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MATE SELECTION IN THE ZEBRA FINCH, *POEPHILA GUTTATA*: THE RELATIONSHIP OF SPECIFIC HORMONE DEPENDENT MALE BEHAVIORS TO FEMALE CHOICE

by

Kevin Sheridan

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

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Abstract

MATE SELECTION IN THE ZEBRA FINCH, POEPHILA GUTTATA: THE RELATIONSHIP OF SPECIFIC HORMONE DEPENDENT MALE BEHAVIORS TO FEMALE CHOICE.

by

Kevin Sheridan

Adviser: Dr. Cheryl F. Harding

Because individuals birds vary in their quality as mates, it is critical to reproductive success that animals choose a mate rather than mate randomly. The most widely held view is that, because they invest more in reproduction, they make the final choice of a mate. The present investigation examined the role of male behaviors as criteria for female choice in a songbird, the zebra finch, Poephila guttata. In a series of experiments, three behavioral attributes of males, song, courtship dance, and nestbuilding, were varied to determine their relative importance. Triads of birds, a female housed between two behaviorally distinct males, were observed for a period of two weeks to determine female mating preferences. In the first experiment, the overall importance of male behavior to female choice was established; females preferred to mate with behaviorally intact males over males deficient in all three behavioral attributes. In the second experiment, females failed to reliably indicate a preference when given a choice between males equivalent in singing and nestbuilding, but differing in the frequency of courtship dances. The failure of females to make a choice was attributable to the fact that song equivalence was accomplished by muting both males and substituting playback for their song. In the third experiment, females preferred as mates males that sang, although these males couldn't nestbuild, over muted nestbuilding males, demonstrating the primary importance of song. However, when these females chose a male nestbox site for egg laying, the poor quality of the song male nests appeared to cause some females to switch their preference. In the final experiment, half the males received implants of an androgen, androstenedione (AE) raising their circulating hormone levels. Although the frequencies of behaviors of the AE males were not different from those of normal males, some measures of mate selection indicated that females preferred the AE treated males. This suggested that some other parameter of behavior may have been changed in the AE treated males, and was attractive to females. The possibility that female zebra finches may be able to detect the hormonal condition of males through their behavior was discussed.

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Kevin Sheridan
April, 1985

Dedication

I could have never come this far without the love and support of my parents, Helen and William Sheridan,. I owe so much to you. Throughout my years, you have always believed in my abilities and taught me that there was no limit to what I could achieve. Your belief in me did more for my health than any "vitamin" I could have taken. You continually encouraged, and never questioned, my idealistic goals. Thank you for your support, your patience and, most of all, your love.

My wife, Patricia, turned my study of mate choice into a personal preoccupation. As our relationship has progressed from fellow students to husband and wife, you have taught me more than any book or research project about the real benefits of being chosen as a mate. It was your love that enabled me to survive. You understood what I was going through like no one else could, and you were always there with the counsel, the sympathy, and the empathy that I needed. "This one's goin' out to you Dr. P. from your Dr. K.!"

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INTRODUCTION

STATEMENT OF THE PROBLEM

In order to maximize her reproductive success, a female must be very selective in her choice of a mate. In many avian species it is crucial for the female to be the primary determinant of whether a pair will mate, since her reproductive investment is believed to exceed that of the male; i.e., a mistaken choice would have a more profound effect on her reproductive success. The available evidence indicates that a female's decision may be based on a preference for some male attributes which, in addition to stimulating her reproductive physiology, are reliable indicators of the male's potential for successfully rearing offspring. The attributes which she finds "attractive" may also, ultimately, be phenotypic indices of the quality of the male's genes which would be expected to contribute to the the pair's inclusive fitness.

Although this view is widely accepted, we do not know what criteria females use in selecting their mates. The purpose of this dissertation project was to determine in a songbird species if particular behavioral characteristics of males are found attractive by females and used in selecting a mate. Previous investigations have determined: 1) that females respond selectively to variations in the stimulus quality of male behavior, and 2) individual differences in the behavior of males account for non-random mating patterns by females. It has not, however, been determined whether particular male behaviors actually direct female choice.

In the present investigation, female zebra finches, a monogamous

Australian grassfinch, were given the opportunity in an experimental setting to choose between two males for a mate. The attributes of the males were systematically varied in such a way that it was possible to assess the relative importance of various behaviors to female choice and determine which of three male behavioral characteristics, song, dance, or nestbuilding are of primary importance in female choice.

MATE CHOICE

Selecting a mate, in terms of its proximate as well as evolutionary consequences, is the most important choice an animal has to make. Potential mates may vary in quality, and it is assumed that natural selection has favored animals that can distinguish this variation and choose appropriately (Darwin, 1871). An individual, then, should be able to select a mate that will maximize its likelihood of reproductive success. The entire process, known as mate choice or mate selection, can be operationally defined as a pattern of behavior, or preference, shown by members of one sex that leads to their being more likely to mate with certain members of the opposite sex (Halliday, 1983).

Since first proposed by Darwin (1871), the predominant view has been that in most species females make the final choice in mate selection (O'Donald, 1983; Trivers, 1972). Justification for this assumption is that, in general, females are more limited than males in the number of gametes they can produce and the number of progeny they can successfully raise. In addition, compared to males, they invest more time and energy in reproduction including gamete production and progeny care, although recently it has been suggested that the male reproductive investment has been underestimated (Partridge and Halliday, 1984). However, even when there is considerable male involvement in reproduction, for instance when parental responsibilities are shared, the female investment is still assumed to exceed that of the male (Partridge and Halliday, 1984). It is crucial, therefore, in species where males do contribute to parental care that females pick a parenting male that will insure the survival of their offspring.

AVIAN MATE CHOICE

Perhaps the most extensive body of research on mate choice comes from the study of birds. In this family, the evolution of elaborate epigamic displays and unique mating systems has led to the assumption that certain traits are "attractive" and females choose selectively from among their suitors based on these traits. In fact, Darwin (1871) based much of his theory of sexual selection, individuals of one sex gaining an advantage over others of the same sex in gaining mates, on observations of avian species. For males the advantages can occur in either of two ways. First, males gain advantage over other males for access to females because they have evolved traits which enable them to dominate in inter-male competition; this is termed intrasexual selection. Second, males have evolved traits which are advantageous in "attracting" females and thereby increasing their mating success. This is termed epigamic or intersexual selection. These two processes are interrelated; male mating success is the result of both inter-male competition and the ability to "attract" females. As will become evident below, it is often difficult to discern whether a trait has evolved as a result of an intrasexual or intersexual advantage. For example, the elaborate plumage of males once thought to function primarily in attracting females, appears now to be of less importance in intersexual attraction than in intrasexual competition among males (Halliday, 1983).

