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INTRA- AND EXTRA-PAIR BEHAVIOR
AND PRODUCTIVITY
IN CAPTIVE ZEBRA FINCH COLONIES

by
JOANNE OLIVA-PURDY

A dissertation submitted to the
Graduate Faculty in Psychology in
partial fulfillment of the
requirements for the degree of
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29/1/96
Date

Cheyl F. Harding
Chair of Examining Committee

1-29-96
Date

Kary Deary
Executive Officer

Robert Rockwell

Carol A. Simon

Howard Topoff

Supervisory Committee

The City University of New York

Abstract

INTRA- AND EXTRA-PAIR BEHAVIOR
AND PRODUCTIVITY IN CAPTIVE ZEBRA FINCH COLONIES

by

Joanne Oliva-Purdy

Adviser: Professor Cheryl F. Harding

Observations were conducted on three colonies of 16 (8 male, 8 female) mature but sexually naive zebra finches (*Taenopygia guttata*) for 13 weeks and the full range of their behavior recorded. During this time, most birds completed at least one breeding cycle. Of the 44 birds which formed pair bonds, 43% of females and 38% of males did not form exclusive male-female pairs, but instead were members of ten alternate nesting groups of various types, some with multiple pair bonds. Birds in groups bonded at the same time as those in pairs; however, females from groups took longer to start their first clutches and if their young died, offspring of groups died earlier than those of pairs. In productive groups, there was no intra-sexual competition among those occupying the same nest.

During the first breeding cycle of all birds which completed incubation (n=32) and an equivalent period for all other subjects (n=6), pairs and groups did not differ in courtship or copulation behavior. Males directed courtship and copulation behavior towards 1) females during their fertile periods, 2) females outside their fertile periods,

3) other males. Males who were bonded to females (n=20) directed 21% of their courtship bouts to other birds, and 73% of the males that raised young to independence (n=11) courted extra-pair. Extra-pair copulations constituted 21% of male and 13% of female copulations. Extra-pair courtship displays included more songs than intra-pair displays. Courtship and copulation occurred at all stages of the breeding cycle and both during and outside females' fertile periods. The frequency of intra-pair, but not extra-pair, copulations dropped during incubation.

Among pairs which fledged young, three characteristics distinguished the most successful: 1) they took longer to initiate these clutches, 2) the males courted their mates relatively more than they courted other birds, and 3) both males and females engaged in fewer extra-pair copulations during the fertile periods for these clutches. A variety of factors appear to be involved in total clutch loss. The data reported support the theory that there is a mix of copulation and nesting strategies in this opportunistic species and that it is important for finches to form a strong pair bond well before breeding occurs.

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CHAPTER 1:
INTRODUCTION

Zebra finches (*Taenopygia guttata*) are small passerine birds native to Australia. They belong to the family Estrildidae, which includes the Australian, African and Asian waxbills or grass finches. Zebra finches are very gregarious, breed in colonies and feed in flocks on the rapidly maturing grasses of the arid or semi-arid Australian interior. Historically, they were found in areas with unpredictable rainfall, such as the Outback region. Like many Australian bird species, they are not photoperiodic as are many northern temperate species, probably as an adaptation to the unpredictability of food for their young. They are opportunistic breeders, using rainfall as an environmental cue for breeding. Wherever and whenever standing water and seed are available and the temperature is high enough, zebra finches will breed. They are very nomadic and will move from areas with bad breeding conditions to areas where conditions are better. When man started clearing, irrigating, and farming the areas in or near zebra finch habitat, this species started breeding almost year round, as long as the weather was warm. They are very prolific and have become very common throughout the

continent, except for some wetter habitats in the cold south or hot north.

As far back as 1870, zebra finches were exported to Europe as cage birds, and aviculturists easily bred them in captivity (Sossinka 1982). Since Australia halted the exportation of their wildlife in the forties, the captive population has been more or less isolated from the wild population. Zebra finches have not been intentionally bred for traits except for feather mutations (mainly color) and size. Except for differences in color, there are few apparent physical differences between wild and domesticated zebra finches. However, there are some behavioral differences due simply to being bred in captivity and to selection for traits besides breeding ability. Most differences are related to a reduction in sexuality compared to wild birds. Historically, wild zebra finches had very little time to take advantage of favorable breeding conditions and so were selected to respond rapidly. Domesticated zebra finches do not mature or ovulate as rapidly, nor court as much as wild birds (Sossinka 1970, 1982).

Early descriptive studies (Morris 1954; Immelmann 1965; Butterfield 1970), classified zebra finches as monogamous birds which paired for a lifetime. Considering how numerous they are in the wild and how popular they are in captivity, studies of feral birds have been rare and have

concentrated on generalized descriptions or breeding seasonality (Frith & Tilt 1959; Davies 1977, 1979; Kikkawa 1980). These studies did not use color-banded populations, thus limiting conclusions about social behavior. Since zebra finches are nomadic, they have been difficult to study in the wild. It can be hard to predict where a colony will form, and breeding proceeds very rapidly once one does form. Zann (Zann & Straw 1984; Zann 1990) has established stable study colonies in an irrigated area of northern Victoria by banding the constant flow of immigrants. Using these colonies he has been able to produce some of the most detailed field studies involving banded zebra finches (Birkhead et al. 1988, 1990; Zann 1994; Zann & Runcimann 1994).

Zebra finches are one of the most easy and therefore popular song birds to keep in captivity. Other seed eating finches, such as canaries, are widely kept; however, any northern species is likely to breed seasonally. Since with sufficient water, food and nest material, zebra finches breed rapidly and almost continuously in captivity, they are very popular birds for laboratory studies on reproductive behavior and neurobiology. Often within a week of introduction, individual captive finches will associate with one particular bird and show behavior patterns indicative of pair bonding such as clumping, allopreening, following and investigating potential nest sites together. Both male and

female participate in care of the young, starting with nest building.

Most laboratory studies concerning zebra finch breeding behavior have focused on the earliest portion of the breeding cycle and/or examined the behavior of pairs in individual cages. The housing of birds in pairs creates an artificial social environment since these gregarious birds normally breed in colonies. In spite of the abundance of publications on zebra finches (over 500 in the last 20 years), I noticed a lack of detailed longitudinal studies on colony behavior. I felt that many assumptions used in the reproductive behavior studies of individuals or pairs in cages had very little "baseline" data to support them. In the relatively short colony studies on hormones and behavior we had done, we had seen much behavior that deviated from these assumptions. I decided that a detailed observational study of domestic zebra finches in captive breeding colonies was needed. The focus would be on variations of sexual behavior and productivity, but data would be gathered on a wide range of behaviors, to avoid making assumptions on where differences would lie. I chose a colony size as large as possible while still allowing focal observation of each bird every observation day. A limited number of nest boxes was used to create some competition for nest sites, since this might stimulate variation in aggression and affect productivity. Data were gathered from 1985 to 1988.

Because of problems with the computerized event recorder, data processing proved to be very time consuming. Although well over 700 hours of behavioral observations were recorded, only about 200 hours were processed for use here and I focused on the relatively rare sexual behaviors.

The following three chapters are in the form of ready-to-publish papers each with its own introduction, so there will be some repetition of information. In Chapter 2, I describe and examine the bonds formed by all birds studied. It includes examples of finches forming nesting groups other than male-female pairs and compares the social behavior and productivity of these birds with that of pairs. In Chapters 3 and 4, I examine courtship and copulation. In Chapter 3, I consider all birds studied, with comparisons between the behavior of pairs and groups. In Chapter 4, I focus on the behavior and productivity of pairs.

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CHAPTER 2:
PRODUCTIVITY IN CAPTIVE ZEBRA FINCH COLONIES: MALE-FEMALE
PAIRS VERSUS NON-PAIR NESTING GROUPS

ABSTRACT

Observations were conducted on three colonies of 16 (8 male, 8 female) mature but sexually naive zebra finches (*Taenopygia guttata*) for 13 weeks and the full range of their behavior recorded. During this time, most birds completed at least one breeding cycle. Of the 44 birds which formed pair bonds, 43% of females and 38% of males did not form exclusive male-female pairs, but instead were members of alternate nesting groups (called here "groups"), some with multiple pair bonds. Ten groups of various types were formed, and even groups of similar composition were clearly differentiated by their behavior. Birds in groups did not differ from pairs in their latency to form bonds, however females from groups took longer than those from pairs to start their first fully-incubated clutches. Across all offspring losses, offspring of groups died earlier than those of pairs. However, if one examines data from only failed nests, those of pairs were more likely not to hatch, whereas those of groups were more likely to lose all young in the first few days. In productive groups, there was no intra-sexual competition among those occupying the same

nest. Among all nesting units that had second clutches, birds tended to switch nest sites for their second clutch more often if their first clutch failed than if it was successful. These data support the theory that there can be a mix of copulation and nesting strategies in this opportunistic species.

In describing avian reproductive strategies, bird species have typically been classified as monogamous, polygynous, polyandrous, or promiscuous, with 90% of species being classified as monogamous (Lack 1968). Monogamy has been considered an evolutionarily advantageous mating system for birds, since, unlike male mammals, male birds can assist in nest building, egg incubation and the care and feeding of their young offspring. In populations where the sex ratio is not badly distorted, both males and females will probably raise more offspring on average if they are monogamous and both help in raising the brood. Some advantages of biparental care are increased diligence at the nest, since one can incubate or brood while the other feeds, and greater ease in providing food for the young, leaving both the parents and the young in better condition. However, since not all bird species are monogamous, biparental care does not seem to be the most advantageous strategy under all conditions.

Lack (1968) stated that in many passerine species polygyny is rare and selected against, but mentioned bird species in some families, such as some Icterids, wrens and flycatchers, in which males can be either monogamous or polygynous. For example, wrens and flycatchers are usually monogamous, but males of some species become polygynous when good nest sites or foraging territories are in short supply.

At the other end of the spectrum, redwinged blackbirds are typically polygynous, but there is great regional variation. It is not unusual for a male in the rich marshes of Washington or California to have as many as 15 females on his territory, while males which inhabit marginal habitat on the east coast of the United States are usually monogamous. In these cases, the abundance of food in the richer habitats allows females to incubate and feed young by themselves, only needing males to defend nesting territories. With this arrangement, the male can defend the nests of more than one female and sire more offspring than if he were monogamous. Verner and Willson (1966) coined the term "polygyny threshold" to explain that under conditions of rich but clumped resources females may gain greater reproductive success by becoming second females on the better territories of mated males rather than mating with unpaired males defending lesser resources. More recent studies have found further examples of additional species using mixed mating strategies that are more flexible than was previously thought (reviewed by Gladstone 1979; McKinney et al. 1984).

Zebra finches are small passerine birds native to Australia. They are opportunistic breeders, using rainfall as an environmental cue for breeding. With sufficient water, food, and nest material, they breed rapidly and almost continuously, a fact which makes them very popular birds for laboratory studies on reproductive behavior.

Often within a week of introduction, individual captive finches will associate with one particular bird. Behavior patterns indicative of pair bonding include clumping, allopreening, following, and investigating potential nest sites together. Both male and female participate in care of the young starting with nest building. The female typically lays 4-5 eggs, and both birds share incubation and feeding of the altricial young when the eggs hatch about 14 days later.

Early descriptive studies (Morris 1954; Immelmann 1965; Butterfield 1970) classified zebra finches as monogamous birds which paired for a lifetime. There have been very few studies of captive zebra finch colonies (Burley 1981, 1985, 1986a, 1977; Burley et al. 1989; Ratcliffe & Boag 1987; Birkhead et al. 1988, 1989, 1990). Most studies concerning zebra finch breeding behavior have focused on the earliest portion of the breeding cycle and/or examined the behavior of pairs in individual cages. Yet, housing finches in pairs creates an artificial social environment, since these gregarious birds normally breed in colonies. Observing zebra finches in colonies allows one to see a much wider range of their social behavior, including both within-pair and extra-pair behavior.

Most studies on zebra finch colonies reported deviations from monogamy, usually extra-pair matings (Birkhead et al. 1988, 1989). However, Burley (1986b) in

her studies of color-banded zebra finch colonies reported instances of polygyny and polyandry that produced young. There were no detailed behavior observations in this study to investigate the differences, if any, between birds nesting in pairs and those that did not. In previous studies on reproductive behavior in our laboratory we also noticed nesting situations other than male-female pairs. I therefore decided to study pair bonding, mating strategies, and productivity in this species.

What would prompt these normally monogamous birds to nest in something other than a male-female pair? Are they forced to pair with mated birds because there are no unpaired birds left? Or are they choosing these nesting situations over the opportunity to form male-female pairs? The latter hypothesis is similar to the explanation given by the polygyny threshold hypothesis (Orlans 1972) mentioned previously.

From previous studies in which zebra finches were observed to "mate for life", it is obvious that they are capable of strong pair bonds. Yet, variations occur in their nesting patterns in captivity. In the present study I asked the following questions: in a small captive colony of naive zebra finches, 1) what mating strategies appear, 2) which are the most prevalent and 3) which are most successful? One would expect from the literature that male-female pairs would be overwhelmingly the most common pattern

and that they would have the highest productivity.

METHODS

The subjects were sexually mature but naive zebra finches, raised in our breeding colony at the American Museum of Natural History. They ranged in age from four to seven months at the time of colony formation. From the time of their juvenile molt, males and females had been housed separately. During this study, birds were housed in a 6 X 8 X 6 foot observation aviary. The aviary contained 8 nest boxes and 23 perches along one wall. Directly opposite this wall, separated from the aviary by an entire wall of one-way plastic, was the observation blind. Through the wall of plastic, the observer could see the entire aviary. To encourage breeding, the temperature was kept over 65°F and humidity was kept over 50%. Food, water, and nest material were available ad lib. Lighting was fluorescent and on a 14:10 light:dark cycle.

Three successive groups of eight males and eight females were housed together in the aviary and allowed to pair and breed for at least 13 weeks. No bird was related to any other bird in its group. Each bird was individually and randomly marked with color bands for identification. Starting within 24 hours of colony establishment, each bird was observed for 10 min. per day, six days per week. The full range of behavior was recorded using a computerized

(SSR) event recorder (Stephenson & Roberts 1977; Lamb et al. 1979). Also noted were the number and date of eggs laid and hatched, and the number of days the young survived, up to independence.

A widely accepted criterion for pair bond establishment is clumping (sitting in contact) or, when more assurance is desired, clumping at a nest site (Butterfield 1970; Slater & Clements 1981; Silcox & Evans 1982; Böhner et al. 1984). Two birds (whether a male and a female, two males, or two females) were considered to have formed a pair bond when they occupied a nestbox together or sat together at a possible nest site. In most cases, birds which met these criteria also performed many other affiliative behaviors. Exceptions are discussed below. For the purposes of this study, subjects were classified based on their nesting and pair bond behavior, specifically, whether or not they bonded (i.e., at least attempted to establish a nest) exclusively with one other bird which bonded exclusively with them. Birds which bonded with only one bird of the opposite sex, which, in turn, did not bond simultaneously with any other bird, were considered a part of a male-female nesting pair (hereafter called "pair"). In each colony observed, all birds defended and built nests at various available sites, but only some birds formed male-female pairs. The behavior and initial clutch success of male-female pairs are reported in more detail elsewhere (Chapter 4). The other birds

nested either singly (called "single nesters"), as single sex pairs, or as members of multi-bond nesting groups. The latter two categories, in which the nest was built or eggs were incubated by a group of birds other than a male-female pair, are hereafter labeled "groups" and all three of these categories are called "atypical nesting units". Any two birds in these groups were considered bonded if they habitually performed affiliative behaviors, such as clumping or allopreening, in addition to occupying the same nest. If they did not, they were considered nesting together, but not bonded. Any number of birds which nested or attempted to nest together (i.e., pairs, groups and single nesters) are referred to as "nesting units" or just "units".

The analyses of productivity include only the 45 birds belonging to the 20 units in which at least one bird completed incubation (that is, incubated eggs for the 14 days necessary for hatching). Comparisons between pairs and groups excluded the one successful single nester. Various numerical and categorical measures of clutch success were calculated for clutches in which females had finished depositing eggs at least 14 days before the end of the observation period. Some of the numerical measures included were: (1) number of eggs laid, (2) number of eggs hatched and (3) number of young which survived to feed independently (which usually occurred about 35 days after hatching). Some of the categorical measures used were: (1) whether or not

the clutch failed, i.e., no young survived to feed independently, (2) total hatching success or whether or not pairs hatched the entire clutch, regardless of how long the hatchlings survived.

All statistical tests were nonparametric and two-tailed, and all differences reported are significant at the 5% level or better.

RESULTS

Pair bonds

Although all 48 subjects defended nest sites at some point, only 44 formed bonds with other birds. All 23 females and 21 males which formed pair bonds had done so by day 17. Of the bonded birds, 18 (41%) did not form exclusive male-female pairs, but instead became members of groups. This was the case for 43% of the bonded females and for 38% of the bonded males. Including the three males and one female which nested singly, there were 23 nesting units, 20 of which incubated eggs. Figure 1 displays the composition of the 13 male-female pairs, six groups and four single nesters. There were many different combinations of males and females in the six groups formed, and even the ones of similar composition were clearly differentiated by their behavior.

Over half (55%) of the birds which bonded formed their first bond within three days of introduction. Within six

days of introduction 82% had bonded. All bonds had formed by 17 days. There was no significant difference between birds in pairs and those in groups in the number of days taken to form the first pair bond (See Table I). Although almost half of the nesting units had one clutch fail at some point during the study, there were no instances of "divorce" or pair bonds breaking, among either pairs or groups, once birds had completed incubation of a clutch.

