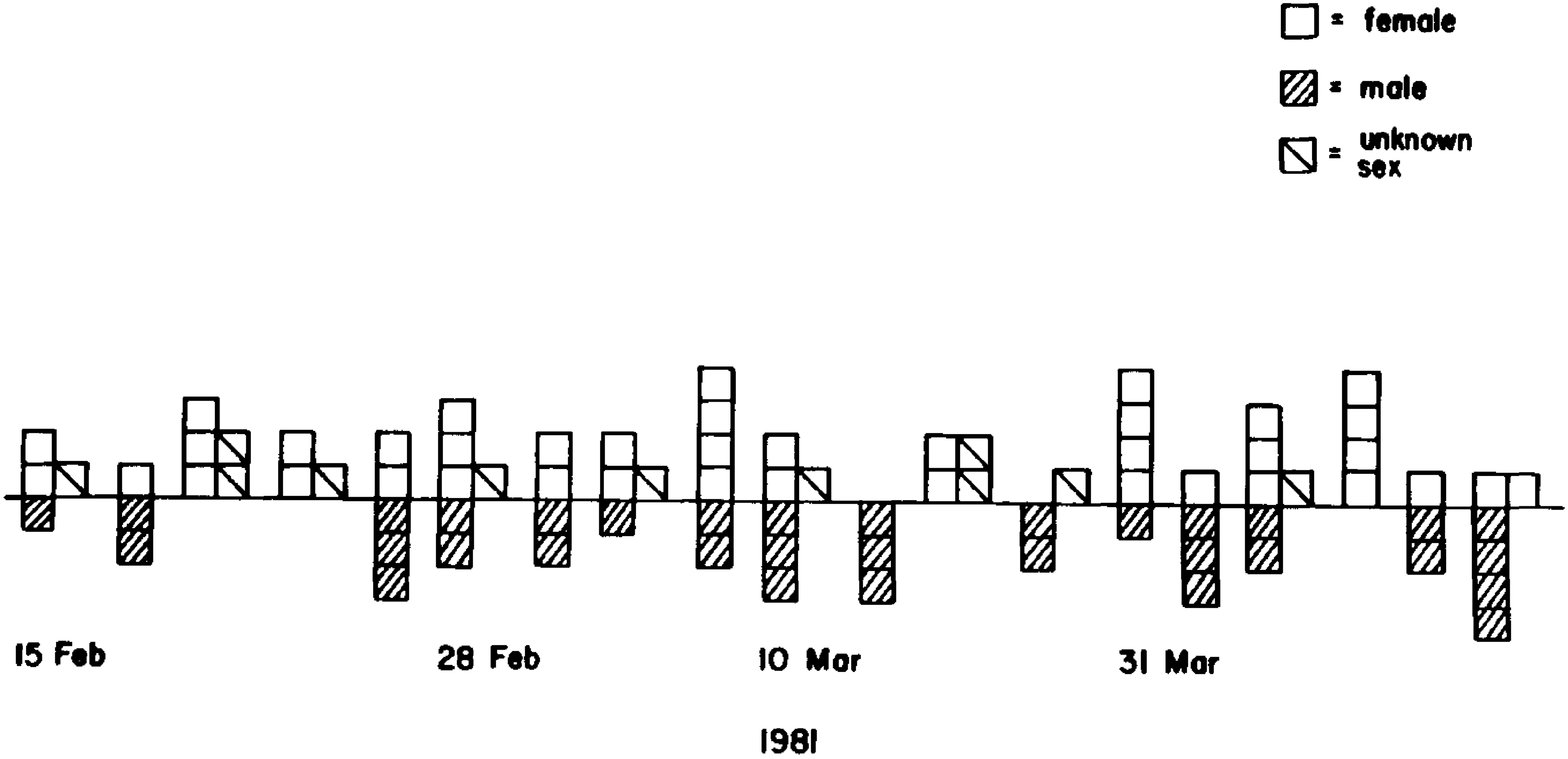