For intersexual selection to benefit a female, the traits she assesses must be reliable predictors of the benefits a male offers to her reproductive success. In some species, reliability can be assured when the characteristics assessed are also the benefits. Female choice based on the qualities of territories held by males, such as food resources would be a good example. In other species, however, a male trait may only predict his beneficial attributes. In a monogamous species where the male contributes to parental care, an important factor for offspring survival, females must choose prior to mating for a behavior that will occur after mating. Selection should favor females which assess traits which reliably predict parental investment by the male and are not used by the male to deceive the female. In addition, in species where a pair form a long-term pair bond, the male trait should not only predict the male's behavior for the first mating, but reflect some invariant quality of the male to insure reproductive success in subsequent matings.

THE BENEFITS OF FEMALE CHOICE

Genetic benefits

The advantages of a female selecting an appropriate male as a mate may come from either influences on the quality of genes passed on to offspring or a more immediate factor for fitness such as offspring survival. Genetic fitness may be enhanced through the quality of the genes that are passed on to her offspring. This in combination with the later reproductive success of the offspring determines the female's ultimate reproductive success. Three subcategories of the genetic benefits which could accrue through female choice have been distinguished (Searcy, 1982). A female may choose so that: 1) her offspring inherit a high degree of fitness, 2) the genes of the mate are compatible with hers, or 3) to insure that "attractive" traits of the male will be inherited by offspring and, in turn, benefit their mating success (Fisher, 1930).

Unfortunately, there are no avian data demonstrating choice for the benefits a male provides to the genome of his offspring. The possibility of selecting a mate for his genetic fitness has been questioned because of the likelihood of low heritability (Maynard-Smith,1978; Partridge, 1983; and Searcy, 1982), and probable difficulty in detecting reliable phenotypic indices of genetic fitness (Halliday, 1983). Halliday (1983) suggests that the only tenable evidence for choice based on genetic fitness may be examples of preferences for older males, since age may indicate an ability to survive that could be heritable. In those species where epigamic characters take several breeding seasons to fully develop, a preference for fully developed males could, then, have a genetic benefit.

Choice based on compatibility of genes is primarily a matter of being able to detect relatedness. Phenotypic indices of genetic relatedness may play a role in the prevention of inbreeding within a species. In addition, females could also select a mate to optimize outbreeding (Bateson, 1983), picking both to maximize heterozygosity of offspring and maintain a gene complex adapted to a particular environment. The problem, here, is in detecting genetic features in the phenotype which indicate this. While it is likely that there are phenotypic indices of relatedness to avoid incestuous matings, being able to determine relatedness to optimize outbreeding is far more complex and would require a more precise indicator of relatedness. No evidence of such an indicator has been reported, although some studies have found preferences for related individuals as a consequence of sexual imprinting (Bateson, 1983; Slater and Clements, 1982).

The third subcategory of genetic benefits, "attractive" or epigamic characteristics directly related to genotype, was a basic tenet of Darwin's (1871) theory of intersexual selection in which characteristics of males which attract females evolved through sexual selection. In a recent article (Halliday, 1983), evidence for an epigamic function of morphological characteristics, particularly plumage, was reviewed and the author concluded that, based on available data, there is little direct evidence of an intersexual "attractive" function for plumage. Rather, plumage characteristics function primarily in interspecific reproductive isolation and intrasexual competition between males and thereby increase the likelihood that a male will become available to females or aid him in securing optimal resources. Thus, a female would indirectly choose a male with attractive plumage, either because he became available to her following competition with other males, as in lekking species for example, or because he controls the resources which she finds attractive in choosing a mate.

There may be no simple relationship between genotype and phenotype when it comes to characteristics which females use in selecting mates. However, it may not be necessary to use a genetic quality argument to explain the adaptive value of female choice. The benefits of choosing for qualities that affect the likelihood of offspring survival may be so substantial that it may be irrelevant whether or not the criteria for choosing can be passed on to progeny genetically (Halliday, 1983). Thus, through natural selection, females may have evolved mechanisms which enable them to select mates which have the important advantage of increasing reproductive success through benefits to offspring survival.

Benefits to the immediate reproductive effort

In contrast to research on female choice for male genetic quality, research directed at the more immediate benefits of female choice has been able to correlate male attributes which could increase female reproductive success with female choice. Factors which could benefit an individual's immediate reproductive success fall into four general categories: fertility, safety from interference, resource quality, and parental care (Halliday, 1983; Searcy, 1979, 1982; Trivers, 1972). While it has generally been assumed that males of most avian species are fertile once they reach sexual maturity and are ready to breed, recent evidence (Wingfield, pers comm.) indicates that hormonal condition and the related display rates of males may not be correlated with gametogenesis. How females could assess fertility independent of these other cues to reproductive readiness remains an important unanswered question. Safety from interference incorporates choosing dominant males, or those able to protect females' nests, eggs, or progeny by other means, such as aggressive behavior. Choice based on resource quality could also, although indirectly, select for dominant males or those who successfully gained control of better territories, nest sites, or food sources through intrasexual competition. Finally, choice for parental care involves selecting males that will engage in behaviors such as nestbuilding, incubation, brooding, and feeding which enhance the chances of successfully raising progeny. These categories are not mutually exclusive and males may have qualities related to any or all of them.

For avian females, the relative importance of these benefits will depend on the mating system of the species, length of pair association, male parental investment, and number of successive matings between a male and a female. The red-winged blackbird (*Agelaius phoeniceus*), for example, is a territorial polygynous species, and it is predicted that females would benefit more from the territory the male controls than other male characteristics, since he contributes little beyond fertilization and territory defense. In the redwing, territory quality is highly correlated with the harem size a male attracts (Searcy, 1979), and the quality of the territory is correlated with reproductive success as measured by number of young fledged (Lenington, 1980). The stonechat (*Saxicola torquata*), in contrast, is a monogamous passerine species. Males establish territories and provide substantial care for the young including nest defense. Nest defense seems to be more important to offspring survival than territory quality (Greig-Smith, 1980), and it has been suggested that a behavioral attribute of the male, song rate, which is positively correlated with male nest defense, is assessed by females in selecting a mate (Greig-Smith, 1982).