Table 2-I: Comparisons made between pairs and groups on various measures of productivity. The one measure significantly different was the number of days to initiate the first completely-incubated clutch.

	PAIRS	GROUPS	COMPARISON
Days from introduction to formation of pairbond (all bonded birds, n=44)	n=26 X=4.96 SEM=0.76	n=18 X=5.40 SEM=0.67	MWU U=189.0 p=0.27
Days to first egg of 1st fully-incubated clutch (bonded females, n=23)	n=13 X=28.08 SEM=5.04	n=10 X=53.70 SEM=7.89	MWU U=22.5 p=0.008
Productivity within 90 days for all nesting units with bonded birds (n=19)	n=13	n=6	MWU
Number of clutches laid	X=2.08 SEM=0.18	X=1.83 SEM=0.31	U=31.5 p=0.46
Number of clutches completely-incubated	X=1.62 SEM=0.14	X=1.50 SEM=0.22	U=34.5 p=0.65
Number of clutches producing some young	X=0.92 SEM=0.18	X=0.67 SEM=0.33	U=30.5 p=0.41
Total eggs laid (in completed clutches)	X=10.62 SEM=1.14	X=8.83 SEM=1.92	U=29.0 p=0.38
Total eggs incubated	X=7.54 SEM=0.83	X=7.33 SEM=1.43	U=36.0 p=0.79
Total eggs hatched	X=3.77 SEM=0.81	X=4.0 SEM=0.82	U=35.0 p=0.72
Percent of incubated eggs that hatched	X=53.46 SEM=10.55	X=54.83 SEM=5.90	U=38.5 p=0.97
Percent of hatchlings that survived	X=60.23 SEM=11.55	X=43.33 SEM=20.28	U=30.5 p=0.44
Total young fledged	X=2.54 SEM=0.54	X=1.33 SEM=0.62	U=24.5 p=0.19

Behavior and relative productivity of atypical nesting units.

Single nesters

Four birds built and defended nests alone in the first two colonies: one male in the first colony, one female and two males in the second colony. Another female in the second colony started a clutch alone, then six days after laying the first egg (or after day 17 of the study), abandoned it and paired with a male, resulting in the longest latency to bond before the first fully-incubated clutch. The single males courted females, but no females accompanied these males into their nests. In fact, these males often defended their nests against females. They did, however, obtain some copulations. No evidence was ever found suggesting that eggs had been laid in their nests. The lone female copulated with males but did not engage in affiliative behaviors typical of bonded birds and defended a nest against all males. She raised three young to independence. During this first clutch, she was often followed by one male in particular but did not allow him into her nest. However, after she finished feeding this brood, on day 90, she bonded with this male.

Two-bird groups.

There was only one pair not composed of a male and a female. This was a pair of females who defended a nest against all males. Initially, only one laid eggs in their

nest, and they both incubated the eggs and raised two young to independence. Later, they both laid clutches almost synchronously in this nest. From these clutches, only one egg hatched.

Three-bird groups.

There were four groups of three birds. Superficially, there seemed to be two polygynous and two polyandrous trios. However, the social dynamics of the four groups were very different. In one male-male-female group, the two males bonded to the female while in the second, both the male and the female bonded to the second male. In one polygynous group, all three occupied the same nest; whereas in the other, the male built a second nest with the second female at a separate site. This second female never laid a clutch. The first female, although not able to prevent the male from accompanying the second female, did prevent this female from entering the pair's nest most of the time. Two of these trios raised young and one trio raised more than the median number.

Four bird group.

The most complicated group was a quartet. In this group, affiliative behaviors occurred within two male-female pairs, but also between the male of one pair and the female of the other, resulting in the following pattern of bonds: male-female-male-female. This was one of the more unstable

groups. There was much intra-sexual aggression between the males and between the females. Although all four birds did not occupy a nest at the same time, the bigamous male and the two females often did. Most often it was one of the three male-female pairs possible with the pattern of pair bonds presented above which occupied a nest site. Sometimes one pair, which eventually laid a clutch, would be in a nest box and the other couple would be on top of the box, with the two females threatening each other. One of the pairs laid a clutch which partially hatched but the young did not survive long. They then switched nests and laid again, but the eggs did not have time to hatch within the observation period. Since this group was extended for use in another study, more anecdotal data are available. They did not have a successful clutch until the bigamous female, debilitated from frequent fighting with the competing female, separated the group into two pairs by attempting to nest with the male bonded exclusively to her. Soon after this, the bigamous male and the other female successfully nested as a pair and in the next four months had two clutches with a total of seven young.

PRODUCTIVITY

The productivity of the three colonies within the 90 day observation period is graphed in Figure 1. Comparisons between pairs and groups were made on many different

numerical measures of productivity (See Table 2-I). Only one comparison was significant, the latency to first clutch. Group females took significantly longer than pair females to lay the first egg of their first fully incubated clutch. The other significant differences found were on categorical measures.

The percent hatching success of the initial clutches of pairs and groups was very close (65% and 68% respectively), while that of second clutches differed more (28% and 41% respectively). Seventeen nesting units (12 pairs, 5 groups) started second clutches, but only eleven of these (8 pairs, 3 groups) started them early enough to complete incubation before the end of the 90 day observation period. Six of these nesting units (3 pairs, 3 groups) hatched their second clutches and two pairs raised young to independence.

No pair or group fully incubated a third clutch within the 90 day observation period. Seven nesting units started third clutches (5 pairs, 2 groups), but five of these (3 pairs, 2 groups) had raised no young, one pair had no eggs hatch in the second clutch and one pair started a third clutch before the second brood fledged. Therefore, since most of these birds were able to renest earlier than they could have if they had raised two broods, the number of clutches started was not a valid measurement of productivity.

The two pairs with successful second clutches produced

the most young. There was no other relationship between the total number of eggs laid by a nesting unit during the 90 days and total number of young fledged by that "nest" within that period.

Male-female pairs produced an average of 2.5 independent young ($SEM=0.5$) during the study, compared to 1.3 young ($SEM=0.6$) for groups (difference not significant, Mann Whitney U, $U=24.5$, $p=0.19$). There were no significant differences between pairs and groups in the numbers of eggs, hatchlings, or independent young produced (see Table 2-I), however, no groups were in the top 20% in terms of the number of young raised to independence. No groups had over three young or more than one successful clutch, whereas pairs had up to six young, and two pairs had two successful clutches.

Survivorship of individual young fell into the following three qualitative categories depending on the point at which failure occurred: 1) the egg did not hatch, 2) the egg hatched, but the hatchling died within the first four days, 3) the egg hatched, but the chick died after nine days. Of the young lost, 81% died in the first four days after hatching. Only 6 died later, between 9 and 16 days after hatching. Within a clutch, if some chicks survived to four days, then at least one survived to independence.

There were many clutches which failed completely, i.e., no young survived to independence. Of the 31 clutches

incubated completely, 14 (45%) did not produce any independent young. There was no significant difference between pairs and groups in the tendency for individual clutches to fail. Of these 14 clutches, 7 did not hatch, 6 had some hatchlings but they died within four days, and one had all eggs hatch but the young died within four days. There was a significant difference between pairs and groups in the point at which nests failed. Once they had incubated a clutch for the full 14 days, pairs were more likely not to hatch any eggs, whereas groups were more likely to hatch at least some eggs but have the young die in the first few days (Fisher's Exact Probability, $n=14$, $p=0.02$). Of those hatchlings which died before becoming independent, from both failed and successful nests, groups lost young sooner than pairs (Mann Whitney U, $U=53.5$, $p=0.004$, pairs: mean= 5 days, SEM=1.29, groups: mean=1.53, SEM=0.54). Of the six atypical units that incubated a clutch, the four that raised young did not have a polyandrous or polygynous pattern of bonds within one nest and all three of the unsuccessful groups did have this pattern (a significant difference, Fisher's Exact Probability, $p=0.03$).

Among all nesting units that had second clutches, birds tended to switch nest sites for their second clutch more often if their first clutch failed than if it was successful (Fisher's Exact Probability, $n=17$, $p=0.04$). Pairs and groups did not differ on this measure.

DISCUSSION

Pair bonds

Based upon early descriptive studies (Morris 1954; Immelmann 1965; Butterfield 1970), zebra finches are typically classified as monogamous birds which mate for life. This classification is not unusual because Lack (1968) classified the great majority of birds as monogamous. Monogamy has been considered an evolutionarily advantageous mating system for birds, since, unlike male mammals, male birds can assist in all parental care except egg-laying. However, not all bird species are monogamous; so biparental care does not seem to be the most advantageous strategy under all conditions.

The polygyny threshold model (Verner and Willson 1966; Orians 1969) predicts that when resources are uniformly distributed, sex ratios are equal, and food is not plentiful birds should choose monogamy as a mating strategy. When resources (such as nesting sites) are clumped and food is plentiful, polygyny should occur more often because there is a "threshold" above which females are more successful mating with a male who is already bonded.

Even as early surveys determined that most birds were monogamous, there were reports of variable breeding strategies in birds. Sometimes, as the polygyny threshold predicts, this is correlated with richer or more concentrated resources than in monogamous populations. For

example, wrens, flycatchers, and dickissels are usually monogamous, but in some environments the males become polygynous (Lack 1968). At the other end of the spectrum, redwinged black-birds are typically polygynous, but there is great regional variation and in some habitats they are typically monogamous (Orians 1972). In recent years, feral populations of many species have been reported as having variable mating systems (Ford 1983). For example, Shugart et al. (1988) documented normally monogamous herring gulls forming female pairs and polygynous trios, often in years when the sex ratio is skewed towards females. There have also been reports of birds of supposedly monogamous species forming pair bonds with more than one bird (Ford 1983; Fitch & Shugart 1983; Davies 1986; Wheelwright et al 1992) and/or engaging in extra-pair mating behaviors (reviewed by Gladstone 1979; McKinney et al. 1984; Westneat et al. 1990; Birkhead & Møller 1992). Although many scientists tend to classify a species as either monogamous, polygamous, or promiscuous, in many cases this is an oversimplification. Careful research has shown intra-species variation in reproductive strategies. Such variation is common in certain species.

Detailed field studies of zebra finch social behavior are rare. In what may be the only large-scale study of behavior in marked colonies, Zann (1994) did not report any instances of nesting groups besides male-female pairs. From

the perspective of the polygamy threshold theory, this finding is surprising, considering the opportunistic nature of this species, the greater amount of food available in the irrigated land finches now inhabit and the clumping of nest sites in bushes.

Even though all birds in the present study attempted to defend a nest site and build a nest, a large percentage (41%) of the birds did not form exclusive male-female pairs. These other birds either 1) formed multiple bonds, 2) formed bonds with birds that formed multiple bonds, 3) bonded with birds of the same sex, or 4) did not bond. Since birds formed these types of bonds at the same time other birds were forming exclusive male-female pairs, it seems unlikely that birds were forced into these choices entirely through lack of available birds. In all cases of a female choosing to nest in a group rather than a pair, there was at least one unpaired male available and in at least three cases a single male consistently pursuing her. The two female-only units raised at least one clutch before the females bonded with pursuing males. In the case of the quartet, the female bonded with an attached male and then bonded with the pursuing male. For some reason, these females preferred one of the three alternatives mentioned over bonding to the available single males. It is possible that in some cases, birds were available but the attempt to form a bond was not reciprocated. However, this was obviously not true in all

cases. For instance, why did one female in the third colony continue literally to fight for a paired male when she bonded with an unattached male a day later, forming the quartet? Why did the lone female in colony two raise her first clutch by herself, when an unattached male persistently followed her during this time? After the observations reported here ended, she nested with him and started a second clutch; so, it seems they were compatible. It is interesting to note that this was the only bird who switched from an alternative strategy to nesting as a pair (or vice versa); yet, she successfully raised her initial clutch. Birds in this study which nested in unsuccessful groups were surprising for their persistence in maintaining these bonds even though some groups were so aggressive that a bird's health suffered.

In an early report on zebra finches from the field, Tubman (1923) said "I saw a considerable number of nests with ten to fifteen eggs in them". Since the normal clutch size is about 5 eggs, this could be evidence that more than one female was laying in these nests. Until the last few years, there have been very few reports from the field on the behavior of individual finches and none on tagged birds. Even though Birkhead et al. (1988) reported extra-pair copulations occurring in the field, as mentioned before, there have been no reports of groups sharing a nest in the wild, as occurred in these captive colonies. Admittedly,

these were artificial conditions but they were not entirely unnatural. The size of the colonies was within the range of 5-25 pairs reported in the wild. Also, there were unoccupied nest boxes in all three colonies and, as mentioned, unpaired birds in the first two colonies which had the highest number of birds opting for alternate strategies. Although not enough is known of population dynamics in the wild to be certain, there may be, on average, more prospective mates available in feral colonies, especially those with the high level of immigration reported by Zann (1994). However, in small, isolated colonies the choices can be expected to be similar to those in this study.

One explanation for the formation of groups rather than pairs is that it is an aberration of captivity. The lower number of unattached birds from which to choose, compared to what is assumed to be available in the wild, might cause groups to form at a higher rate in captive colonies. Ours is not an isolated finding. Other laboratories working with zebra finch colonies have anecdotal evidence that groups have formed in their colonies. There are reports of female pairs, male pairs, polygynous and polyandrous trios in captive colonies (Burley 1986b; Ratcliffe, personal communication). Perhaps if there were greater choice, these birds could have paired monogamously. For the second female in a polygynous group

or the second male in a polyandrous group, perhaps they could find an unattached bird with characteristics similar to the attached one they preferred. Bonding to birds of the same sex has been reported in the wild when sex ratios were skewed (Shugart, et al. 1988). Perhaps with more choice of birds, these subjects could have found mates of the opposite sex.

A similar explanation could account for the lack of mate desertion in these colonies. There was one instance (involving four birds) of pairs bonding then switching mates; however, this switch occurred before either pair finished incubating a clutch. Mate switching before breeding has been documented in other species (Rowley 1983) and is not unusual. What is surprising is that, although there were numerous cases of nest failure, there were no cases of mate desertion after the first clutch. Studies on mate desertion in birds have found that younger birds and pairs which fail to raise young are more likely to break pair bonds (Coulson 1966; Bradley et al. 1990). Since these were all naive, young finches and there were many unsuccessful nests, from the literature one would expect mate desertion after some of these failures. It is likely there are other factors at work here. Much of the work on mate desertion has been in long-lived seabirds which are only paired during the breeding season. In these studies, nest failure does not account for all cases of mate

desertion (Coulson & Thomas 1983). When mates do switch after nest failure, it may be more because the pairs split and leave the breeding ground early when their nest fails. With not as much time to reinforce the pair bond, the pair may not reform next season (Coulson & Thomas 1983; Rowley 1983). Zebra finches are different from such seasonal breeders in that their bond is maintained year round. In this study, there is the added factor of restricted choice. There may not have been enough better options available to these captive birds for mate switching to be advantageous.

The polygyny threshold model (Orians 1969, 1972) may help to explain some of the non-monogamous nesting behavior reported here. In this captive situation, resources (food and nest material) were plentiful, and females did not need to be as concerned with males' contributions to parental care. Evidence for this suggestion includes the ability of females in these colonies to fledge three clutches with no help from males. Under these enriched conditions, some females may have used different criteria to choose a mate.

There seemed to be more variation than similarity between groups in composition and affiliative behavior patterns. The greatest similarity was that all groups persisted in this strategy, even following total nest failure. Since 1) these birds took longer to initiate completely-incubated clutches, 2) these clutches were often (although not more often than pairs) unsuccessful and 3)

affiliative behaviors were not exclusive, there must have been some criteria for mate retention other than the rapid achievement of a successful first clutch.

Productivity

It is hard to explain why the failed nests of pairs were more likely to be because of unhatched eggs rather than mortality of hatchlings. There were no obvious differences in copulation rates between pairs and groups, so it's unlikely that a difference in fertility caused this. Most of the unhatched clutches were second clutches from pairs whose first clutches were fertile.

It seemed counter-intuitive and was not consistent with our experience with our own breeding colonies that there was such a drop in hatching success for second clutches. In our laboratory breeding colonies, which typically had at least 40 birds, first clutches often failed, but later clutches usually had at least two-three hatchlings survive. All of the unhatched second clutches in this study were laid within 11 days of each other by pairs in the third colony, making us wonder if some unknown environmental perturbation might have been responsible.

The data on productivity were surprising for their lack of significant differences between pairs and groups on most numerical measures. The average number of young raised by pairs was higher than that of groups, but not significantly

so. This difference might have increased and become significant over time had the observation period allowed for more clutches. One reason for the lack of difference could have been that success or failure depended more on the type of group rather than anything intrinsic to being a group versus a pair.

The failure of many groups was associated with intra-sexual competition within a nest. The successful units were the two nests with only females, one male-male-female trio and one female-male-female trio. In both trios, there was only one female in a nest. In the first trio, a bond first formed between the two males and then a female bonded to one of the males. This resulted in some initial aggression towards the female from the other male, but there was no intra-sexual aggression. In the second of these trios, the male successfully raised young with one female while building a another nest with the second female. The first female successfully defended her nest from the second female, so the intra-sexual aggression was kept outside the nest. The unsuccessful male-female-male and female-male-female trios had much intra-sexual aggression occurring in the nest and this persisted into incubation. Unsuccessful trios were either not able to hatch eggs or lost their young in the first several days after hatching.