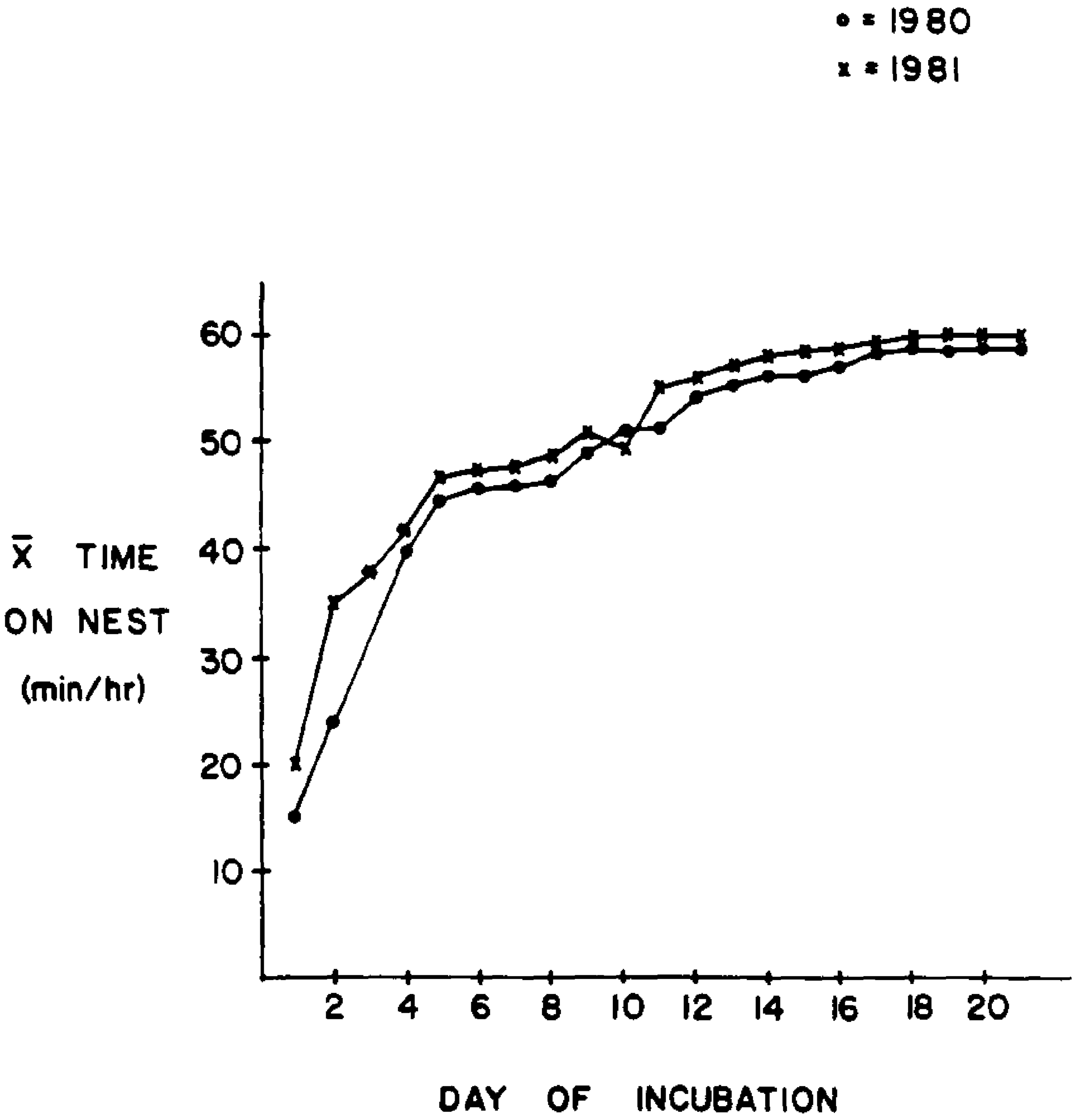