MALE ATTRIBUTES POTENTIALLY IMPORTANT TO FEMALE CHOICE

What then are the traits of males which could vary in their "attractiveness" to females? The characteristics which females may use in making their choice fall into three categories: male morphology, male resource quality, and male behavior. In addition to their potential intersexual function for "attracting" females, both morphological and behavioral traits may also influence the quality of the resources a male controls by functioning in intrasexual competition among males. The dual function of the traits in these categories, as well as the fact that most mate choice data is correlational and derived from field investigations, often makes it difficult to discern whether particular male attributes have a direct influence on female choice. The alternative is that the influence was indirect as a result of inter-male competition either to gain access to females or to gain resources which directly attract females. For example, among songbird species in which males hold territories, females may either choose a male directly based on his song, or song may indirectly influence choice by enabling the male to gain control of a quality territory - the trait actually chosen by the female. The emphasis of this dissertation project is upon the direct importance of male behavior in female choice, but because of the difficulty in separating the interaction of behavior with the other attribute categories a brief discussion of choice based on morphology and resource quality is necessary.

Morphological traits

The assumption about the existence of elaborate morphological characteristics, particularly plumage, in birds has been that these features evolved because they were "attractive" to females (Darwin, 1871). Some have suggested that plumage is a phenotypic index of genetic fitness (Halliday, 1983), and another suggestion (Fisher,

1930) has been that a female's inclusive fitness is enhanced because heritable morphological characteristics are passed on to sons whose success at mating will be greater resulting in a larger number of progeny in subsequent generations. This may explain how choice based on these characteristics is sustained, but it cannot explain how it became established; it is not clear what the initial advantage for a female would be to select males with elaborate plumage (Halliday, 1978). Andersson (1982) has demonstrated that female widow birds (*Euplectes progne*) prefer to nest on the territories of males with experimentally elongated tails. The preferences were independent of male display rates and any intersexual advantage longer tails may have had, suggesting that female choice was based primarily on this plumage characteristic. Male widow birds only develop long trails during the breeding season, and it was not demonstrated that longer tails have any advantage related to genetic fitness.

In some birds, morphological development takes several breeding seasons. In the argus pheasant (*Argusianus argus*), for example, the length and number of ocelli in a male's tail increases over a number of years (Davison, 1981; cited in Halliday, 1983). In such species, choice based on plumage might have an advantage for females, since it indicates the age of males which may reflect males' ability to survive. But no data yet support this contention. Rather, in the argus pheasant plumage is more likely to function in intrasexual competition; older males have a more dominant status because of their plumage.

In fact, an intrasexual function may best explain elaborate plumage in some avian males (Halliday, 1983). Data from the literature on lekking species, where males display in large groups, each defending a small territory within the display ground, were reviewed by Bradbury and Gibson (1983). They could find no consistent evidence that females chose males based on their morphological characteristics. It appears, rather, that plumage may function to get the male to the central display territory where he may then use his display to try to attract females. In the sharp tailed grouse, fully developed adult male plumage was found to be an important advantage in establishing a more central territory on the lek (Moyles and Boag, 1981). Data from other species support this view. Thus, while females may mate with males that have more elaborate plumage it is more likely that the choice is due to some other male characteristic such as resource control. The males either gain access to a resource or gain access to the females through intrasexual competition for which plumage was an advantage.

Plumage may, however, provide other information for a female to assess. Williams' (1983) and Klint's (1980) studies of mallards (<u>Anas platyrhynchous</u>) have found that females preferred males in nuptial plumage over males with non-mallard or incomplete mallard plumage. But these data suggest a species-recognition function rather than a sexual preference for individual males. In snow geese, Cooke and Davies (1983) report non-random mating based on color, but these data are based on two distinct color types (white and dark gray) and, again, not individual variation. The authors could provide no explanation of a functional advantage for the preferred dark gray males.

Resource quality

Investigations of resource quality and its relationship to mate choice in birds have been primarily concerned with territory quality as measured by features such as: number and quality of nests or nest sites, food sources, structure of vegetation, and territory size. There is evidence from a variety of polygynous species that suggests that females directly assess the quality of the territory a male controls. In the red-winged blackbird, Searcy (1979) found that over three breeding seasons female harem size was correlated with specific territories and not with the males that occupied them from season to season. Lenington (1980) confirmed this finding and found that the territories preferred by females produced the greatest number of fledgings, probably because of high food productivity. A similar relationship has been found between the quality of food available on a territory and female choice in the long-billed marsh wren (Telmatodytes palustris) (Verner, 1964; Verner and Engelson, 1970). In other species, the vegetative structure of the territory has also been found to influence female choice. Female lark buntings (Calamospiza melanocorys) prefer territories with more shade, and if shading is experimentally altered by changing the vegetative covering, female preferences change as well (Plesyczynska,1978; Plesyczynska and Hansell, 1980). In the yellow warbler (Dendroica petechia), females prefer males whose territories contain an abundance of shrubbery (Ficken and Ficken, 1966), again demonstrating a preference for the vegetative structure of a territory. Available nests in a male's territory may also be important to the female's choice of a mate. Unfortunately, most investigations of the relationship of nest quality to female choice are confounded by the nestbuilding behavior and nest displays of males, and these may be the traits actually assessed by females. In European wrens (Troglodytidae troglodytes), a preference for nests independent of behavior has been suggested. Garson (1980) found a correlation between the number of nests built on a territory and the number of females that were attracted to the territory, but was unable to demonstrate a relationship between nestbuilding behavior or displays and female choice. A similar relationship between the number of nests and the number of females on a territory has been found in the long-billed marsh wren (Verner and Engelson, 1970). In both these investigations, the apparent preference for more nests was independent of the number of nests available for females since there were usually many more nests than females on the territories; a large number of nests was simply more attractive.

The quality of resources found on a territory do appear to directly influence female choice in some avian species and these features are quite likely to benefit female reproductive success. It is difficult, however, to completely exclude the possibility that other factors, especially a male's behavior on the territory, are not also directly assessed by females even if they are of only secondary importance.

Behavioral traits

A third factor which females may utilize in their selection of a mate is male behavior. In comparison to other more static qualities, like resource quality and morphological characteristics, investigations of female preferences for male behavior are far more problematic. While "display" may be the unit of behavior believed to "attract" females, individual males may vary in several of the behavioral components making up the display. It is, therefore, difficult to ascertain which particular characteristics might be attractive to females. In addition, male behavior encompasses more than those behaviors commonly referred to as courtship displays. Other behaviors, such as the act of nestbuilding, may also be assessed by females in choosing a mate. The variability and complexity which makes the study of behaviors more difficult, nonetheless emphasizes the potential importance of behavior for female choice; male behavior may be very informative. A female could use individual variation in the behavior of males to choose the most appropriate mate from her available suitors.

Specific benefits of female choice based on male behavior.

If a female selects a mate based on some behavioral trait, what benefit to reproductive success is she likely to derive? For many avian species probably the most important behavioral information to assess would be the quality of the male as a parent. Trivers (1972) emphasized that the relative parental investment of the sexes in their young is the key variable controlling sexual selection. He proposed that in species where males contribute little beyond fertilization, female choice should be based on genetic or resource quality. In those species where males make a parental investment, females should have evolved mechanisms to assess the qualities that would predict a male's parental contribution. A female should prefer a male that can build a better nest, will incubate the eggs, feed the young and defend the nest and offspring, because without such contributions the females reproductive success will be diminished.