It is hard to say without more data, whether the strategy of breeding as a group rather than as a pair could

be adaptive. The finding that birds in groups are less successful than pairs on several measures of productivity says more about the ability of these groups to function effectively together than about the genetic contribution of these birds to the next generation. From their copulation behavior, some of the birds in groups did not seem to contribute genetically to the clutches they incubated. However, many males engaged in extra-pair copulations and therefore may have contributed to other clutches. Females also can contribute to other clutches by egg-dumping, or intra-specific brood parasitism, when a female lays and abandons an egg in a conspecific's clutch, leaving it to be raised by the conspecific if not discovered. Although there was no evidence of egg dumping in fully-incubated clutches, this may have been attempted by unsuccessful females. However, unless a large number of eggs were dumped without being detected, most of the females in groups were not likely to have contributed to young which were successfully reared. This may point to a difference between males and females in the effectiveness of groups as a strategy; however, there would need to be data on parentage to support any hypothesis on this subject.

In conclusion, captive zebra finches display a flexible reproductive strategy and do not conform to the standard definition of monogamy. In a captive colony, they form nesting units other than one male and one female, in spite

of unpaired birds present in the colony, and persist in this strategy despite the failure of their clutches. There is some evidence from other species that this happens in the wild, although it may be exaggerated in captivity. In the current study, groups with no intrasexual competition were cooperative enough to raise as many and sometimes more young than some pairs, but often took longer to initiate a clutch. Groups with intrasexual competition, although they hatched young, lost them all within the first four days. It is clear that avian reproductive strategies are more plastic than was initially thought.

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FIGURE CAPTIONS

Figure 2-1: Three measures of productivity of the first clutch for the 13 male-female pairs(a & b), six groups and four single nesters(c); eggs = number of eggs laid; hatchlings = number of eggs hatched; fledglings = number of chicks raised to independence. Data are arranged in descending order of productivity. For those units having second clutches, horizontal lines divide the data for the two clutches.

Figure 2-1a

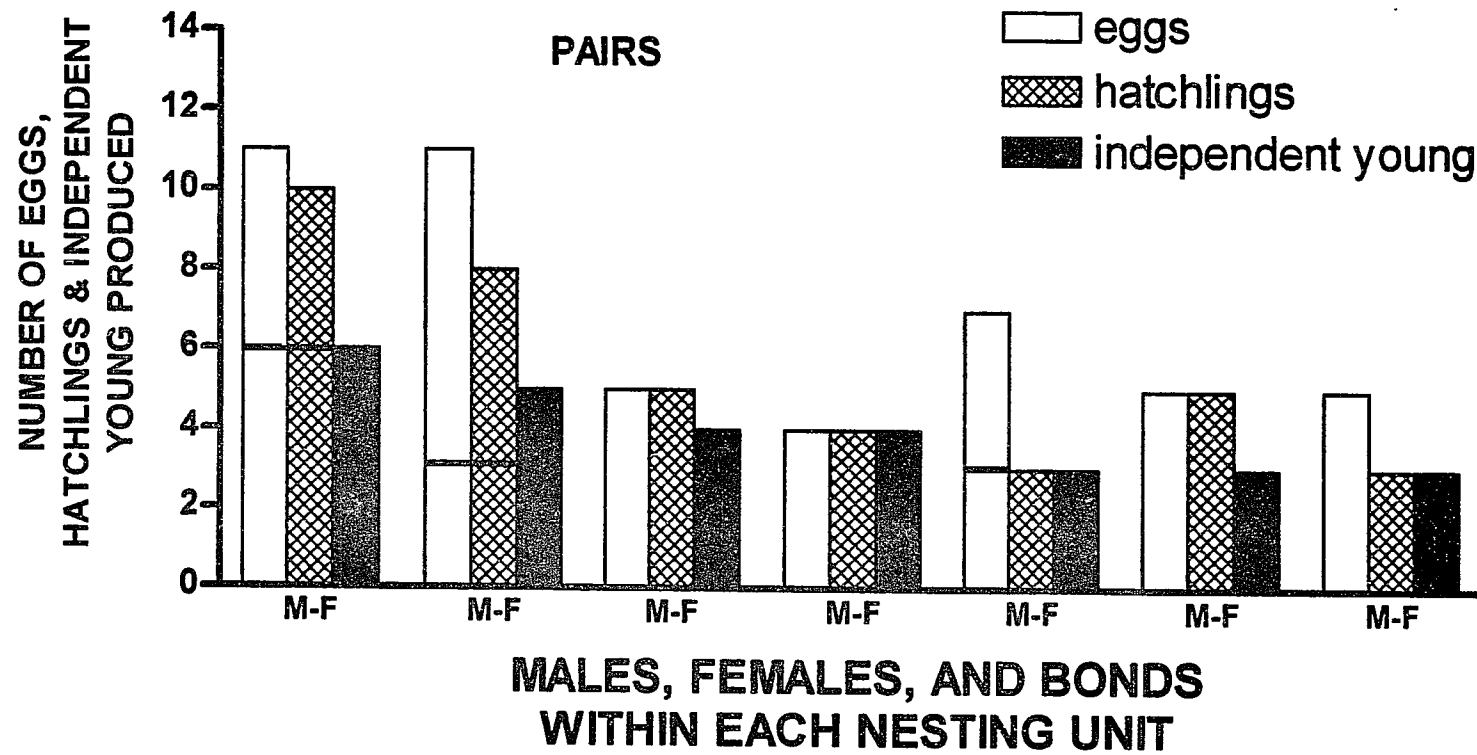


Figure 2-1b

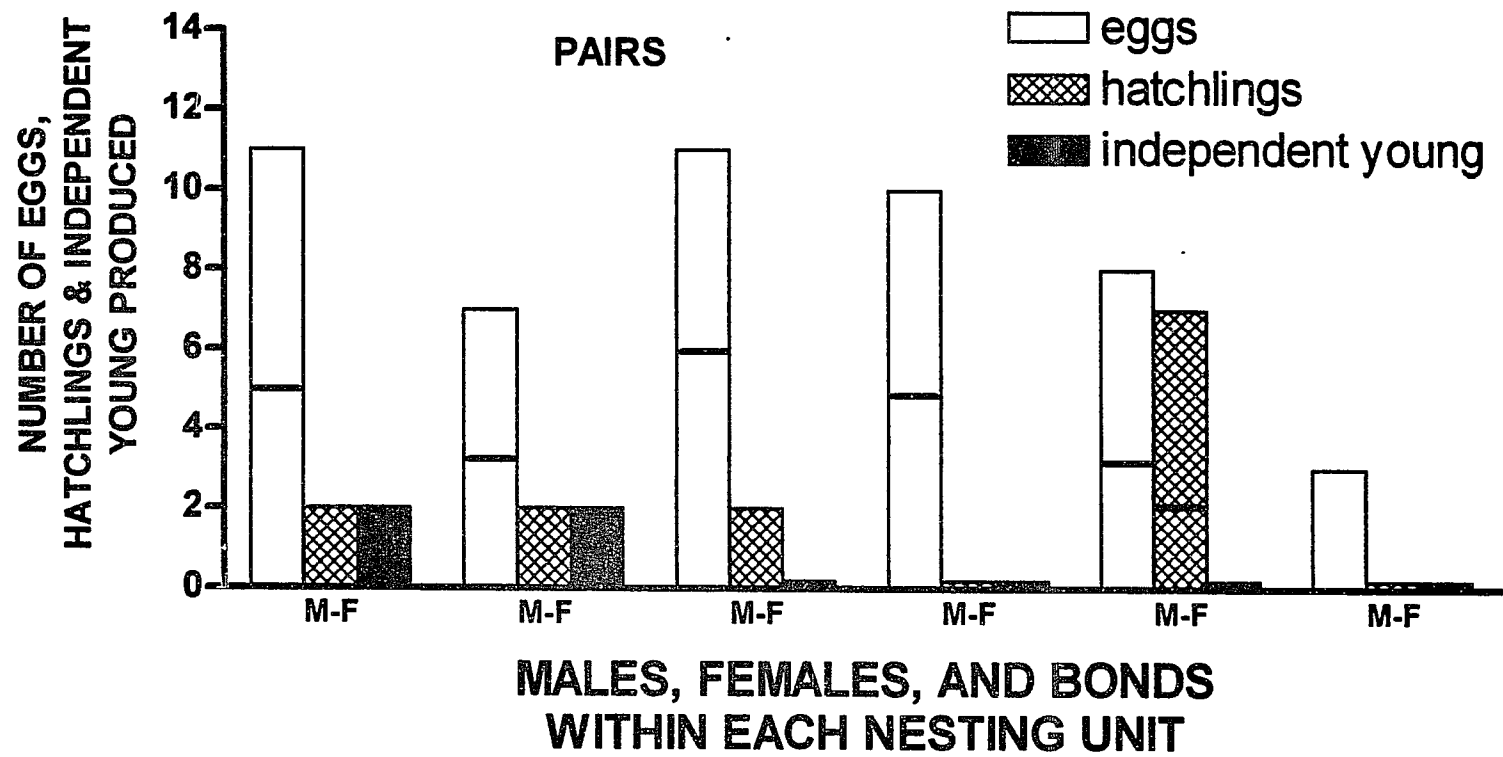
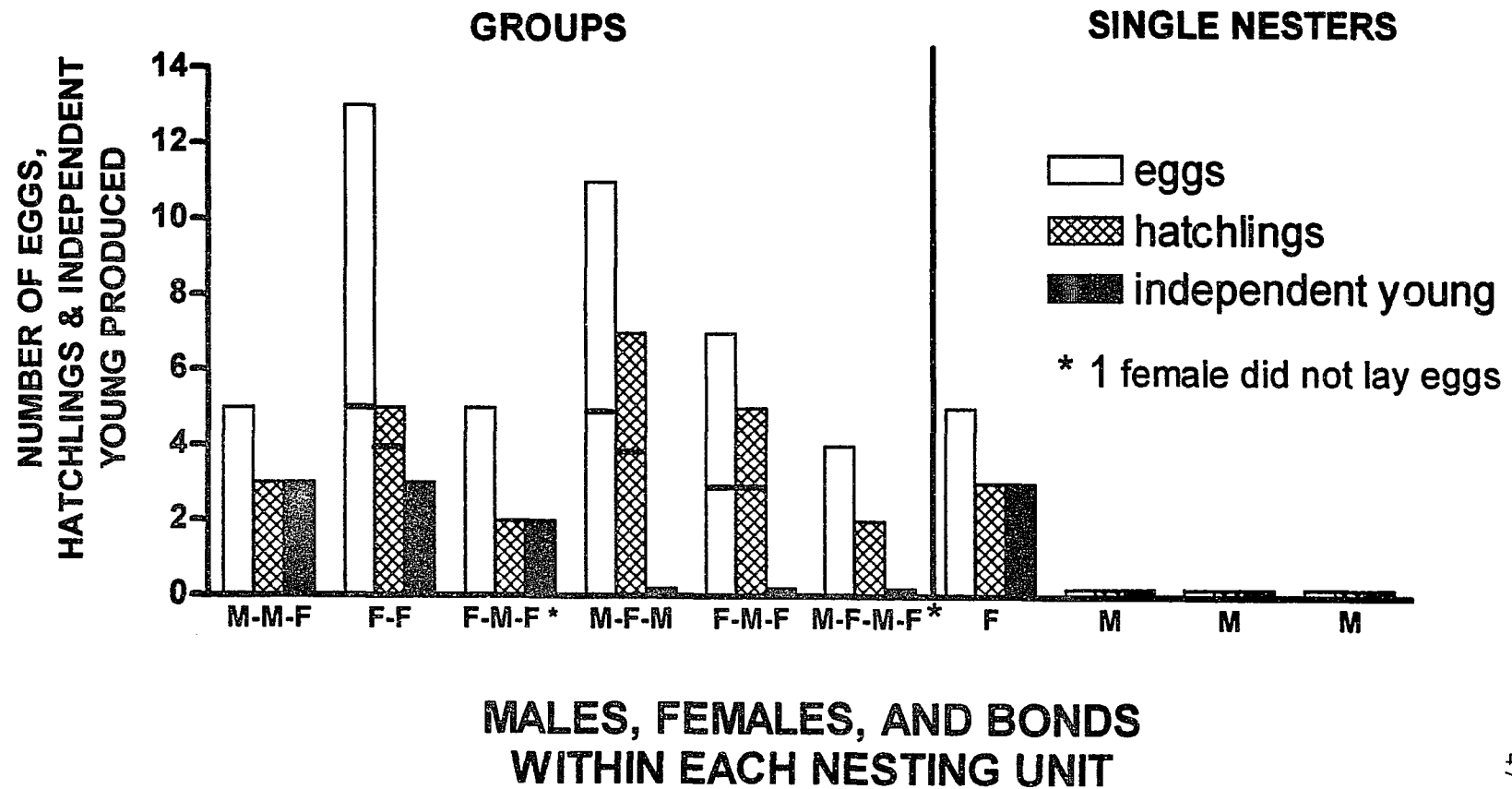


Figure 2-1c



CHAPTER 3:**COURTSHIP AND COPULATION BEHAVIOR IN CAPTIVE ZEBRA FINCH
COLONIES: MALE-FEMALE PAIRS VERSUS NON-PAIR NESTING GROUPS****ABSTRACT**

Observations were conducted on three colonies of 16 (8 male, 8 female) mature but sexually-naive zebra finches (*Taenopygia guttata*) over 13 weeks and the full range of their behavior recorded. During this time, most birds completed at least one breeding cycle. Reported here are data from the first breeding cycle of all birds which completed incubation (n=32) and from an equivalent period for all other subjects (n=6). Males directed courtship and copulation behavior towards 1) females during their fertile periods, 2) females outside their fertile periods, 3) other males. Males who were bonded to females (n=20) directed 21% of their courtship bouts to other birds, and 73% of the males that raised young to independence (n=11) were observed courting females other than their mates. Extra-pair copulations constituted 21% of male and 13% of female copulations observed during this period. Extra-pair courtship displays included more songs than intra-pair courtship displays. Courtship and copulation occurred at all stages of the breeding cycle and both during and outside females' fertile periods, but the frequency of copulations dropped during incubation. Total and intra-pair copulation

behavior was less frequent during incubation than during the fertile period, but extra-pair sexual behavior was not. As reported previously, over 30% of the 44 birds which formed pair bonds did not form exclusive male-female pairs, but instead were members of nesting groups (called here "groups"), some with multiple pair bonds. There were no significant differences in courtship or copulation behavior between pairs and groups. However, the data support the theory that males from groups increased their sexual behavior to achieve a constant rate of courtship and copulation per mate, unless they were competing with another male for that mate.

Based on observations of unmarked populations, most species of birds have been classified as monogamous (Lack 1968). These classifications were based on the assumption that nesting patterns are a good indicator of copulation patterns. Later studies which used plumage or artificial marking to identify individual birds reported individuals of supposedly monogamous species seeking or engaging in extra-pair copulations (EPCs) (reviewed by Gladstone 1979; McKinney et al. 1984). Initially, it was difficult, if not impossible, to say whether EPCs were successful in fertilizing eggs. However, in the last ten years, the great advances in molecular biology have enabled investigators to confirm that EPCs often resulted in offspring (reviewed by Westneat et al. 1990; Birkhead & Møller 1992). DNA fingerprinting has been used to demonstrate extra-pair paternity and maternity in supposedly monogamous species (reviewed by Zajac 1991; Gowaty & Gibbs 1993). These new data have revealed differences in mating strategies between species previously classified as monogamous and have lead to theories of more complex mating systems (Gowaty 1983; Wagner 1991; Morton et al. 1990).

Gowaty (1983) proposed a new classification system which assessed a species' typical nesting pattern (or "apparent mating system") separately from determining which individuals make a genetic contribution to the next

generation (i.e., actually contribute eggs or sperm). In this theory, mating system classifications refer to the genetic contribution ratios of a species (or sub-population of a species), and these classifications are not necessarily consistent with the "observed consort patterns among breeding adults" or "apparent" mating system of the same species. For example, in an apparently monogamous population, the genetic contribution ratio would be one if every pair caring for a brood were the biological parents, because for every male contributing genes, there is a female contributing. Whereas, this ratio would be skewed in one direction or the other if the male sired the young of more than one female or if the female laid fertile eggs in the nest of more than one successful male.

In species which typically breed in pairs, there are two general ways individual birds deviate from monogamy. The first is in their nesting behavior, such as forming pair bonds with additional birds (Ford 1983; Fitch & Shugart 1983; Davies 1986; Wheelwright et al. 1992). The second deviation from monogamy is in birds' mating behavior; they solicit, court, and/or copulate outside their pair bonds ("extra-pair" behaviors) without showing any other affiliative behavior indicative of a pair bond (reviewed by Gladstone 1979; McKinney et al. 1984; Birkhead & Møller 1992).

Both types of variation have been reported in the

literature with increasing frequency as more bird populations are marked and closely studied. Variations have been reported disproportionately more in colonial birds, probably because one can observe large samples of birds in a small area with these species (Ford 1983). Sea birds and waterbirds are popular subjects for research on mixed mating strategies for the same reason. In addition, these species are particularly easy to observe because their open nests allow a clear view of behavior throughout the colony (common guillemots, Hatch 1987; northern fulmar, Hatchwell 1988; razorbill, Wagner 1992; white ibis, Frederick 1987; white spoonbill, Aguilera & Alvarez 1989; cattle egrets, Fujioka & Yamagishi 1981). Many songbirds have nests that are not as open and observable, and their matings, especially extra-pair matings, can be secretive, making it difficult to obtain comparable detailed data on large numbers of birds.