□ = female
▨ = male
⧄ = unknown sex
15 Feb
28 Feb
10 Mar
31 Mar
1981

Figure 4. Blue Jay courtship activities.

1980 : n = 14 pairs, 64 hours observation

Figure 5. Female incubation patterns.



1980 : n = 8 females, 59 hours observation

1981 : n = 10 females, 66 hours observation

Figure 6. Vocalizations given at or approaching the nest during incubation.

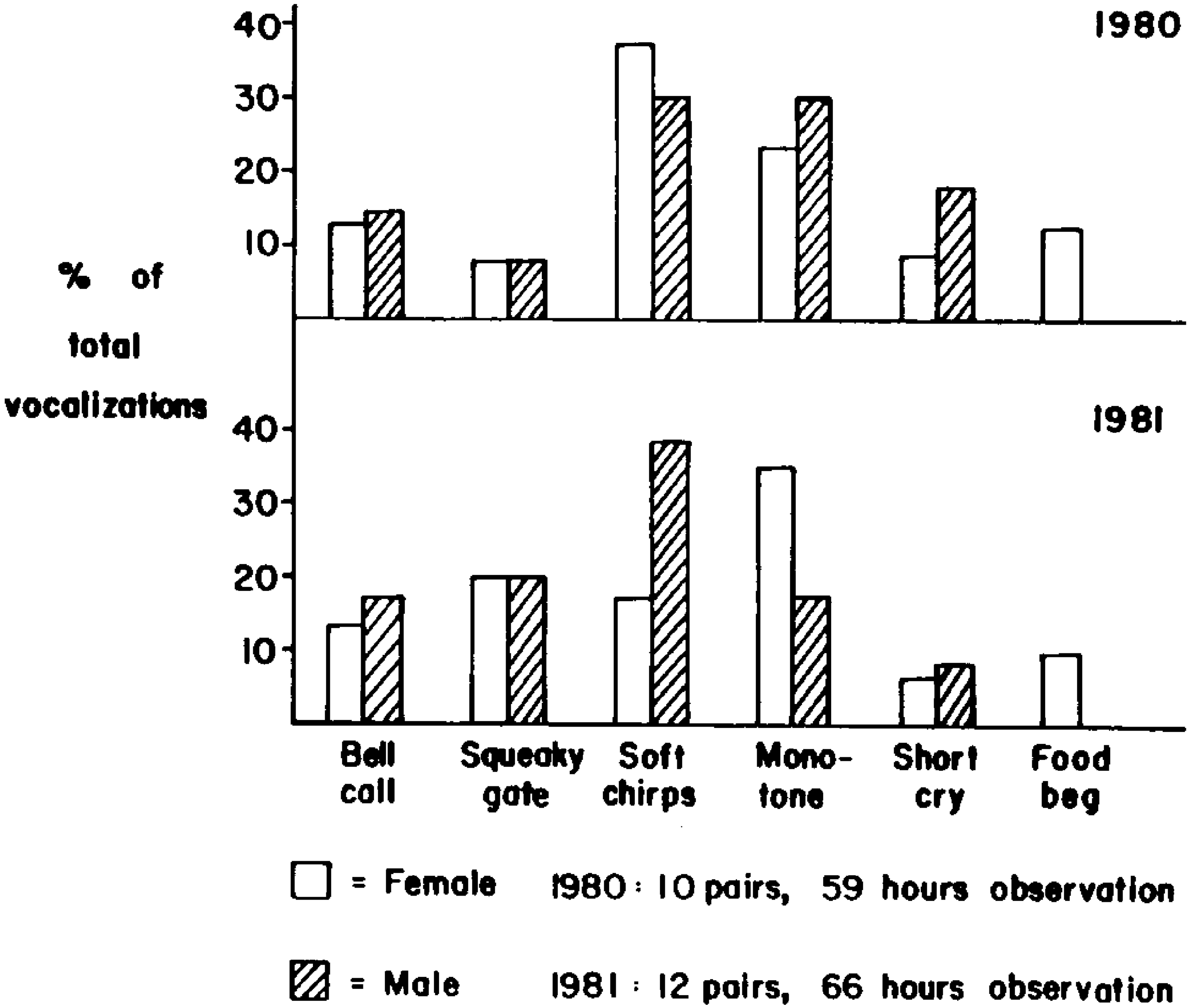
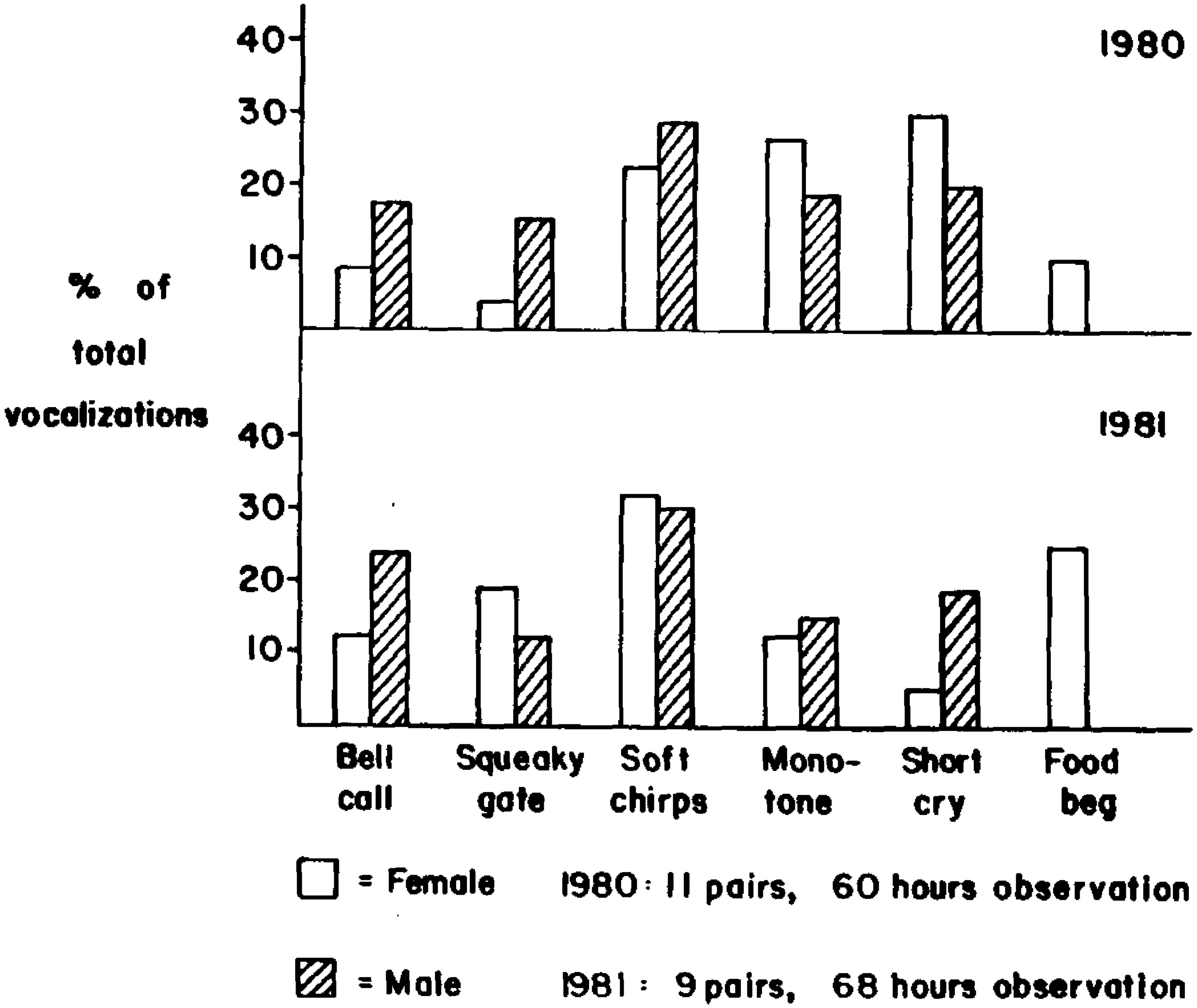

% of total vocalizations
1980
1981
40
30
20
10
Bell call
Squeaky gate
Soft chirps
Mono-tone
Short cry
Food beg
☐ = Female
▨ = Male
1980 : 10 pairs, 59 hours observation
1981 : 12 pairs, 66 hours observation

Figure 7. Vocalizations given at or approaching the nest during nestling.


1980
1981
% of total vocalizations
40
30
20
10
Bell call
Squeaky gate
Soft chirps
Mono-tone
Short cry
Food beg
□ = Female
▨ = Male
1980 : 11 pairs, 60 hours observation
1981 : 9 pairs, 68 hours observation