The inherent problem in choosing a male based on parental characteristics is that females must find some premating behavior of the male which predicts later parental involvement. In many birds, it has been established that the reproductive activity of males is dependent on the presence of gonadal hormones (See Balthazart, Prove, and Gilles, 1983). While there may be no simple direct hormonal relationship between a male's courtship behaviors and his willingness or preparedness to engage in parental behavior, aspects of early reproductive behavior may be indicative of later parental participation (Erickson, 1978). No data yet demonstrate that behaviors determined to be critical to female choice are indicative of parental care, although there are two examples of early reproductive behavior in males correlating well with later parental investment. In the stonechat, the pre-mating song rates of males correlate with later male nest defense activity and the number of feeding visits to the nestlings by males (Greig-smith, 1982). In the common tern (Sterna hirundo), the amount of food fed females by males during courtship is correlated with the amount of food fed later to the chicks (Nisbet, 1973). And while the majority of courtship feeding occurs after pairing and has considerable impact on reproductive success, early carrying and feeding of fish by males during courtship may predict later feeding of offspring. It is not known if the song rates of male stonechats or the courtship feeding of male terns are utilized in female choice.

In species that find new mates with each successive breeding, females may prefer more experienced males since experience may help to insure reproductive success. Behavioral changes as males age could then be used by females to pick a mate of considerable experience and avoid inexperienced males. In many of the species in which males build nests, including the zebra finch (*Poephila guttata*) (Sargent, 1965), the quality of nests built improves with experience and the selection of a male who builds a good nest could affect reproductive success. Song repertoire size is another behavior that has been found to increase with the age of a male in several species (canary, *Serinus canaria*: Nottebohm and Nottebohm, 1978; red-winged blackbird: Yasukawa, 1981b; See Krebs and Kroodsma, 1980 for review) and this could be used by females to select more experienced males. Other aspects of learned behavior may also be critical to females. For example, male behavior may be important in preventing incestuous matings. Australian grassfinches learn their songs from their fathers and by avoiding their father's songs, females can avoid mating with their brothers as well as their fathers. The ability of female zebra finches to recognize the song of their fathers has been demonstrated (Miller, 1979a).

Male behaviors and behavioral displays, therefore, have the potential to reliably convey information about a male for a female to assess. The reproductive and parental behavior of a male can have a profound influence on the proximate requirements for reproductive success.

Specific male behaviors relevant to female choice

Which male behaviors are important in female choice? Male displays particularly male singing behavior have traditionally been assumed to attract females. In those species in which males actively build nests, behaviors associated with nest building, including nest soliciting displays and displays near completed nests, may also provide clues about the quality of a male as a mate. Nest building by males, when it occurs following mating, is considered part of a male's parental contribution. In species where it occurs before mating it may predict later parental investment. These three classes of behavior: vocalizations (song), visual displays, and nestbuilding are male attributes which could be used by females to choose a mate. While they may not encompass all the behaviors females assess when choosing a mate, they provide a starting point to determine the relative importance of various male behaviors to mate selection by females.

Some data on this problem are available from investigations of a variety of avian species. The data come from two different lines of research. Field studies have attempted to define the relationship between these behavioral traits and mate choice or reproductive success. They have primarily used correlational techniques which, although they may find positive relationships, don't provide direct evidence that females use behavioral criteria to choose mates. Laboratory studies on the other hand, have focussed on the stimulating effects of male behavior on females, measuring changes in reproductive physiology or behavioral receptivity. These studies don't address the question of mate choice specifically, but do provide evidence that females respond differentially to variations in male behavior. A synthesis of these two lines of research can, however, contribute to an understanding of the role behavior plays in female choice of a male as a mate.

Both laboratory and field studies have tended to emphasize song at the expense of the other behaviors. The evidence suggesting the importance of male behavior in female choice will be reviewed according to their relative importance in the literature.

Song

Marler (1959) proposed that, in addition to its role in species recognition, song might function in individual recognition as well. Both of these functions have now been well documented (Falls, 1982; Miller, 1979a, 1979b). While individual recognition of song does not indicate that it is used in selecting a mate, per se, the ability to discriminate parameters of individual song plus the evidence of selective responsivity to song parameters does indicate that females can discriminate qualitative differences in male songs.

One of the problems in establishing the role of song in female choice is in distinguishing song's function in intrasexual competition among males from its direct intersexual function as a character assessed by females. This is especially true in polygynous species where theoretically the territory should be assessed by the female (Orians, 1969; Emlen and Oring, 1977) with song functioning to enable males to gain and maintain control of a quality territory. It is possible, however, that song may also function to "attract" females as well. Studies of several species demonstrate the difficulty of distinguishing the two functions of songs: the same song types are used in both contexts (village indigobird, Vidua chalybeata - Payne, 1979), the same parameter of a song is important for both functions (repertoire size in: red-winged blackbirds - Yasukawa, Blank,and Patterson, 1980; and mockingbirds, Mimus polyglottos - Howard, 1974), or a component of a song serves the second function (the presence of terminal phrases in songs used for territory control attract females in boat tailed grackles, _Cassidix mexicanus_ - Kok, 1972). In other species, distinct differences in the song-types used in different contexts are suggested based either on changes in frequency through the breeding season (black-throated green warbler, _Dendroica virens_ - Morse, 1970; Lein, 1972) or the frequency of occurence in the close presence of females (Cuban grassquit, _Tiarus canora_ - Baptista, 1978).