Swallows are small songbirds which often nest in colonies near open areas so they can feed on flying insects, making them relatively easy to observe. A number of detailed studies have used them as subjects (barn swallow, Møller 1991, purple martin, Morton et al. 1990; cliff swallow, Medvin et al. 1992, Dunn & Robertson 1992; welcome swallow, Tarburton 1993). Morton et al. (1990) found that older males establish nests early, attract younger birds to their colony, then obtain more extra-pair fertilizations with the females of these younger pairs. Møller (1988)

found that females were attending to physical indicators of fitness, when choosing which males to solicit for EPCs. These surprising and informative observations resulted from detailed, long-term studies on entire colonies. I felt that a laboratory study would provide greater opportunity to study these behavioral phenomena in birds that don't normally breed in open areas.

Early descriptive studies (Morris 1954; Immelmann 1965; Butterfield 1970) classified zebra finches as monogamous birds which paired for a lifetime. There are very few studies of captive zebra finches breeding in colonies (Burley 1981, 1985, 1986a, 1977, Burley et al. 1989; Ratcliffe & Boag 1987, Birkhead et al. 1988, 1989, 1990), but most of these reported deviations from monogamy. We also noticed such deviations in our breeding colony and Burley (1986b) reported nesting groups other than pairs. Birkhead, et al. (1988, 1989) found evidence of extra-pair paternity in 11% of captive zebra finch broods and 8% of wild broods. Studies examining zebra finch breeding behavior have typically focused on the earliest portion of the breeding cycle and/or examined the behavior of pairs in individual cages, creating an artificial social environment since these gregarious birds normally breed in colonies. A study of zebra finches breeding in colonies offered the opportunity to observe both pair and extra-pair behavior.

The current study examined the behavior of small

colonies of captive birds across the entire breeding cycle, concentrating on within-pair and extra-pair courtship and copulation behavior. The study included both the pairs and the other nesting groups which formed allowing comparisons between birds using different nesting strategies.

METHODS

Male courtship is the most frequent and the most noticeable sexual behavior in zebra finches. Both males and females have many calls, but only males sing. Male courtship consists of songs directed toward the female, often accompanied by a visual dance display. In the course of normal pair bond formation, the female initially responds to courtship by moving away, but eventually solicits copulation by crouching and tail quivering. This tail-quiver display is often followed by the male mounting and copulation culminating in cloacal contact. Both male and female participate in care of the young, including nest building, incubation and feeding.

Subjects were sexually mature but naive zebra finches ranging in age from 4 to 7 months at the time of colony formation. From their juvenile molt, males and females had been housed separately. For this study, birds were housed in a 6 X 8 X 6 foot observation aviary, containing 8 nest boxes, 23 perches, and an observation blind with a view of the entire aviary. To encourage breeding, the temperature

was kept over 65°F and humidity was kept over 50%. Food, water, and nest material were available *ad libitum*. Lighting was fluorescent and on a 14:10 light:dark cycle.

Three successive groups of 8 males and 8 females were housed in the aviary for at least 13 weeks. No bird was related to any other bird in its group. Each bird was individually and randomly marked with color bands for identification. Starting within 24 hours of colony establishment, each bird was observed for 10 min. per day, six days per week. The full range of behavior was recorded using a computerized (SSR) event recorder (Stephenson & Roberts 1977; Lamb et al. 1979).

A widely accepted criterion for pair bond establishment in zebra finches is clumping (sitting in contact) or, when more assurance is desired, clumping at a nest site (Butterfield 1970; Slater & Clements 1981; Silcox & Evans 1982; Böhner et al. 1984). Two birds (whether a male and a female, two males, or two females) were considered to have formed a pair bond when they occupied a nestbox together or clumped together at a nest site. Birds which met these criteria usually performed many other affiliative behaviors such as allopreening (which was not as exclusive) and synchronized behaviors, such as foraging and searching for a nest site.

Subjects were classified based on their nesting and affiliative behavior, specifically, whether or not they bonded (i.e., at least attempted to establish a nest) exclusively with one other bird which bonded exclusively with them. Birds which bonded with only one bird of the opposite sex, which, in turn, did not bond simultaneously with any other bird, were considered a male-female nesting pair (hereafter called "pair"). In each colony, all birds defended and built nests but only some birds formed male-female pairs. The behavior and initial clutch success of male-female pairs are reported in more detail elsewhere (Chapter 4). The other birds nested either 1) singly, 2) as single-sex pairs, or 3) as members of multi-bond nesting groups. The latter two categories, in which the nest was built or eggs were incubated by a group of birds other than a male-female pair, are hereafter labeled "groups" and all three of these categories are called "atypical nesting units". The behavior and productivity of male-female pairs compared to atypical units are reported in more detail elsewhere (Chapter 2). Any two birds in these groups were considered bonded if they habitually performed affiliative behaviors, such as clumping or allopreening, in addition to occupying the same nest. If they did not clump, they were considered nesting together, but not bonded. Any number of birds which nested or attempted to nest together (i.e., pairs, groups and single nesters) are referred to as

"nesting units" or just "units".

Birds began nesting at different times. Behavioral frequencies, especially those of sexual behavior, varied over the course of the breeding cycle. To study a comparable period of time across birds, I used the day females laid their first egg of the first clutch they incubated completely as day 0 and compared behavior based upon when it occurred in relation to this day. For courtship and copulatory behavior, I included only behavior occurring during the females' fertile periods for these first clutches unless otherwise stated. Birkhead et al. (1989) defined the fertile period as day -11 to the day before the last egg is laid based upon his work on sperm competition in zebra finches. Since clutch sizes varied, the length of fertile periods also varied. To correct for the differing number of observation days during fertile periods, I report frequencies per day of observation unless otherwise stated.

Behavioral data collected during fertile periods refers to observations of females which completed incubation (that is, incubated eggs for the 14 days necessary for hatching) and males in those females' nesting units. For females which never laid a clutch or males which never bonded, behaviors were measured during the "average fertile period" of the colony. This was calculated using the first six fertile periods in a colony which included 75% of the

females in each colony. It started on the average start date of these fertile periods and continued for the average number of observations in those fertile periods, overlapping with 5-6 of the fertile periods in each colony. The incubation period is defined as the period from the end of the fertile period until 14 days after the first egg was laid.

The measurement of male courtship behavior is complicated by the female's behavior. For example, the frequency of a male's courtship display is determined, in part, by the female's response (Collins 1994). A male could sing and dance once or many times depending upon whether the female solicits, or stays but does not solicit, or dances with the male first and then solicits, or moves away after which the male could follow, or stop. Male courtship bouts were used as a variable in the analysis in addition to individual courts or songs, to correct for the confounding effect of the courted female's response. A courtship bout was defined as a group of songs beginning when the male first approached and sang to a bird and ending when the male initiated any non-sexual behavior or behavior not directed at the original bird. Courtship bouts were counted for each male during his mate's fertile period. Courts were counted during the 10 minute period per observation day during which each male was observed. Copulations were counted during the time any bird was observed in the colony, at least 160

minutes per observation day.

All statistical tests were nonparametric and two-tailed, and all differences reported are significant at the 5% level or better.

RESULTS

BEHAVIOR OF GROUPS VS PAIRS

Table I compares courtship and copulation data of pairs versus that of groups for the three colonies (see Table I). All summaries of intra- and extra-pair behavior included only males bonded to females, excluding the three single males and the one male member of a trio who was bonded to a male (described in Chapter 2). Although this latter group male eventually sat in the nest with the female to incubate or brood, he did not perform any affiliative behaviors with the female characteristic of a pair bond and was aggressive towards her until incubation. His affiliative behaviors were directed towards the other male in the trio, and his copulations, instead of being with the group female, were with other females.

Table 3-I. Median and range of male courtship and copulation behavior per observation day during mate's fertile period for all males, males which formed pairs, and males which formed groups.

	ALL MALES (n=24)	MALES IN PAIRS (n=13)	MALES IN GROUPS (n=11) *(n=7)	COMPARISON OF PAIRS VS. GROUPS (MANN WHITNEY U)
TOTAL COURTSHIP BOUTS	0.33 0 - 1.22	0.30 0.08 - 1.08	0.36 0 - 1.22	U = 40.5 p = 0.64
TOTAL INDIVIDUAL COURTS	0.47 0 - 2.18	0.44 0.08 - 2.18	0.55 0 - 1.88	U = 62.5 p = 0.56
INTRAPAIR COURTSHIP BOUTS*	0.31 0 - 1.11	0.30 0 - 1.00	0.32 0 - 1.11	U = 37.0 p = 0.45
INTRAPAIR COURTS*	0.28 0 - 1.67	0.22 0 - 1.36	0.32 0 - 1.67	U = 45.5 p = 0.94
EXTRA PAIR COURTSHIP BOUTS*	0.11 0 - 0.70	0.11 0 - 0.70	0.11 0 - 0.17	U = 24.0 p = 0.08
EXTRAPAIR COURTS*	0.17 0 - 3.20	0.27 0 - 3.20	0.17 0 - 0.23	U = 33.0 p = 0.29
TOTAL COPULATION	0.28 0 - 1.36	0.36 0.08 - 1.36	0.18 0 - 1.08	U = 44 p = .10
INTRAPAIR* COPULATION	0.27 0 - 1.08	0.25 0.08 - 0.91	0.29 0.17-1.08	U = 37 p = .45
EXTRAPAIR* COPULATION	0 0 - 0.56	0.10 0 - 0.56	0 0 - 0.09	U = 24 p = .08

* Does not include the 3 single males or the one male trio member who bonded to a male (n=7).

There were no significant differences between males in groups and those in pairs on any of these measures of courtship or copulatory activity (see Table 3-1).

The following data are from all birds, whether from pairs or groups, unless otherwise mentioned.

COURTSHIP

The social behavior of bonded males and females consistently indicated the existence of stable pair bonds (Chapter 2). However, birds often engaged in extra-pair courtships, solicitations, and copulations, the most common activity being extra-pair courting by males. When courtship displays of males bonded to females ($n=20$) were divided into intra- and extra-pair bouts, 21% of all courtship bouts were directed outside pairs, and 73% of the males that raised young to independence ($n=11$) courted females other than their mates. Males with all levels of hatching success and success in raising young to independence (see Chapter 2) engaged in some extra-pair courtship. However, in general, males courted their mates significantly more often than they courted other females (Wilcoxin Matched Pairs Signed Rank Test, $n=19$, bouts: $p=0.001$; courts: $p=0.03$). The frequency of individual courts by any male towards any female was significantly higher than the frequency of courtship bouts (Wilcoxin Matched Pairs Signed Rank Test, $n=16$, $p=0.0004$). However, when comparing extra-pair and intra-pair courtship separately, there was no difference between the frequency of

courtship bouts and that of individual courts by males towards their mates, while there was a difference in extra-pair courts (Wilcoxin Matched Pairs Signed Rank Test, intra-pair: $n=8$, $p=0.12$; extra-pair: $n=10$, $p=0.005$). Bouts of extra-pair courtship were longer, i.e., had more individual courts per bout, than intra-pair courtship (Wilcoxin Matched Pairs Signed Rank Test, $n=11$, $p=0.033$).

COPULATION

The most dramatic variation in copulatory behavior was the difference between the frequency of behavior during the fertile period and immediately thereafter. Copulation occurred at all stages of the breeding cycle, but dropped in frequency during incubation. For males and females, both total rates of copulation and rates of intra-pair copulation decreased significantly during the incubation period; however, the rate of EPCs did not drop significantly for either sex (See Table 3-II).

Table 3-II: Copulation per observation day for all bonded males (n=17) and all bonded females (n=16) during fertile periods and during incubation (does not include two late nesters).

	Fertile Period median (range)	Incubation median (range)	Comparison (Friedman 2-way ANOVA by ranks)
MALES			
Total Copulations	0.41 (0.17-1.36)	0.09 (0 - 0.45)	p=0.029
intra-pair copulations	0.29 (0.08-1.08)	0 (0 - 0.10)	p=0.0001
extra-pair copulations	0 (0 - 0.56)	0 (0 - 0.33)	p=0.63
FEMALES			
Total Copulations	0.30 (0.09-1.75)	0.00 (0 - 0.17)	p=0.0002
intra-pair copulations	0.26 (0.08-1.60)	0 (0 - 0.10)	p=0.0002
extra-pair copulations	0.04 (0 - 0.17)	0 (0 - 0.10)	p=0.21

Eighty-five ($n=20$) intra-pair copulations, or IPCs, were observed. During this time, males ($n=20$) engaged in a total of 23 extra-pair copulations, or EPCs, (21% of copulations by males) and females ($n=21$) accepted 13 (13% of female copulations). The EPC frequency was significantly lower than that of IPCs for both males and females (Wilcoxin Matched Pairs Signed Rank Test, males: $n=20$, $p=0.0007$; females: $n=19$, $p=0.0002$).

In 69% of pairs, males and females were consistent with each other on whether or not they had EPCs, i.e., either they both did or both did not engage in EPCs (Chapter 4). This was true in only two of the five male/female groups. Among pairs with EPCs, females had significantly fewer observed EPCs than males (Chapter 4). There seemed to be a trend in the opposite direction for groups. Only one group male copulated with a female other than one of his mates (and only during the fertile period of the mate which also had EPCs). Yet, half of the group females engaged in EPCs, a difference which was not significant.

Females did not resist during any observed EPCs. One EPC occurred through interrupted pair courtship. In this case, the female responded to her mate's courtship by soliciting, and another male flew over and copulated with her. This occurred so rapidly, it seemed possible that the female mistook the other male for her mate until after copulation.

COURTSHIP, SOLICITATION AND COPULATION

There were some unexpected dynamics in the copulatory behavior observed. As one might expect, not every copulation was preceded by a solicitation. More surprisingly, not every solicitation was followed by a copulation. There were many more observed courts, mounts and attempted mounts than completed copulations and even males with no observed EPCs during the fertile period had extra-pair courts during that time. And, although solicitations were less common than courts, many females had more observed extra-pair solicitations than copulations. Seven males and three females which had no observed EPCs, nevertheless, did have extra-pair courts or solicitations, respectively.

COPULATION WITH NONFERTILIZABLE PARTNERS

Males courted and copulated with both their mates and other females outside of their fertile periods. During the fertile periods of their mates, the group female or the average fertile period of the colony, males' extra pair courtships and copulations were towards nonfertilizable females twice as often as towards fertile females. All of these behaviors were demonstrated both by males from pairs and from groups and by those whose nesting units produced and did not produce young. Although there were a few males from pairs which courted fertile females, productivity did not predict which males showed extra-pair courts.

Males sometimes courted and copulated with other males. Seven percent of male courtship bouts were directed towards other males, 3% for pairs (2 birds) and 13% percent (4 birds) for groups. Three percent of the copulations by males were with other males, 2% for pairs (1 bird) and 6% for groups (1 bird). Both males which copulated with males during this period also copulated with females. Unpaired males had the highest numbers of both courtships and copulations directed toward other males. Only unpaired males had frequencies of courtship or copulation towards males higher than that towards females. During the period of observations encompassing the first six fertile periods of each colony, six males were observed copulating with other males, including three paired males, an unpaired bird and the two male members of a trio who behaved as if bonded.

There was also one pair which engaged in female-female copulations and one which engaged in reverse copulations, i.e., copulations in which the female mounts the male. The female-female copulations occurred in the female pair which raised young together (Chapter 2). The reverse copulations occurred in one of the male-female pairs which was not successful in raising young from their first clutch.

DISCUSSION

The median rate of copulations found in these colonies was consistent with that found by Birkhead in his captive colonies but lower than he observed in the wild (Birkhead et al. 1988). The drop in frequency of intra-pair copulation behavior during incubation is consistent with behavior in a number of species (Birkhead & Møller 1992). Not only are both the male and female spending a large proportion of their time in the nest, the start of incubation is an obvious indicator of the end of the female's fertile period. In swallows, Møller (1987) demonstrated that the male normally decreases his mate guarding frequency when his mate has a full clutch and spends more of her time in the nest; but, he will continue guarding at a high rate if the clutch is artificially kept at one and the female defers incubation. The lack of decrease in EPCs during incubation here may be because of the availability of other females who are or seem to be fertile.

There were no occurrences of forced EPCs except for the interrupted pair courtship mentioned previously. Birkhead et al. (1989) define interrupted pair courtship as a category of "forced" copulation, meaning the female did not seem to accept the male's advances. They also describe males forcing IPCs after their mates engaged in EPCs, which would devalue the EPCs through sperm competition. Although males in the present study vigorously chased their mates

after some extra-pair encounters, there were no "retaliatory copulations" following the 13 EPCs observed during the fertile periods of bonded females.

There were no significant differences between pairs and groups on any measure of courtship or copulation behavior. This means the rate of copulation or courtship per female did not vary between males in pairs and males in groups. For males bonded with more than one female, this means that they increased their rate of sexual activity to accommodate two females rather than dividing a constant number of behaviors between them. The effect was different in the only case of a group with two males which competed with each other for a female. This group produced two of the four highest rates of intra-pair copulation for males and the highest rate of intra-pair copulation for females, almost twice the second highest rate.

This copulation pattern supports the sperm devaluation sub-hypothesis of the sperm competition hypothesis (Birkhead and Møller 1992). Its predictions are that species with high risks of EPCs also have high copulation rates. The frequent copulations by one male would devalue or replace sperm of a competing male. The last male to copulate before fertilization has an enhanced ability to devalue or replace the sperm of any preceding males. Copulation frequencies are high in species in which females often copulate with more than one male, such as those that are polyandrous. In

this study copulation frequency was highest in the group having a female bonded to more than one male.

There are some data to suggest that females influence the frequency of male courtship. Collins (1994) showed that in a female choice apparatus, male courtship was related to both the proximity of the female and her preference. Males displayed more frequently when females were present and facing them and, while they were, preferred males displayed at higher rates. However, females were equally likely to leave preferred males while they were displaying as non-preferred males. In the apparatus used, males could not follow the females. In the current study, males were able to pursue females and continue courting. In some cases, they did so for protracted periods of time. These pursuits were often unsuccessful extra-pair courtships, which is one explanation for extra-pair courtship bouts being longer than intra-pair courtship bouts. Another explanation, assuming some of these courts were successful, is that females took longer to solicit in response to extra-pair courts. Males directed extended bouts of courtship towards both fertile and unfertile females.

Trivers stated that monogamous males should try to increase their reproductive success by sneaking copulations with other females while preventing other males from copulating with their mates (Trivers 1972). This assumes that the chance of fertilizing another female's clutch is

well worth the time spent away from the male's own mate and brood. Birkhead et al. (1989, 1990) demonstrated in zebra finches that EPCs can and do result in extra-pair sired young when they occur during the female's fertile period. Therefore, it was not surprising that there was a high level of extra-pair courtship and copulation in these colonies. However, it is more difficult to explain why there were more instances of males courting and copulating with nonfertilizable females than fertile females. Extra-pair copulations by males during their mates' fertile periods can carry some risk (Birkhead & Møller 1992). Elsewhere, I have shown that, of males able to raise some young to independence, males who engaged in EPCs during their females' fertile periods raised fewer young (Chapter 4). Therefore, the males from productive units who engaged in EPCs were engaging in risky behavior--if the goal of those EPCs was to increase their reproductive success. The four instances of copulations with fertile females involved 1) either males not bonded to females or 2) males whose own nesting units were unproductive. This may mean that these males actually increased their reproductive success.

This raises the question of whether there was some other motivation for copulations with nonfertilizable females or were the males unable to tell when females were fertile? In birds there are a number of possible indications of female fertility, including copulation

solicitation, flying ability (because of the extra weight of eggs), and nest building and the presence of eggs in the nest (Birkhead & Møller 1992). Females in this study solicited well before the start of the fertile periods for their initial clutches. Some zebra finch females may nest build in only the second half of their fertile periods, since nests are often established only a few days before egg laying, or could start constructing a nest and abandon it without ever laying. Both behavior patterns occurred in this study. Therefore, it may be advantageous for zebra finch males to treat females as if they are fertile at all times, except during incubation.

As used here, the term nonfertilizable simply means outside the fertile period. There were at least a couple of cases of productive males who obtained two (or more) EPCs with the same female, one before and one during her fertile period. The first EPCs, with unfertilizable females, occurred during the males' mates' fertile periods and were included here, but the second when the other females were fertile occurred outside the fertile period of their mates. It is difficult to say whether EPCs with unfertile females happened because the males were being indiscriminate or if perhaps they were increasing their chances of obtaining EPCs from these females when they were fertile.

It would be difficult to come up with a general theory to explain copulations which cannot, or are unlikely to,

result in fertilization, partially because of the range of examples of such behaviors. Examples, in species other than zebra finches, include: copulations without cloacal contact (e.g. kittiwakes: Chardine 1987), copulations well before fertility (e.g. common guillemot, some ducks, and starlings: Birkhead et al. 1987), reverse copulations (e.g. grebes: Nuechterlein & Storer 1989), female-female copulations (e.g. herring gulls: Shugart et al. 1988) and male-male copulations (e.g. pukeko: Jamieson & Craig 1987). Aberrant behavior or "mistakes" by the birds involved do not seem a likely explanation for most of these cases (for review of theories, see Birkhead & Moller 1992, pp. 88-95).

Male-male copulation has been documented in other species, such as the pukeko (Jamieson & Craig 1987). In this species, dominant males solicit copulations from subordinate males. Since a copulation results in some sperm depletion, this may give the dominant male an advantage if he is competing with the subordinate for fertilizations. The male-male copulations in this study were by birds which not only copulated with females, but, in most cases, also raised young. Therefore, it does not seem likely that these birds were sexually imprinted on males. Walters et al. (1991) showed that the structure of male-male courtship songs in zebra finches differs from that of male-female courtship songs. The structure of song directed towards males resembled that of undirected song, song not directed

at another bird, rather than that of song directed towards a female. The function of undirected song is not well understood. Although it is very similar to courtship song, closer study revealed that it is slower, has fewer introductory notes, and is less complex and rigid than courtship song (Sossinka & Böhner 1980). It also requires lower hormonal levels than courtship song (Pröve 1974) and so may represent lower levels of motivation. If songs directed at males have the same structure as undirected songs, then they could have a different, perhaps agonistic, function, rather than a sexual one and perhaps should not be classified as courtship.

Although on average, birds copulated within their pair bonds more often than outside their bonds, for individual birds copulation was an unreliable indicator of whether two birds formed a social bond and would try to nest together, because some birds engaged in more extra-pair copulation than intra-pair. The courtship and copulation patterns of the birds in this study were consistent with Triver's predictions that males should try to fertilize the clutch of their own mate, while at the same time trying to fertilize the clutches of other females. I found that males copulated more often with their mates during their fertile periods, while copulating with other females about a third of the time. During incubation males all but halted intra-pair copulation when their mates were obviously no longer

fertile, but did not reduce their frequencies of EPCs. However, it does not seem likely that these males were siring more young using this strategy. Males in pairs who engaged in EPCs during their mates' fertile periods 1) tended to produce fewer young (Chapter 4), 2) may not have sired all young in their nests since they had mates who also engaged in EPCs and, 3) in most cases, did not copulate with fertile females during their EPCs. On the other hand, females did copulate with males besides their mates when they were fertile, and so were likely to have a wider range of traits represented in their young. They also seemed to exercise some choice in accepting extra-pair courtship. Since these lasted longer than pair courts, the females were either withdrawing or not soliciting as quickly as with intra-pair courts.

There were some surprising results from this study. Among them were copulations with unfertilizable females, male-male copulations, and the lack of differences in the frequency of courtship and copulatory behavior between pairs and groups. Although there were no consistent differences in sexual behavior between pairs and groups, the variety of association patterns that were considered "groups" and the rarity of any one pattern may have masked any differences present. However, the individual cases of birds in trios adjusting their behavior may indicate a trend that would become more obvious with larger sample sizes of each type of

group. It is difficult to explain why males often copulated with females outside the fertile period and why male-male copulation occurred. Male-male copulation may be structurally (as in the song structure of the preceding courtship) and functionally different from female-male copulation even though they seem indistinguishable visually. Even if there is no structural difference between copulations with unfertilizable females, compared to those with fertilizable females, the former may be for assessment rather than fertilization. On the other hand, due to the uncertain timing of zebra finch breeding, it could be advantageous for both males and females to behave as if females were fertile as long as conditions are favorable to breeding and the females are not incubating.

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CHAPTER 4:
INTRA- AND EXTRA-PAIR BEHAVIOR AND INITIAL CLUTCH SUCCESS IN
CAPTIVE ZEBRA FINCH COLONIES

ABSTRACT

Observations were conducted on three colonies of 16 (8 male, 8 female) mature but sexually naive zebra finches (*Taenopygia guttata*) over 13 weeks and the full range of their behavior recorded. During this time, most birds completed at least one breeding cycle. Reported here are data from the first breeding cycle of all pairs which completed incubation (n=13). Among pairs which fledged young, three characteristics distinguished the most successful pairs: 1) on average, they took longer to initiate these clutches, 2) the males courted their mates relatively more than they courted other birds, and 3) both males and females engaged in fewer extra-pair copulations during the fertile period for these clutches. A variety of factors appear to be involved in total clutch loss. The data reported support the theory that there is a mix of copulation and nesting strategies in this opportunistic species and that it is important for finches to form a strong pair bond well before breeding occurs.

The majority of bird species have been classified as monogamous, based on studies of unmarked populations (Lack 1968). An explanation of this bias towards monogamy has been that, from an evolutionary viewpoint, monogamy is an advantageous mating system for birds, since male birds are as able as females to raise young once eggs are laid. Maintaining a pair bond for many seasons is also seen as advantageous for birds. There are some data supporting this hypothesis, as birds breeding with former mates show lower levels of aggression and higher degrees of within-pair synchronization, allowing them to breed more rapidly and efficiently and leading to demonstrable increases in reproductive success (Emlen & Oring 1977).

Sociobiologists have suggested that "monogamous" males should try to sneak copulations with additional females, but at the same time try to prevent other males from copulating with their mates (Trivers 1972). Many recent studies using individually marked birds have reported birds of supposedly monogamous species seeking or engaging in extra-pair copulations or EPCs (reviewed by Gladstone 1979; McKinney et al. 1984; Birkhead & Møller 1992). Advances in molecular biology have been used to confirm that some of these EPCs were successful in producing young (reviewed by Westneat et al. 1990; Gowaty & Gibbs 1993). These new data have led to new theories of mating system classification (Gowaty 1983; Wagner 1991).

Gowaty (1983) proposed a new classification system which assessed the "observed consort patterns among breeding adults" or "apparent" mating system of a species separately from determining which individuals make a genetic contribution to the next generation (i.e., actually contribute eggs or sperm). Wagner (1993), whose hypotheses were based upon observations of razorbills, suggested that one of the selective pressures for colony formation comes from males and females clustering to facilitate EPCs. Morton et al. (1990) theorized that purple martin colonies form because the older males establish nests early, attract younger birds to their colony, then obtain a majority of the extra-pair fertilizations with the females of these younger pairs. It seems that there are many selective pressures for the use of EPCs in a mating strategy. However, if too much time is spent seeking extra-pair copulations or mate guarding, this may interfere with parental care toward the brood in a pair's nest (Daly & Wilson 1983). The question remains whether there are selective pressures against exclusive pair bonds.

Zebra finches (*Taenopygia guttata*) are small passerine birds which have been described as forming long term monogamous pair bonds, maintained even when not breeding. These Australian grass finches are opportunistic breeders, using rainfall as an environmental cue for breeding. With sufficient water, food and nest material, they breed rapidly

and almost continuously, a fact which makes them very popular birds for laboratory studies on reproductive behavior. Often within a week of introduction, individual captive finches will associate with one particular bird. Behaviors indicative of pair bonding include clumping, allogrooming, following and investigating potential nest sites together (Butterfield 1970; Slater & Clements 1981; Silcox & Evans 1982; Böhner et al. 1984).

Early descriptive studies (Morris 1954; Immelmann 1965; Butterfield 1970) classified zebra finches as monogamous birds which paired for a lifetime. Most studies concerning zebra finch breeding behavior have focused on the earliest portion of the breeding cycle and/or examined the behavior of pairs in individual cages. Housing birds in pairs creates an artificial social environment since these gregarious birds normally breed in colonies. The current study was one of the few which investigated the behavior of colonies of birds across the entire breeding cycle.

Although Birkhead, et al. (1988, 1989) found evidence of extra-pair paternity in 11% of captive zebra finch broods and 8% of wild broods, there have been no published quantitative studies investigating how extra-pair social interactions affect the productivity of a pair's nest. In the only published study examining the relationship between individual behavior and reproductive success in zebra finches, Delesalle (1986) demonstrated that prior breeding

experience with a particular partner increased productivity. These data support the theory that the pair bond is important to productivity. Yet, EPCs are common in zebra finches. If one assumes that EPCs disrupt the pair bond, EPCs should also affect productivity. The present study addresses the question of whether males and females are less successful at raising their primary clutch if they seek or engage in extra-pair interactions.

METHODS

Both males and females zebra finches have many calls, but only males sing. Male courtship consists of songs directed toward the female, often accompanied by a visual dance display. In the course of normal pair-bond formation, the female initially responds to courtship by moving away, but eventually solicits copulation by crouching and tail quivering. This tail-quiver display is often followed by mounting and copulation culminating in cloacal contact by the male. Both the male and the female participate in care of the young starting with nest building. The female typically lays 4-5 eggs, and both birds share incubation and feeding of the altricial young when the eggs hatch about 14 days later.

The subjects were sexually mature but naive zebra finches, raised in our breeding colony at the American Museum of Natural History. From the time of their juvenile

molt, males and females had been housed separately. During this study, birds were housed in a 6 X 8 X 6 foot observation aviary. The aviary contained 8 nest boxes and 23 perches along one wall. Directly opposite this wall, separated from the aviary by an entire wall of one-way plastic, was the observation blind. Through the wall of plastic, the observer could see the entire aviary. To encourage breeding, the temperature was kept over 65°F and humidity was kept over 50%. Food, water, and nest material were available *ad libitum*.

Three successive groups of eight males and eight females were housed together in the aviary and allowed to pair and breed for at least 13 weeks. No bird was related to any other bird in its group. Each bird was individually and randomly marked with color bands for identification. Each bird was observed for 10 min. per day, six days per week. The full range of behavior was observed and recorded using a computerized (SSR) event recorder (Stephenson & Roberts 1977; Lamb, et al. 1979). The number and date of eggs laid and hatched, and young fledged were noted.

The current analyses of reproductive behavior and latency to nest include only the 13 male-female pairs which nest built exclusively with each other once pair bonds were established and which completed incubation (that is, incubated eggs for 14 days). The behavior and initial clutch success of birds which did not meet these criteria

(some of which occurred in each colony) are reported elsewhere (Chapter 2). A widely accepted criterion for pair bond establishment is clumping (sitting in contact) or, when more assurance is desired, clumping at a nest site (Butterfield 1970; Slater & Clements 1981; Silcox & Evans 1982; Böhner et al. 1984). Birds were considered to have pair bonded when they occupied a nestbox together or clumped together at a possible nest site. Birds which met these criteria also performed many other affiliative behaviors such as allopreening (which was not as exclusive) and synchronized behaviors, such as foraging and searching for a nest site.

Individual pairs began nesting at different times. Behavioral frequencies, especially those of sexual behavior, varied over the course of the breeding cycle. Conditions varied between the first and second clutches because the second clutch is often laid while the first brood is fledging and still dependent on the parents. To study a comparable period of time across pairs, I used the day females laid their first egg of the first clutch they incubated completely as day 0 and compared behavior based upon when it occurred in relation to this day. For courtship and copulatory behavior, I included only behavior occurring during the females' fertile periods for these first clutches. The fertile period has been defined by Birkhead et al. (1989), based upon his work on sperm

competition in zebra finches, as day -11 to the day before the last egg is laid. Courts were counted during the 10 minute period per observation day during which each male was observed. Copulations were counted during the time any bird was observed in the colony, at least 160 minutes per observation day.

The measurement of male courtship behavior is complicated by the female's behavior. For example, the frequency of a male's courtship display is determined, in part, by the female's response. A male could sing and dance once or many times depending upon whether the female solicits, or stays but does not solicit, or dances with the male first and then solicits, or moves away after which the male could follow or stop. Male courtship bouts were used as a variable in the analysis instead of individual courts or songs, to correct for the confounding effect of the courted female's response. A courtship bout was defined as a group of songs beginning when the male first approached and sang to a bird and ending when the male initiated any non-sexual behavior or behavior not directed at the original bird. Courtship bouts were counted for each male during his mate's fertile period.

Two measures of initial clutch success were calculated for the first clutch. The first was whether or not pairs hatched the entire clutch. The second was the number of young raised to independence, which was usually around 35

days after hatching. Birds successfully fledging young which survived to independence (termed "successful") were divided into those who raised the median number of two young (considered "moderately successful") and those who raised more than two (considered "the most successful"). Those raising no young were termed "unsuccessful".

All statistical tests were nonparametric and two-tailed, and all differences reported are significant at the 5% level or better.

RESULTS

PAIR BOND BEHAVIOR

Pair bond establishment was defined as the first day two birds were seen sitting together in or on a nest or investigating a nest together. Once this occurred, clumping (sitting in contact with another bird) was exclusive within a pair, with rare exceptions. Pairs clumped only with each other during the first 36 days of individual observations on Colonies 2 (four pairs and 18 occurrences) and 3 (six pairs and 30 occurrences). These data were not available for Colony 1.

Another common avian social behavior is one bird preening another or allopreening. This also tended to occur exclusively between paired birds; however, allopreening outside the pairbond was seen more often than extra-pair clumping. In Colony 2, during the first 36 days of individual observations of four pairs, there were 9

occurrences (out of 68 or 13%) of extra-pair allopreening between a male and female, 2 between females (involving an unpaired female) and one between males (involving an unpaired male). In Colony 3, during the first 38 days of individual observations of six pairs, there were 17 occurrences (out of 209 or 8%) of extra-pair allopreening between a male and female, 6 between females and one between males (an unusually brief bout).

Almost two thirds (62%) of the birds which formed pairs bonded initially within three days of introduction. Within six days of introduction, 89% had bonded. All the pairs were formed by 17 days. Although over half of the pairs had one clutch fail at some point during the study, there were no instances of "mate switching" or pair bonds breaking once birds had completed incubation of a clutch.

PRODUCTIVITY

Since unsuccessful pairs lost their young within a few days of hatching, they were unsuccessful both at fledging young and at raising young to independence. (See Fig. 1) The moderately successful birds lost some young early on; so, for them, fledging success equalled success in raising young to independence. Only for pairs in the most successful group, which did not lose any hatchlings, were there young that left the nest but did not survive.

COURTSHIP

The social behavior, such as that mentioned above, of

male-female pairs consistently indicated the existence of stable pair bonds. However, birds often engaged in extra-pair courtships, solicitations, and copulations, the most common activity being extra-pair courting by males. When male (n=13) courtship displays during their mates' fertile periods were divided into intra- and extra-pair bouts, 29% of all courtship bouts were directed outside the pair, and 78% of the males that raised young to independence (n=9) were observed courting females other than their mates.

A ratio was computed of intra-pair courtship bouts divided by extra-pair courtship bouts observed during each female's fertile period (computed after adding 0.1 to each numerator and denominator to avoid division by zero). The ratios of males from pairs hatching all their eggs were significantly higher than those of males from pairs with lower hatching success (Figure 2). Nevertheless, males at all levels of hatching success and success in raising young to independence engaged in some extra-pair courtship during their mates' fertile periods.