Laboratory investigations have emphasized the stimulus quality of male vocalizations in inducing changes in female reproductive physiology as well as changes in behavioral responsivity and proceptivity. Data from several species are available detailing the requirements for responses from the simple presence of vocalizations to the specific parameters of song causing the response. In the ring dove (_Streptopelia risoria_), ovarian development is stimulated by auditory, visual, and tactile cues. Females do not lay eggs in isolation from males. The visual presence of a conspecific or of a female's own image in a mirror (these birds are not sexually dimorphic) in concert with the sounds of the colony result in ovulation (Lott and Brody, 1966), but auditory stimulation alone is sufficient to induce the same result (Lehrman and Friedman, 1969). Auditory stimulation is, however, not necessary; deafened females will lay eggs with just visual and tactile stimulation, but the onset of nestbuilding and ovulation are delayed (Nottebohm and Nottebohm, 1971). Thus, while all three stimuli are important, vocalizations from the colony are most important in inducing ovulation at the normal rate. The behavior of individual males is also important. Females, when separated from a male by a transparent partition, do not ovulate in the presence of castrated males who no longer visually or vocally display (Erickson and Lehrman, 1963). Castrated males given androgen which restores behavior are able to provide sufficient behavioral stimulation for females to lay eggs just as intact males do (Erickson, 1970). Thus, ovulation can be induced by individual males only if they are behaviorally active. The primary importance of the vocal component of courtship was established by Friedman (1977) who exposed females to male courtship vocalizations in combination with different degrees of male visual stimulation. All females were stimulated by vocalizations including those deprived of any visual stimuli, but those who saw males actually courting them had the greatest ovarian response, demonstrating that the visual component of courtship was also important. In budgerigars (Melopsittacus undulatus), Brockway (1962) reported that while seeing and hearing other breeding pairs enhanced breeding, hearing pairs was sufficient. Ovarian growth can be stimulated in female budgerigars by the sounds of conspecifics (Ficken, van Tienhoven, Ficken, and Sibley, 1960), but it is male vocalizations which induce ovarian growth and nest building activity. This response is specific to the duration of the soft-warble vocalization which is closely associated with pre-copulatory behavior (Brockway, 1962). Similarly, Hinde and Steele (1978), studying the influence of external stimuli on the effectiveness of gonadal hormones in restoring behavior, found that hearing male vocalizations facilitated nest box entry by females. The effect was also species specific; the vocalizations of male canaries were not effective. Brockway (1964a, 1964b), however, reported that females do not solicit males for copulation unless males show a high level (frequency) of both visual and vocal display. Thus, while vocalizations are sufficient to induce ovarian growth and nesting activity, proceptive behavior was dependent on both the visual and vocal components of display.

In female canaries (Serinus canaria), and in many other seasonal breeders, reproductive development is initiated by increases in photoperiod. Stimulation from male vocalizations accelerates development, and decreases the latency to nestbuilding (Warren and Hinde, 1961). The playback of male song is sufficient to cause this effect when photoperiod is less than the spring optimum (11 hr., day vs. 14 hr. day) (Hinde and Steele, 1978). In Hinde and Steele's work on the influence of external stimuli on hormone effectiveness, photoperiod appeared to be primary to the initiation of nestbuilding in females, but male song playback again decreased the latency to nestbuilding and increased the amount of nestbuilding. As in budgerigars, the response to song was species specific; canaries did not respond to budgerigar song playback.

Female canaries also respond to specific parameters of male song. Kroodsma (1976) used artificial songs of different complexity (simple - 5 different syllables vs. complex - 35 different syllables), but identical duration, and played them to isolated females. The females exposed to complex songs gathered significantly more nest material and laid more eggs than females hearing the simple songs. Therefore, a parameter of song known to differ between individual males differentially stimulated female reproductive development.

Behavioral specificity in female responsiveness to parameters of male song has also been demonstrated in the song sparrow (Zonotrichia melodia). In a study testing the potency of certain parameters of song on female behavior, Searcy and Marler (1981) primed females with a dosage of estradiol sufficient to induce a selective behavioral response to song, the copulation solicitation display, and then played tapes of a variety of male songs. Not surprisingly, females responded preferentially to songs of conspecifics compared to those of heterospecifics (sympatric, swamp sparrow, Zonoitrichia georgiana; allopatric, chaffinch, Fringilla coelebs). When the syllabic structure and temporal pattern of the songs of the three species were interchanged, the response of the females was significantly greater to songs with both the syllabic structure and temporal pattern of their own species. In addition, female responses also favored variable conspecific songs (4 song types vs. 1 song type) and songs of eventual variety (repetition of initial song type followed eventually by a new song type-AAAAABBBCC) over songs with immediate variety (ABCABCABC). Thus, species specific selectivity in proceptivity based on the temporal pattern and syllabic structure of song was found. In addition, a preferential discrimination of traits typical of individual differences between males was suggested by selective responses to repertoire length and song-type variety, which may be a species-specific trait. These data suggest that a female may selectively mate with a male based on the quality of his song.

The selective copulation solicitation response of females has also been used to study male song potency in cowbirds (Molothrus ater). In this species, prior isolation is sufficient to make females responsive to song. Females respond preferentially to songs of the males of their own subspecies (M. a. ater vs. M. a. obscurus) (King, West, and Eastzer, 1980). Females also prefer the songs of isolated males compared to wild-caught males (King and West, 1977); and this is dependent on the presence of the second phrase of the song (a very brief modulation and tone in the range of 8-12 khz.) (West et al., 1979). In the wild, only dominant males have these potent songs and they appear to earn the right to sing them (West and King, 1980; West, King, and Eastzer, 1981). The use of this phrase is normally related to male dominance status, and isolated birds appear to sing them due to a lack of negative feedback from conspecifics. If males with low potency songs were placed in isolation they soon developed the high potency song, but when placed back in the colony were attacked by more dominant males. High potency songs did not insure a male's dominance. A male needed a higher status in order to be able to sing the more potent song. Potent songs, therefore, while necessary to achieve copulations, do not assure a dominant status or insure mating success. Males will learn to sing the songs of both subspecies when both males and females of the other subspecies are present, and females choose mates whose song repertoires contain a greater percentage of the females' native song variant (West, King, and Harrock, 1983). Thus, female cowbirds appear to use characteristics of the male song to choose mates of their own subspecies and, also, selectively solicit males whose songs contain a potent phrase related to dominance.

The research reviewed above indicates that the quality of male songs can differentially stimulate both internal gonadal responses and behavioral responses directly related to copulation and egglaying. While there is no apparent heterospecific consistency in the parameters which influence the stimulus quality of vocalizations, they do indicate that variations in song parameters result in female selective responses. However, it is still unclear whether song parameters differ between males in such a way that they are responsible for selective matings by females, beyond inter-species reproductive isolation.

Field investigations have provided correlational evidence of the relationship between male singing and female choice. In the village indigobird, a brood parasite of the African finch, both number of female visits to male territories and male mating success were found to be positively correlated with the mean number of minutes per hour a male sang (Payne and Payne, 1977). But further work (Payne, 1979) indicated that in addition to their apparent attractive function these same songs were used in inter-male aggressive contexts. Songs, therefore, appeared to have an inseparable dual function of excluding other males and attracting females.

Male mockingbirds have elaborate songs. In studying the behavior of these birds, Howard (1974) found that song repertoire size influenced the quality of the territory that males eventually obtained, and that the quality of male territories was inversely related to pairing date; males with better territories paired sooner. He also found that repertoire size itself was inversely related to pairing date. A partial correlation analysis revealed that while territory took higher priority in female choice, repertoire size also significantly influenced female preference for mates.