When comparing all males that successfully reared at least one chick to independence with those that were unsuccessful, there were no differences in either courtship ratios, total courtship bouts, or total courts, (See Table 4-I).

Table 4-I. Median male courtship behavior during mate's fertile period for males successful versus unsuccessful at raising some young to independence.

	SUCCESSFUL	UNSUCCESSFUL	COMPARISON
	MALES	MALES	MWU
	(n=9)	(n=4)	
Total Courts	8	7	p = 0.76
Total Courtship bouts	5	6	p = 0.82
Courtship ratios	3.86	2.50	p = 0.44

COPULATION

There were a total of 41 ($n=13$) intra-pair copulations observed during the females' fertile periods. During this time, males engaged in a total of 21 ($n=13$) extra-pair copulations, or EPCs (34% of copulations by males), and females ($n=13$) accepted 8 EPCs (16% of female copulations). These numbers differed because other birds in these colonies participated that did not belong to these 13 pairs.

Females did not resist during any observed EPCs. One EPC occurred through interrupted pair courtship. In this case, the female responded to her mate's courtship by soliciting, and another male flew over and copulated with her. This occurred so rapidly, it seemed possible that the female mistook the other male for her mate until after copulation.

Among all male-female pairs fledging chicks, females that had 100% hatching success had no observed EPCs during their fertile periods and all females with unhatched eggs had EPCs during these periods, a significant difference in behavior between the two groups (Fishers Exact Probability, females with 100% hatching, $n=5$ v.s. other females $n=4$; $p = 0.008$). Among successful male-female pairs, there was a significant difference between the most and the moderately successful pairs in whether or not they engaged in EPCs during the female's fertile period (20% of most successful, $n=5$; 100% of moderately successful, $n=4$; Fisher's Exact

Probability, $p=0.04$). Four of the five most successful pairs had no observed EPCs during this period (Fig. 3). The only observed EPC in this group was an unusual one. Early in her fertile period, the female had the EPC through interrupted pair courtship mentioned above. Only after this copulation, during egg laying, did the male engage in EPCs. This pair was the only one of the most successful pairs that did not hatch all their eggs (Fig. 3).

In 69% of the pairs, males and females were consistent with each other on whether or not they had EPCs during the female's fertile period, i.e., either they both did or both did not engage in EPCs. Successful pairs were significantly more likely to be matched than unsuccessful pairs (Fig. 3). Among pairs with EPCs, females had significantly fewer observed EPCs than males.

To compare copulation behavior measured during females' fertile periods, I used a ratio of intra-pair to extra-pair copulations (computed after adding 0.1 to each numerator and denominator to avoid division by zero). For both males and females, these ratios were significantly higher for the most successful birds than for moderately successful birds (Fig. 4 & 5).

There were some unexpected dynamics in the copulatory behavior observed. As one might expect, not every copulation was preceded by a solicitation. More surprisingly, not every solicitation was followed by a

copulation. There were many more observed courts, mounts and attempted mounts than completed copulations, and even males with no observed EPCs during their mates' fertile periods had extra-pair courts during that time. And, although solicitations were less common than courts, many females had more observed extra-pair solicitations than copulations. Three males and three females which had no observed EPCs, nevertheless, did have extra-pair courts or solicitations, respectively, during the females' fertile periods.

LATENCY TO FIRST CLUTCH

The latency from pairing to initiation of the first fully incubated clutch was significantly longer for the most successful than for moderately successful pairs (Fig. 6), while the latencies of unsuccessful pairs fell between those of these two groups. However, the latency to pair did not differ between the most successful and moderately successful pairs. Among successful male-female pairs, the more successful birds started their clutches later, which may have involved abandoning nests started early on. No above-the-median broods were started earlier than 20 days after introduction (Fig. 7).

DISCUSSION

In these captive colonies of inexperienced zebra finches, the sexual behavior observed was consistent with data reported for many birds, both captive and in the field, in that extra-pair activity was common and was shown by both successful and unsuccessful males and females. In addition, our data show that productivity varied with the dynamics of the pair bond and that there was some advantage associated with exclusive pair bonds. Among successful males, the more males courted their mates rather than other females, the more eggs they hatched. Among successful pairs, the more males and females copulated with their mates relative to other birds, the more young they fledged. There was also some advantage to mate familiarity. Successful pairs that were bonded longer before initiating their first clutch were more likely to have higher than median success in raising chicks. To summarize, among successful pairs, those having had more time as a pair and not engaging in EPCs had greater hatching success and raised more young than birds having had less time as a bonded pair and engaging in EPCs.

Most observed differences in behavior were between the most and the moderately successful birds, rather than between successful and unsuccessful birds. Therefore, there are likely to be different processes interfering with breeding in completely unsuccessful pairs compared to pairs raising some young. It is surprising that although there

were numerous cases of nest failure, there were no cases of mate desertion after the first clutch. There was one instance (involving four birds) of pairs bonding then switching mates; however, this switch occurred before either pair finished incubating a clutch. Mate switching before breeding has been documented in other species (Rowley 1983) and is not unusual. Studies on mate desertion in birds have found that younger birds and pairs which fail to raise young are more likely to break pair bonds (Coulson 1966; Bradley et al. 1990). Since these were all naive, young finches and there were many unsuccessful nests, previous data from other species would lead one to expect mate desertion after some of these failures. It is likely other factors are involved. Much of the work on mate desertion has been in long-lived seabirds which are only paired during the breeding season. In these studies, nest failure does not account for all cases of mate desertion (Coulson & Thomas 1983). When mates do switch after nest failure, it may be more because the pairs split and leave the breeding ground early when their nest fails. With less time to reinforce the pair bond, the pair may not reform the following season (Coulson & Thomas 1983; Rowley 1983). Zebra finches are different from the seasonal breeders in these studies in that their bond is maintained year round. In this study there is the added factor of restricted choice. There may not have been better options available to these captive birds so that mate

switching was not advantageous.

There were significant differences between the most successful pairs and the moderately successful pairs in both the time from colony formation to the first egg and the time pair bonded before the first egg. Most birds established pair bonds within six days after introduction, so it is not surprising that these two measures gave similar results. However, since there was a 15 day range in date of pair bond formation, the two measures may reflect different phenomena. It may be that pairs need both a minimum amount of time in a certain environment and a minimum amount of time to become familiar with a mate to achieve above median success.

It does not follow from these data that delaying the first clutch is necessarily an adaptive strategy in the wild. Wild zebra finches typically form pair bonds before conditions become favorable for breeding. The maintenance of year-round pair bonds has been cited as an adaptation to the dry, unpredictable climate of the Australian outback. Zebra finches feed their young fresh grass seed which in parts of their range is available only following unpredictable rainfall during warm temperatures (Davies 1977). By forming long-term pair bonds early in life and remaining with the mate even when not breeding, zebra finches are ready to take advantage of any brief improvement in environmental conditions. Since my subjects were already mature and in breeding condition before being grouped, the

lower success of clutches started before day 20 may indicate that birds are at a disadvantage if they are not already pair-bonded when conditions become favorable for breeding. In the field, the grass that is their primary food source only takes approximately 21 days to mature and seed. If a pair takes 21 days to develop a strong pair bond, then 14 more days to hatch eggs, it may not have the best food available for the young unless the rains continue. The more successful strategy seems to be to form pair bonds before conditions are favorable for breeding and thus be able to start a successful clutch within a week of rainfall--which is fairly typical of wild birds. As mentioned before, Delesalle (1986) demonstrated that prior breeding experience with a particular partner increased breeding success in this species. Our data support the theory that time spent together as a pair, even before the first breeding attempt, is valuable in this species. Therefore, it should be advantageous for zebra finches to pair bond as early in life as possible in order to gain time together before breeding, rather than breeding as a newly-formed pair.

Although there are many other behaviors besides courtship and copulation which may more directly affect a pair's success in raising young, there is evidence of indirect relationships between sexual behavior and productivity. Research from our lab (Sheridan 1985) has shown that females choose their mates primarily on the basis

of male courtship song, which suggests that this behavior should have some value in predicting reproductive success. Various workers have suggested that birds should invest less in their offspring if paternity or maternity assurance is low (Reviewed by Schwagmeyer & Mock 1993). Since it may be difficult for parents to identify genetic relationships in young birds, the sexual behavior of the mate might be used, instead, as a criterion for determining the amount of parental care to give. The male could use the observation of his mate engaging in EPCs during her fertile period as a criterion to judge whether the offspring he is to care for are his own. On the other hand, it would be important for the female to determine whether she can count on the male to help care for the offspring. The frequency of her mate's extra-pair courtship and copulation during her fertile period could predict the amount of time taken away from paternal care later on.

Recent research, including the present study, has shown that individual zebra finches use a mixed mating strategy. The matching of extra-pair copulatory behavior in pairs in this study may indicate that these birds adjusted their strategies to match their mate's. Birkhead et al. (1989), using DNA fingerprinting, demonstrated that extra-pair copulations by wild zebra finches are often successful in fertilizing eggs. However, the results reported here show that there is some cost associated with using EPCs as part

of a mating strategy, since their use was associated with lower hatching success and fewer chicks fledged in primary clutches.

Among successful pairs, there appears to be a qualitative difference between birds nesting after having been pair bonded for 20 days and those laying more rapidly. The pairs who nested after at least 20 days of experience as a pair were unlikely to engage in extra-pair copulations, did not lose hatchlings, and raised more young to independence compared to those nesting sooner. These data support the theory that there is a mix of copulation and nesting strategies in this opportunistic species and that it is important for them to form a pair bond well before breeding occurs.

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FIGURE CAPTIONS

Figure 4-1: Three measures of productivity of first clutches of the 13 male-female pairs formed which incubated a clutch completely; eggs = number of eggs laid; hatchlings = number of eggs hatched; fledglings = number of chicks raised to independence.

Figure 4-2: Mean ($\pm$ SEM) courtship ratio (number of intra-pair courts observed during fertile period of mate $\pm$ 0.1 over number of extra-pair courts observed during the same period $\pm$ 0.1) for males of pairs successful (N=5) or unsuccessful (N=8) in hatching their entire clutches. The ratios of the two groups were significantly different (Mann-Whitney U, $U = 6.5$, $p = 0.05$).

Figure 4-3: Total observed copulations by individual males during the mate's fertile period and individual females during their fertile periods of the 13 pairs which incubated clutches completely, grouped by pair and number of young raised to independence from their first clutches; male-wpc = male intra-pair copulations; female-wpc = female intra-pair copulations; male-epc = male extra-pair copulations; female-epc = female extra-pair copulations.

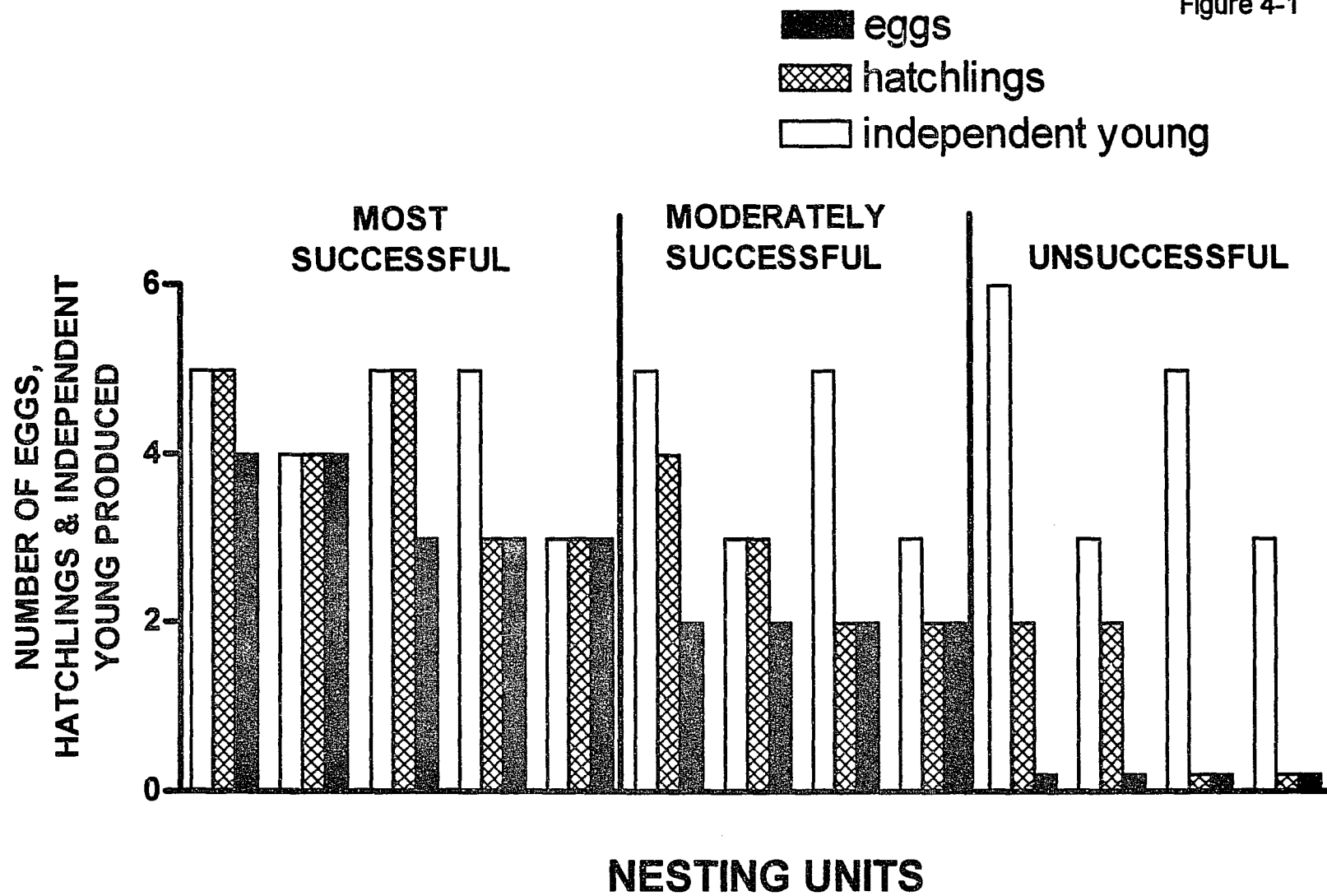
Figure 4-4: The copulation ratio of males which fledged chicks as a function of fledgling productivity. The copulation ratio was calculated as the number of intra-pair copulations observed during the mates' fertile periods, + 0.1, over number of extra-pair copulations observed during the same periods, + 0.1. (Spearman's Rank Order Correlation, $r = 0.72$, $df = 7$, $p = 0.03$)

Figure 4-5: The copulation ratio of females which fledged chicks as a function of fledgling productivity. The copulation ratio was calculated as the number of intra-pair copulations observed during females' fertile periods, + 0.1 over number of extra-pair copulations during the same periods, + 0.1. (Spearman's Rank Order Correlation, $r = 0.69$, $df = 7$, $p = 0.04$)

Figure 4-6: Mean ($\pm$ SE) days of experience with mate (number of days from establishment of pairbond to start of first clutch) for pairs moderately successful ($N=4$) or most successful ($N=5$) in raising some chicks to independence. The two groups were significantly different (Mann-Whitney U, $U = 0$, $p = 0.02$)

Figure 4-7: Number of days from colony formation to the first egg of the first clutch incubated completely as a function of chick productivity. No above the median brood started before day 20. Correlation not significant because of failed clutch started on day 61.