Kok (1972) attempted to determine the relationship of the behavior of males to ultimate breeding success in the boat-tailed grackle, a promiscuous mater. He found a high correlation between territory size and number of young fledged, and territory integrity was related to song rate. The terminal phrases of male songs, which are loud and carry well, appeared to serve as a female attractant and had the highest correlation with the number of young fledged. Here, then, a parameter contained within song was important in intersexual attraction, while the song itself had an intrasexual function in territorial maintenance.

The functional role of male vocalizations in female choice has been investigated more specifically in field research which attempts to correlate them with either the ability to attract females or influence successful matings. In red-winged blackbirds, the necessity of song for establishing and maintaining territories has been repeatedly demonstrated (Peek, 1972; Smith, 1976, 1979; Yasukawa, 1981a, 1981b), but it is the territory that a male controls which females choose in most instances (Lenington, 1980; Searcy, 1979). Other data, however, indicate that courtship intensity (Yasukawa, 1981a) and the frequency of the song-spread display (Weatherhead and Robertson, 1977) are also positively correlated with female nest density on territories and may also have a direct influence on female choice. In addition, song repertoire size has also been found to be positively correlated with harem size on a territory (Yasukawa, et. al, 1980), but repertoire size is also correlated with both male experience and the ability to maintain a territory (Yasukawa, 1981b) and this may explain these findings; the influence of repertoire size on female choice may be indirect.

Song repertoire size has also been hypothesized to have a dual attractive and territorial function in some species. A controversy exists, however, about repertoire length, its function, and its relation to mating system. Kroodsma (1977) found that polygynous North American wrens have more elaborate repertoires than monogamous wrens, presumably to attract more females. Catchpole (1980), on the other hand, reported the converse situation in European warblers (Acrocephalus); polygynous species had shorter repertoires than monogamous species. Based on the assumption that monogamous females place the highest priority on the male himself, and polygynous females on the resources of the male, he suggested that long repertoires would be best suited to monogamous males for attracting females. In the monogamous sedge warbler (A. schoenobaenus), Catchpole (1980) found a significant inverse correlation between repertoire size and pairing date; males with larger repertoires paired sooner. There was no correlation between territory quality and pairing date. Great reed warblers (A. scirpaceus) are polygynous and have both long and short songs in their repertoires. It appears that the long songs of these birds are intersexual in function. Catchpole (1983) determined that unpaired males sang long songs and that females in close proximity inhibited their production. Once a male paired, long songs were deleted from his repertoire, and when a rival male approached, males sang short songs. Using playback of long and short songs, Catchpole found males approached long songs but moved away when the playback was shifted to short songs. Reversing the playback order resulted in closer approaches once long songs were played. In addition, Catchpole (1982) cited unpublished data demonstrating that females approached playback of long songs. These data indicated that short songs have a territorial function, and long song an attraction function. Thus, it appears that, at least in European warblers, long songs attract females in both the polygynous and monogamous species. Krebs and Kroodsma (1980) caution, however, that in many species repertoire size increases with age, and this may be a confounding variable. But choice based on repertoire size as an indicator of age could only emphasize the usefulness of choice based on this attribute.

Another direction for investigations of the role of song as a criterion for mate choice has been to study changes in frequency of song as a consequence of seasonal changes or pair formation. The assumption of this work is that if song has an intersexual function, frequencies should be highest early in the breeding season and decrease following pairing or some other measure of a decreased necessity to attract females. This research is concerned with monogamous species, since there is no reason to assume that polygynous males would decrease their efforts to recruit females over the breeding season unless some parental investment is involved. Monogamous species account for at least 90% of all passerine species (Lack, 1968).

In an investigation of over 20 woodland species of passerine birds, one of the strongest relationships found was that song production peaked several days before the onset of egg-laying (Slagsvold, 1977; cited in Catchpole, 1982). In the white-throated sparrow (Zonotrichia albicollis), there is a significant decrease in male singing following pairing. Removal of females increases singing, and re-pairing produces a second reduction in song frequency (Wasserman, 1977). The implication is that song functions early in the breeding sequence and is being used to attract females. There is, however, another tenable explanation. Pairing could interfere with song production by changing a male's time budget, males simply having less time to sing. According to this explanation, an aggressive or territorial function for songs is be just as tenable; i. e., males would have less time to spend being aggressive.

In monogamous European warblers, similar changes in song production during the breeding season are also found. Male sedge warblers lose their characteristic diurnal pattern of song production after they have paired with a female. But it is not the result of interference with a territorial function of the song. Catchpole (1977), using playback of male song, found that prior to pairing males approached song (8 of 10 males) or gave threat calls (6 of 10), but following pairing, while still approaching (6 of 10), not one male sang (although 8 of 10 produced threat calls). Pairing, therefore, did not interfere with approaching the speaker or giving threat calls; the cessation of song could be related to the end of its functional usefulness.

Visual displays

While it is accepted that visual displays of males may attract females, there are few studies investigating this function. At one time it was thought that behaviors associated with presenting elaborate plumage to females were epigamic in function, but some theorists now argue that morphological traits serve a primarily intrasexual function (Halliday, 1983). In lekking species, for example, males compete for access to a central territory where they can then display to females and those with the more elaborate plumage are more likely to reach this area. In passerine species, the visual components of a display often occur in concert with the vocal component, song, and the functional effects of the two are difficult to separate. Most often, it has been assumed that song is the attribute which attracts the female; non-vocal displays are often ignored or assumed to be of only secondary importance. The occurence of these displays in close proximity to females as well as the fact that they are often directed toward the female suggests that they have an intersexual function and are an assessable attribute for female choice.

Most experimental evidence of the effect of the non-vocal displays of males on female reproduction concerns their stimulating effects on reproductive physiology. While these investigations do not directly demonstrate the effect of male behavior on mate choice, they demonstrate that females are sensitive to the quality of visual displays. In addition, it is not at all clear whether the hormonal responses of females to male behaviors are components of mate choice. Do females choose as mates those males whose behaviors are more effective in stimulating reproductive physiology?

Most investigations of the effects of male social stimuli on females have found auditory stimuli most effective, but other behavioral aspects may also be important. In ring doves, male vocalizations are sufficient to induce ovulation (Lehrman and Friedman, 1969), but they are maximally effective if visual components of the display are present as well (Friedman, 1977). Visual stimuli will produce the effect alone but the latency is delayed (Nottebohm and Nottebohm, 1971). In addition, if both visual and vocal components of courtship are eliminated as a result of castration, the simple visual presence of a male is not sufficient to induce ovulation; normal male behavior is required (Erickson and Lehrman, 1964). Thus, it is only in the presence of hormone activated male behaviors that ovarian activity is induced in females. In budgerigars, vocalizations are sufficient to induce egg-laying in females, but females only solicit copulations in the presence of both visual and vocal components of courtship display (Brockway, 1964a, 1964b), suggesting that both are needed to induce a behavioral preference. In Bengalese finches (*Lonchura striata domestica*), the ovulation of females is affected primarily by two variables, the presence of a mate and the ability to manipulate nest material. Egg-laying is not induced if females can, a) only hear singing males, b) only see nestbuilding males, and c) only have access to nest material without any male stimulation (Slater, 1969). Females will lay eggs with a normal latency only when they can both see males and manipulate nest material. Thus, the visual presence of a male contributes to ovarian development. The particular male behavioral characteristics females are responding to are unclear.

From these data it is apparent that male behavioral displays, other than vocalizations, may be important in some species and essential in others for ovarian development or responsivity to copulation attempts. While the data do not demonstrate that non-vocal behaviors are critical to selection of mate, they do suggest that females may be selectively responsive to male visual displays

There are also limited data from field observations demonstrating the relative importance of the visual components of displays independent of vocalizations in female choice. In a lekking species, the European ruff (Philomachus pugnax), Shepard (1975) reported that mate choice by females was dependent on three factors; possession of a central territory, the presence of satellite males on the territory, and high display rates. While the male residents of territories with the greatest mating success had some optimal combination of these features, which varied for different leks and different males, high rates of visual courtship displays appeared to be the most important factor leading to a high number of female visits and copulation solicitations. Thus, a parameter of visual display influenced female choice.

Another area of investigation has concerned behaviors associated with nestbuilding, including the nest advertisement displays found in some species. A problem, as mentioned earlier, is in distinguishing preferences for the quality of nest-related behaviors from those for the quality of the nests themselves (see above). Emlen (1957) observed that female whydahs (Vidua orientalis) and bishop birds (Euplectes hordacea) appear to assess both the nest and the nest display as they move through a male's territory. In the village weaverbird (Ploceus cucullatus), nest quality, primarily the freshness of the nest, appears to be related to female choice (Collias and Victoria, 1978; Jacobs, Collias, and Fujimoto, 1978), but the high display rates at fresh nests may also account for female preference (Garson, 1979) though Collias (1979) thinks that nest quality is more important.

Summary

The evidence from both laboratory investigations of female responsivity to behavioral stimuli and field investigations of the relation of behavior to female mating preferences, indicate that male behavioral attributes have significant potential to influence mate choice in birds. Male vocalizations have, historically, been presumed to "attract" females and the evidence, while not definitive, supports this contention. Selective responses to various parameters of song indicate that individual differences in songs can be detected. The particular parameters of importance, however, depend upon the species. Non-vocal male behaviors, while less extensively studied, may also influence the mating preferences of female passerines. The visual components which accompany vocal displays make a significant contribution to female reproductive responsivity. And although specific parameters of these behaviors have been largely unstudied, their frequent coincidence with song suggests a supplemental source of information about potential mates. Male nest displays found in some avian species, as well as the activity of nestbuilding itself, may also convey information about male quality.

Rationale

While investigations of a variety of species have implicated the behavior of males in determining a female's choice of mate, there is little evidence demonstrating that individual differences in male behavior direct the selection, although it is often assumed. Investigations in the laboratory have focused on the stimulus quality of male behavior in inducing changes in female reproductive physiology and behavioral receptivity. The data, which demonstrate that particular male behaviors are essential for these responses and that changes in the quality of behavioral stimuli alter parameters of the response, do not, however, demonstrate that females will select from among males based on the quality of their behavior. Investigations in the field attempt more directly to determine what male qualities are utilized by females in choosing a mate. Unfortunately, the limitations of field research enable only a determination of correlations between male behaviors and patterns of female mating preferences, and are not able to demonstrate that specific male behaviors direct female choice.

Historically, it has been assumed that the songs of male passerines attract females. Other non-vocal behaviors including visual courtship displays and nestbuilding behaviors are likely to have a similar function. To date there have been no systematic investigations in the laboratory to determine the effects of these behaviors on mate choice when their presence, quantity or quality are varied. The purpose of the present research was to determine the role of male behavior in directing female choice, and to determine which behaviors are most important to females in making a choice. These questions were addressed in a series of experiments in which three male behavioral attributes, song, visual courtship display, and/or nestbuilding, were varied. In each experiment, females were given the opportunity to select between two males differing in the three behavioral attributes. To insure that the preferences of females were sexual, they were given visual, auditory and some limited tactile access to males for a period sufficient for pair formation under normal circumstances.

The subject of the investigation was the Australian zebra finch. The zebra finch was an appropriate subject for such an investigation for several reasons. 1) According to previous investigations, these birds are monogamous, form long-term pair bonds, and show bi-parental care of the young. A female's reproductive success should, therefore, be greatly affected by the quality of the male and his behavior. 2) Individual males vary greatly in their reproductive behavior, so there is a basis for females to differentiate between them. 3) Measures of female acceptance of males indicate a selective responsiveness to individual males. 4) The male behaviors proposed to be relevant to female choice are sensitive to hormonal status, and preliminary evidence indicates that hormonally induced changes in male behavior do affect pair formation suggesting that females may select mates based on the quality of specific hormone dependent male behaviors.

STUDY I.

Zebra finches are common Australian grassfinches (Family, Estrildidae). Originally found in the semi-arid plains, their range now extends over most of Australia due in large part to the expanded use of irrigation. These birds are extremely gregarious and form large nomadic flocks when not breeding. They are colonial breeders with many pairs nesting in close proximity to one another in shrubbery. Zebra finches are sympatric with several other grassfinches, including the Bicheno finch (P. Bechenovi) and masked finch (P. Personata) (Zann, 1975). These other species sing songs similar in structure to those of the zebra finch, but their plumage makes them easily distinguishable and presumably evolved to aid in species recognition. The plumage patterns of zebra finches are sexually dimorphic; males have more elaborate markings.

Breeding biology

In contrast to most birds which are seasonal breeders, zebra finches are aperiodic, opportunistic breeders who take advantage of changes in the environment which predict optimal conditions for reproduction. The most reliable cue for the onset of breeding is rainfall (Immelmann, 1963), or possibly humidity (Preidkalns and Bennett,1978), and not daylength; only rainfall reliably leads to abundant seed and insects for feeding the young. In situations where this cue is continuous, as in irrigated regions or in humid laboratories, zebra finches will breed continuously. The mating system of these birds is also apparently an adaptation to the aperiodic climatic conditions of their natural habitat. Zebra finches have evolved two characteristics which allow them to take advantage of unpredictable rainfall; they are monogamous and form long-term pair bonds. This assures the availability of a mate to take quick advantage of any sudden improvement in climatic conditions (Butterfield, 1970; Immelmann, 1965).