Figure 4-1



**MEAN INTRA/EXTRA PAIR
COURTSHIP RATIO
(+/- Standard Error)**

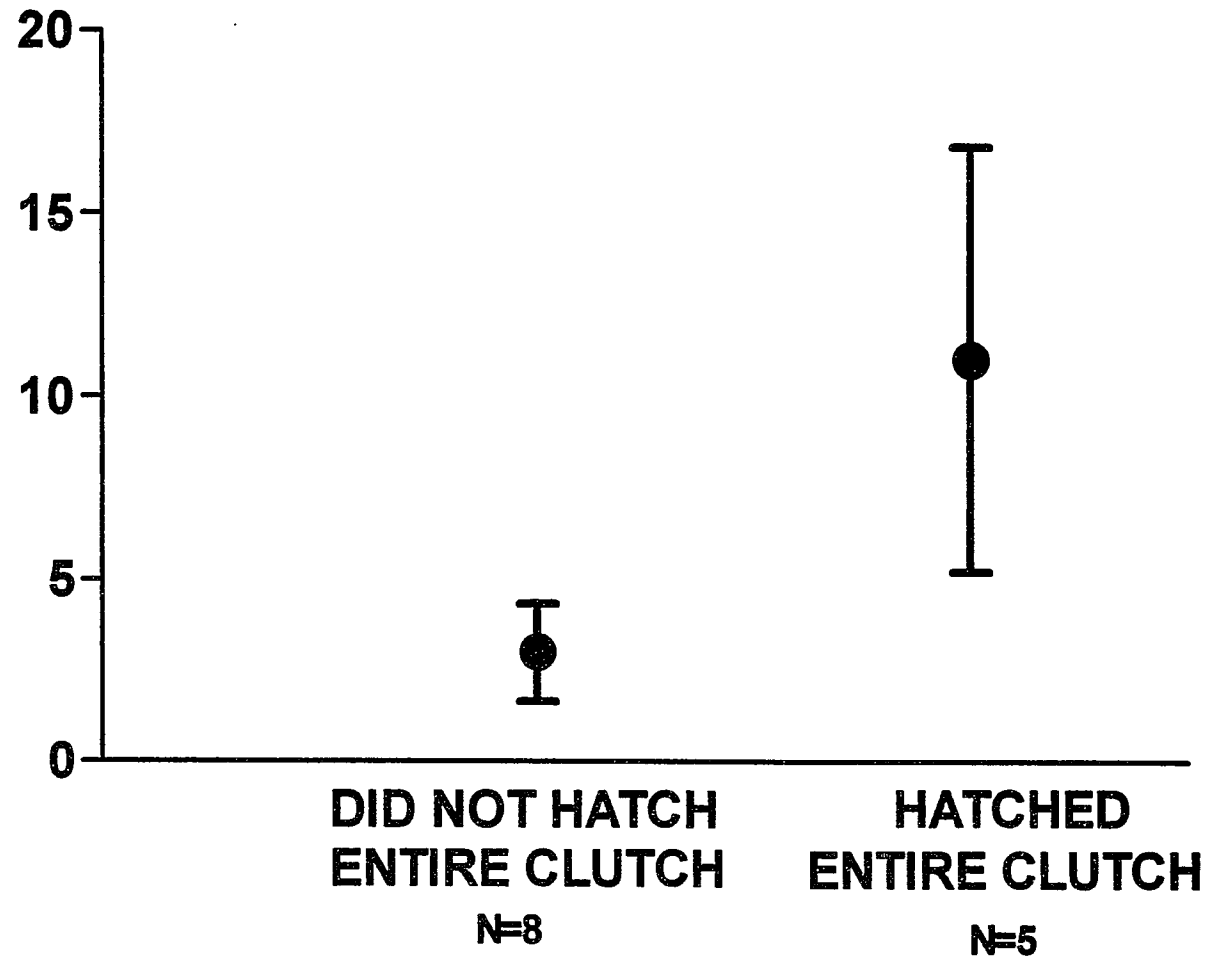
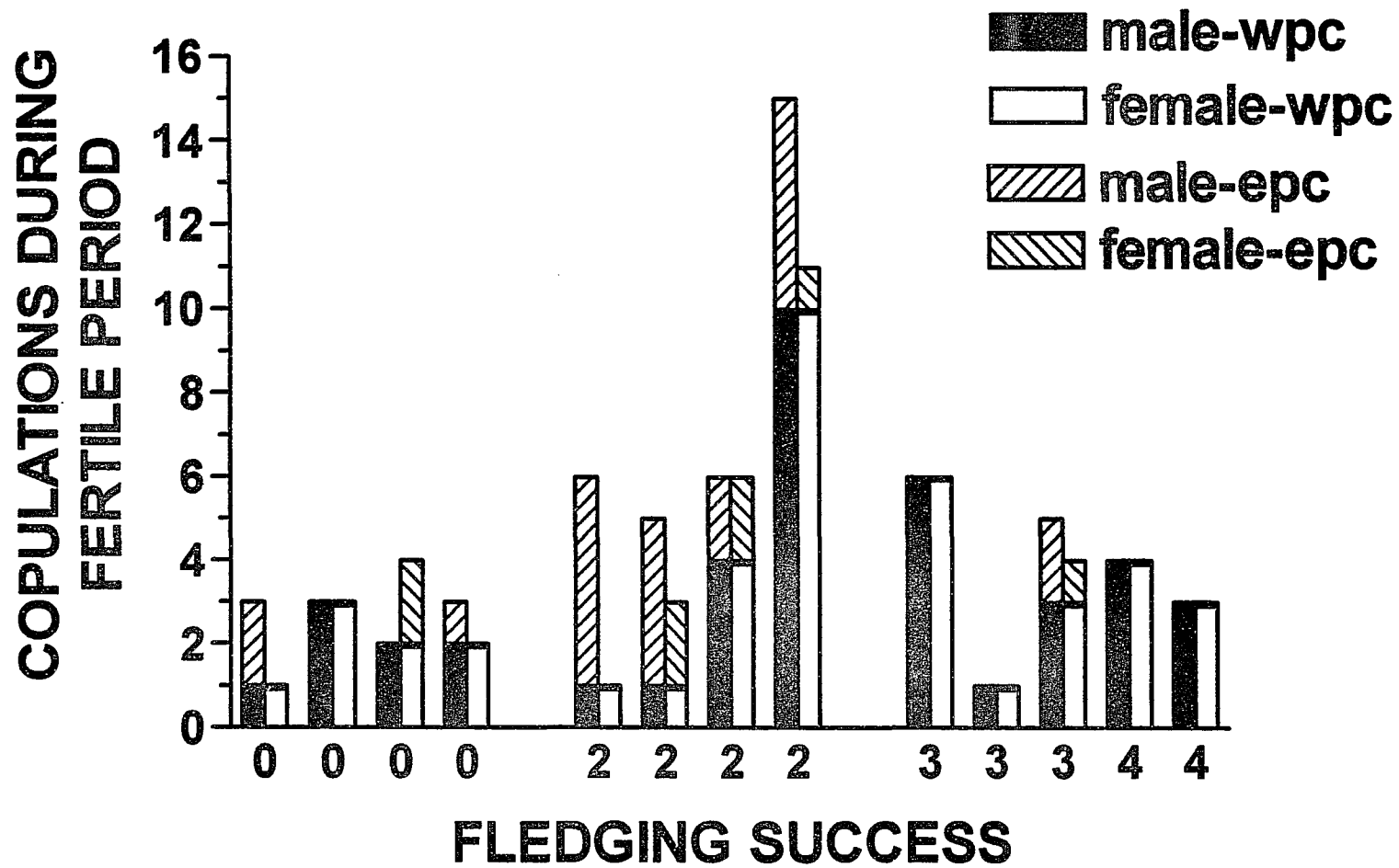


Figure 4-2

Figure 4-3



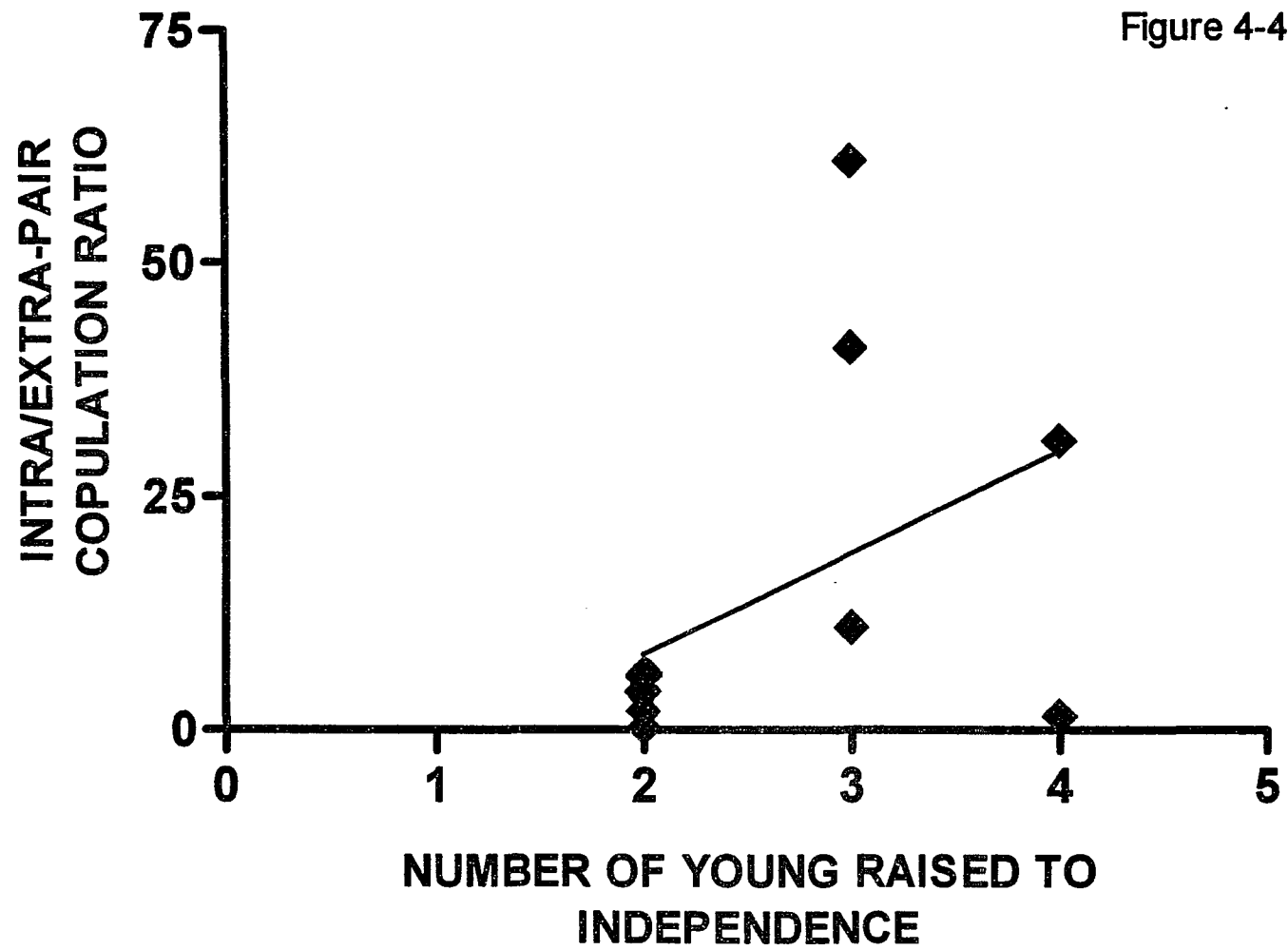
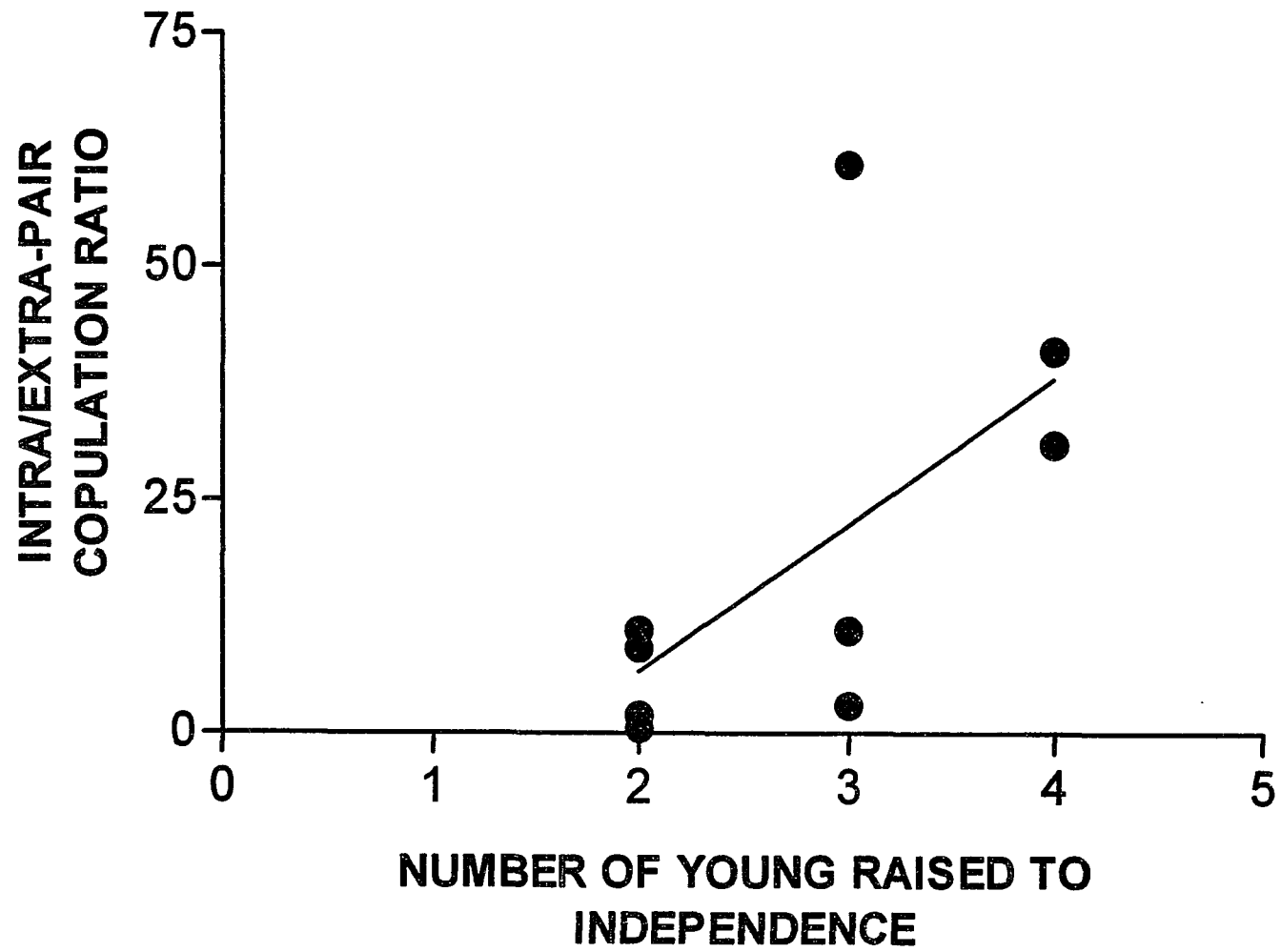


Figure 4-5



DAYS FROM PAIR FORMATION TO START OF FIRST CLUTCH

(MEAN $\pm$ SEM)

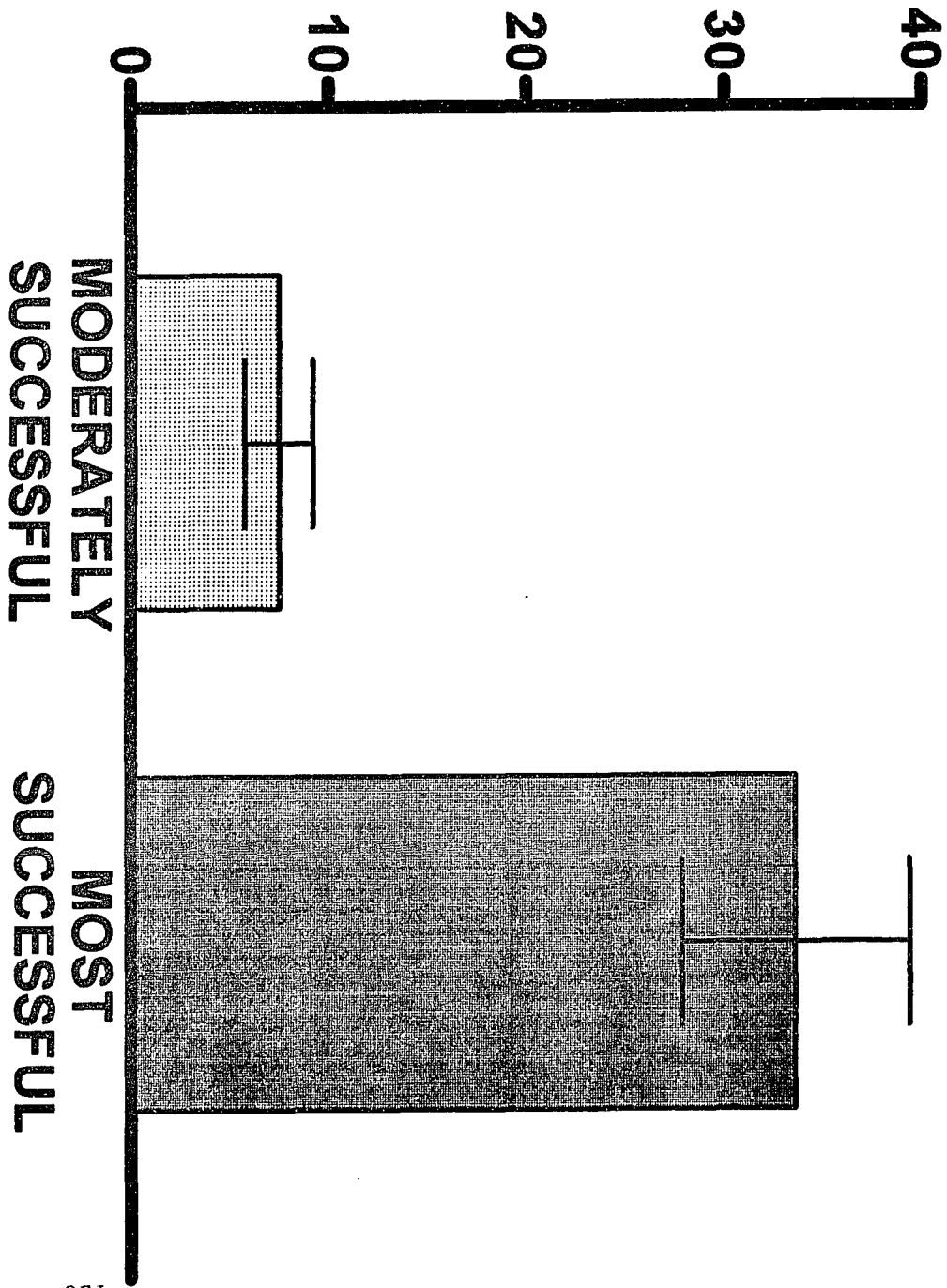
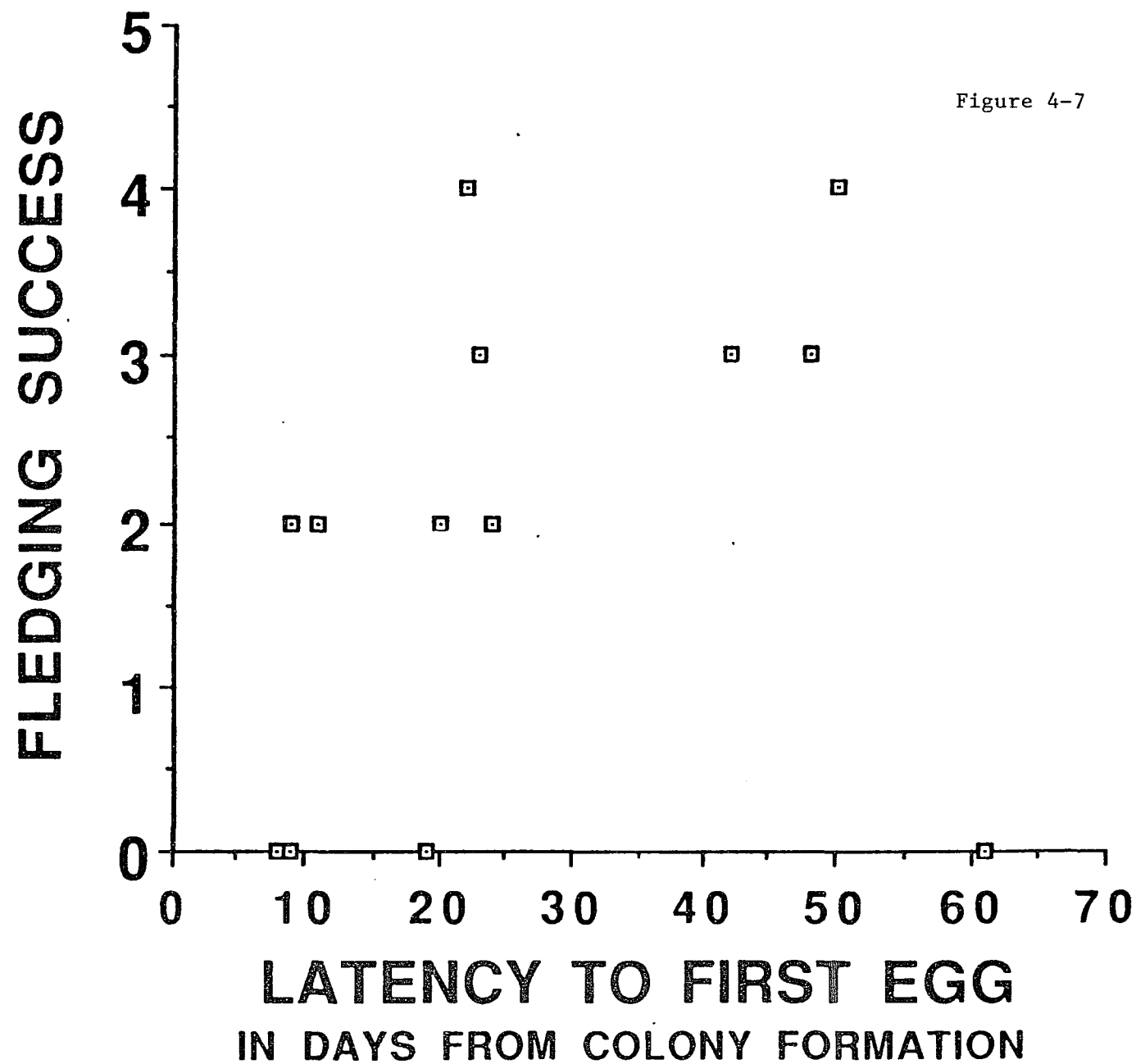


Figure 4-6



CHAPTER 5:

DISCUSSION

Early publications classified zebra finches as monogamous based upon descriptive field studies of unbanded birds. At that time, they were already well established in captivity and soon the captive and feral populations were separated because of the lack of new stock from Australia. Because they were easy to breed year round, domesticated finches became popular research subjects for behavioral and neurobiological studies on reproductive behavior. Researchers assumed that these birds were monogamous and studied pairs in individual cages or artificial choice situations. It was only after detailed behavioral studies on marked populations that deviations from monogamy became apparent. This pattern, of early mating system classification and latter reporting of deviations, typifies research in the field of behavioral ecology and the study of mating systems in many other species. The most common deviation is extra-pair fertilizations among apparently monogamous birds. This has been reported in both wild and captive zebra finches. Less common, is the forming of alternative bond-types. This has only been reported only in domestic zebra finches but occurs in wild populations of other species, especially gulls. In a number of gull species, since males and females look the same, it was only after marking individuals and observing them that it became

clear that there were single-sex pairs and polygynous groupings. In these species, this tended to happen when the sex ratio was skewed towards females. In short studies of zebra finch colonies with equal sex ratios in our laboratory, we had noticed similar groupings as well as many extra-pair copulations. I decided a longer more detailed behavioral study was necessary.

I determined the association patterns of the birds in this study based upon affiliative behaviors such as clumping and allopreening rather than sexual behaviors such as copulations. Although on average birds copulated within their pair bonds more often than outside their bonds, for individual birds, clumping was a more reliable indicator than copulation of whether two birds formed a social bond and would try to nest together, because some birds engaged in more extra-pair copulation than intra-pair.

These indicators of a bond, confirmed by other behaviors including maintaining proximity and behavioral synchronization, appeared not only between males and females, but between males, between females, and by one bird towards two birds. Most of these alternative bond types have been reported in either captive zebra finches or wild gulls or both. Although clumping was a good predictor of which birds established nests together, birds which nested together didn't necessarily show indication of a pair bond. This situation occurred in groups where two birds were

competing for a third bird and only tolerated each other. This has also been reported in other species where there is competition between nest members.

The courtship and copulation patterns of the birds in this study were consistent with Trivers' predictions that a male should try to fertilize the clutch of his own mate, while at the same time trying to fertilize the clutches of other females. I found that males copulated more often with their mates during their fertile periods, while copulating with other females about a third of the time. During incubation, males all but halted intra-pair copulation when their mates were obviously no longer fertile, but did not reduce their frequencies of EPCs. However, it does not seem likely that these males were siring more young using this strategy. Males in pairs who engaged in EPCs during their mates' fertile periods 1) tended to produce fewer young, 2) may not have sired all the young in their nests since they had mates who also engaged in EPCs and, 3) in most cases, their EPCs were not with fertile females. On the other hand, females did copulate with males besides their mates when they were fertile, and so were likely to have a wider range of traits represented in their young. They also seemed to exercise some choice in accepting extra-pair courtship. Since extra-pair courts lasted longer than pair courts, the females were either withdrawing or not soliciting as fast as they did to intra-pair courts.

It is difficult to explain why males often copulated with females outside their fertile periods. It is possible that females behave as if fertile as long as conditions are favorable to breeding and they are not incubating. Some even accepted copulations during incubation.

Some of the variation in sexual activity and affiliative behavior was associated with variation in productivity. Feral zebra finches seem to bond while young, well before breeding occurs. In this study, birds were more successful if they were bonded longer before starting their clutches, which could mean that zebra finches need some time to become familiar with each other before successfully rearing young. Birds also tended to have higher productivity if they had few or no EPCs, which could indicate a more established bond or some advantage in mate quality over less successful pairs. The groups with no intra-sexual competition were more likely to be successful. Those with competition within a nest tended to lose all their young after hatching. It is not clear whether this is a direct result of aggressive interactions or if the aggressive interactions interfered with proper care of the young.

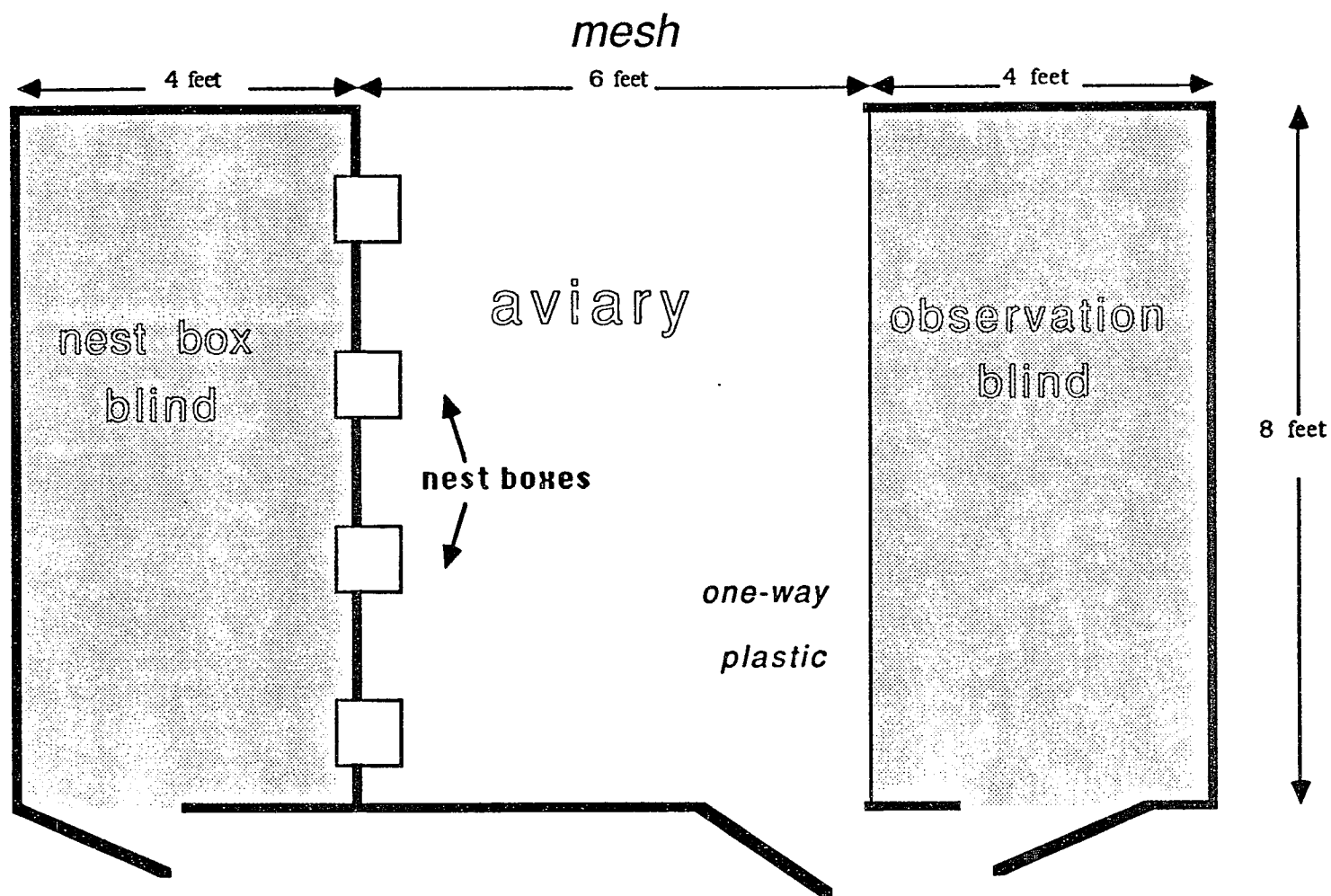
Zebra finches are highly successful opportunistic breeders. Stable, established pair bonds are important to their success in raising young. Although more often than not they breed as male-female pairs and copulate with their

mates, there are variations in their breeding behavior that show up in captive populations or in both captive and wild populations. Some of these variations still allow a median to high level of productivity while others seem to interfere with breeding attempts.

Detailed observations of marked populations of wild birds are necessary to determine the frequencies of these behavior patterns in wild populations and their effects on productivity.

APPENDIX I:
DIAGRAM OF OBSERVATION AVIARY

Figure A-1: During this study, birds were housed in this 6 X 8 X 6 foot observation aviary. The aviary contained 8 nest boxes (in two rows) and 23 perches (not shown) along one wall. Directly opposite this wall, separated from the aviary by an entire wall of one-way plastic, was the observation blind. Through the wall of plastic, the observer could see the entire aviary. From the aviary, the surface of the plastic was irregular enough to prevent a mirror effect. On the opposite side, in back of the nest box wall, was the nest box blind. Boxes could be slid out of their holders from this blind and be checked with minimal disturbance to the colony.



APPENDIX II:
BEHAVIORS RECORDED DURING OBSERVATIONS OF ZEBRA FINCH
COLONIES

SEXUAL BEHAVIORS:

Call-Rapid series of two or more short vocalizations, by male or female

Undirected Song (male)- A song sung while the head is not directed at any obvious object.

Follow- To move in the same direction as another bird, starting after that bird has started, and finishing in approximately the same area after the other has stopped.

Approach- To reduce the distance between the subject and the object of the subject's attention.

Courtship approach- To approach another bird with feathers and body in courtship posture (standing alert with feet stationary and feathers sleeked; in males: cheek, flank, and chest patches puffed).

Synchronous courtship approach- To perform a series of courtship approaches and withdrawals together with another bird.

Court (male)- To sing towards another bird, with or without accompanying species-typical dance.

Tail quiver- (usually female but often by male too) - To move tail up and down rapidly; used as solicitation display by female.

Attempted mount- To hop on the back of another bird but immediately fall off, usually because the mounted bird moves away.

Mount- To hop on the back of another bird and either to stay on for at least a second or to jump off voluntarily.

Cloacal contact (or "copulate") - To press the cloaca against the cloaca of the other bird, while mounted, by twisting the tail around and under other bird's tail.

Allopreen (duration)- To groom another bird's feathers with the beak.

Clump (duration)- To sit in contact with another bird.

NEST RELATED BEHAVIORS:

Approach nest - To move toward a nest to within half a meter.

Enter Nest (duration)- To move the feet into a nest box.

In Nest (duration)- Within edge of nest box.

On Nest (duration)- 1. On top of nest box. 2. To move onto nest box.

At Edge of Nest (duration)- 1. On lip of nest box. 2. To move to lip of nest box.

Leave nest -To move from either on, in or at the edge of a nest to elsewhere.

Peck Nest -To peck the nest box, usually the top.

Nest Call - To make a whining sound while performing stereotypical crouching or sitting movements at a nest site. This is sometimes accompanied by Tail Fan and/or Beak Chatter as well.

Pull Nest Material - To grab nest material held by something at the other end (often another nest), and to dislodge it or attempt to dislodge it.

Mandibulate Nest Material - To open and close beak while holding nest material in it.

Transport Nest Material - To fly while holding nest material.

Drop Nest Material - To let nest material fall after holding it initially.

Nest Build (duration)- To cause any movement of nest material in the nest either with the beak or by pushing it with the body after moving it with the beak.

Push - To apply sufficient pressure with body or head to move another bird.

Mate Pushing* - To grab a feather of another bird and pull it up or down, but not dislodge it.

Tug-O-War - To pull nest material while another bird is holding it.

Incubate (duration)- To sit on one or more eggs.

Feed Young (duration) - To regurgitate food into the beak of a chick.

Guard (duration)- To stand in a still but alert posture around a nest opening, usually while mate is inside feeding young.

Beg (usually young) - To give specific vocalizations with beak open and head wagging from side to side, usually with head lower than body and turned to the side.

LOCOMOTIVE BEHAVIORS:

Fly - To make any change in location that requires flying.

Fly Around - To circle the aviary at least once while flying.

COMFORT BEHAVIORS:

Beak wipe - To swipe first one then the other side of the beak on a perch.

Head wipe - To rub first one then the other side of head on a perch.

Shake - To make a sudden movement while perched that fluffs out the feathers and rapidly flaps the wings in an almost closed position.

Stretch - To extend one leg and the wing on the same side in a slow deliberate movement ending with a fast return to original position.

Scratch - To repeatedly swipe the head or the neck with a toe-nail.

At Cuttle Bone (duration) - To hang onto mesh within reach of cuttlebone.

Feed (duration) - To eat seed, greens, fruit or egg from dishes.

Forage (duration) - To hop along the floor, intermittently stopping and looking at it and/or pecking it and/or eating from it.

Drink - To drink from waterer, bath or any collection of water on floor.

Bathe (duration) - to stand or perform any activity while in a bath dish.

Yawn - Slow stretching open of the beak followed by rapid closing.

Sit (duration) - To have the body resting on a surface (perch, nestbox, or floor).

Head Tuck (duration) - To rest with the head under a wing.

Peck Foot - To peck one's own foot.

Peck Band - To peck the leg band on one's own leg.

AGONISTIC BEHAVIORS:

Threaten - To point a beak at another bird with stretched out neck.

Withdraw - To go from a position near another bird to one farther away.

Beak Chatter - To open and close the beak rapidly, usually, but not always from a threat position.

Tail Fan - To spread and close tail in a stereotypical manner.

Supplant - To land in spot vacated by another bird as it was approached.

Running Chase - To chase another bird along the floor.

Chase - Similar to Follow (q.v.), but faster, starting towards the other bird before they take off.

Peck - To hit another bird with point of beak.

Beak Fence - Mutual pecking or attempts to peck around the beak and face.

Attack - To collide with another bird.

Fight - To collide mutually with another bird.

*Mate Pushing

I measured a mate-pushing behavior, which has not yet been described in the literature. Mary Ann Sydlik (personal communication), while studying incubation behavior, noticed what is probably the same behavior, which she said occurred when birds were trying to replace their mates on the nest. In addition to these occasions, I saw it during the nest building stage. It involved one mate using its beak to lift the other away from the center of the nest. The motion, which resembled a nestbuilding movement, was very stereotyped and quick, since the active bird did not "hold" the push. I measured the frequency of individual lifts by one bird to another.

Mate pushing was sometimes followed by the pushed bird leaving the nest, but could be followed by a number of pushes or both birds pushing alternately with or without anyone leaving.

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