In order to take advantage of optimal breeding conditions which occur so unpredictably, zebra finches should also be in a constant physiological state of near readiness to breed. Farner and Follett (1966) speculated that the zebra finch must maintain a relatively developed gonadal state year round. More recent evidence has demonstrated that for both females (Sossinka, 1980) and males (Preidkalns and Bennett, 1978), the gonads are normally maintained at a "medium" level of development and develop fully when the birds are placed in a humid environment.

Reproductive behavior

The sequence of sexual behavior begins quickly following the onset of the proper climatic cues. A male actively courts his female and the pair soon copulate. Courtship and copulations are repeated daily. Nestbuilding soon begins, with males gathering most of the nest material and both birds sharing in the building and shaping of the nest. Within two weeks the first eggs are usually laid, typically a clutch of 4-5 eggs. Both parents share in parental care, incubating the eggs (12-14 days), and then feeding the young by regurgitating food from their crops. The young fledge 14-21 days after hatching and by 30 days they may be left to feed on their own. The dimorphic plumage develops over the next 30 days, and by 90 days of age the young birds are ready to breed (Butterfield, 1970; Immelmann, 1965; Morris, 1954).

<u>Mate choice in zebra finches</u>

Previous interest in the process of mate choice in zebra finches has focused on the imprinting of preferences for particular color morphs. For males there is good evidence that early experience with parents of a particular color morph, usually all white vs. the wild-type coloration, results in preferences for a female mate of that same coloration (Immelmann, 1972; Walter, 1973). An imprinted preference in females for a particular coloration in males has not been reliably demonstrated (Immelmann, 1972; Walter, 1973; Sonneman and Sjölander, 1977; Immelmann, Kalberlah, Rausche, Stahnke, 1978; tenCate and Mugg, 1984), and the more recent investigations have speculated that male courtship behavior may also be of importance. Because the manipulations in these studies involve either extreme differences in coloration or cross-fostering to other species (usually Bengalese finches), demonstrations of female preferences in these experiments have emphasized their interspecific function in reproductive isolation. Intraspecific mate selection, however, must involve less extreme differences among potential mates.

The effect of color on preference in zebra finches has also been studied in an unlikely way by Burley (Burley, 1981; Burley, Krantzberg, and Radman, 1982). In the first report, aviary observations indicated that successful breeding was related to the color of the leg bands on both males and females, but the study was severely criticized on a number of grounds (Immelmann, Hailman, and Baylis, 1982; Thissen and Martin, 1982). In the second, the researchers found preferences in both males and females for specific leg band colors. Mating preferences, however, were not reliably demonstrated since choice was based on proximity during short choice trials (2 h or less). More reliable measures of mating preference, such as copulation solicitation and cooperative nestbuilding activity, were not employed.

The potential importance of male behavior, particularly hormone-dependent behaviors, for mate choice in zebra finches has been suggested in previous investigations in our lab (Harding, Sheridan and Walters, 1983). Following release into an aviary (Harding, 1983), the overall percentage of males from 8 different hormone treatment groups that kept the female with whom they had been paired for two weeks in isolation was low (26%), indicating that familiarity alone (Butterfield, 1970) was not sufficient for pair formation. Castrated males that received hormone regimens providing both estrogenic and 5&-androgenic metabolites were significantly more likely to keep their original females than males receiving other treatments (46% vs. 10%, respectively). In addition, six of these males (32%) not only kept their original females, but appeared to form a pair bond with a second female based on continued association, nestbox occupancy, and heteropreening. A similar effect from altered male hormonal status on pair formation has been found in the field. Wingfield (1984) has reported that when, normally monogamous, male white crowned sparrows (*Zonotrichia leucophrys*) and song sparrows (*Melospiza melodia*) were given implants of testosterone which increase circulating levels above normal levels, a substantial number of males in both species became polygynous. Thus, it appears that some hormone dependent attribute(s) of males may be important in attracting females.

The hormonal status of the male zebra finches also affected whether females would solicit them for copulation. Although at least one male from each of the eight treatment groups was solicited, a significantly greater percentage of males receiving treatments providing both estrogenic and androgenic metabolites were solicited than males receiving other treatments (62.5% vs. 38%, respectively). In addition, these males were observed copulating with significantly more females, possibly because females were more likely to accept their mounting attempts. It appeared that variation in hormone-dependent male courtship behavior might be responsible for selective solicitation by females.

Male endocrine status also affected male nesting behavior and female nest selection. Males treated with hormones providing estrogens were more likely to acquire good nest sites (in nestboxes) and build nests. More nests of these males had eggs in them; they also had a significantly greater number of eggs per nest. The preference of females for the nests of these males indicated that females might be selecting for behaviors that could affect their reproductive success. Whether females preferred the males because of their nests per se or some nest-related behavior was not apparent from the data. Thus, the data from this group aviary situation suggested that in the zebra finch, the behavioral quality of a male, specifically the quality of hormone-dependent behaviors, might be critical to female choice.

Three types of male behaviors, singing, the visual display which accompanies singing in courtship, and nest-related behaviors, are likely to be among those that females assess. It has been assumed that male courtship functions to "attract" a mate. Courtship behavior in the male zebra finch (Morris, 1954; Immelmann, 1962) consists of the combination of a vocal component, directed song (DSong), and a visual component, dance. While the two components occur simultaneously in courtship, they should not be considered as only a single cue. The parameters of song and dance may vary independently and each may provide distinctly unique information about the male to the female. Females selecting a mate may be responsive to either or both of these components of courtship. Another type of behavior which may be important to females is nest related behavior, primarily nest building. For this monogamous species, in which both male and female engage in parental behavior, the premating behavior of the male may be important in determining later parental involvement. If male nestbuilding activity precedes pair formation, this behavior may well be the best criterion for females in making a choice for a partner who will share parental duties, although some aspect of song or dance may also predict parental quality. For zebra finches, then, the behaviors with the greatest potential importance to female choice are song, dance and nest-related behavior, since they may be indicative of qualities of males critical to female reproductive success.

Before conducting experiments to determine which specific behaviors might "attract" females, it was necessary to establish that differences in male reproductive behaviors were detected by females and played a critical role in female mate choice. Female zebra finches were given a choice between behaviorally intact males which showed normal levels of directed song, the accompanying visual courtship, and nestbuilding and experimentally manipulated males which showed significantly lower frequencies of all these behaviors. It was hypothesized that when given a choice between behaviorally intact males and males deprived of these behaviors, females would select behaviorally intact males. We also predicted that some parameters of the quality of these behaviors would influence the choices made by females such that they would suggest specific aspects of behavior which serve an "attractive" function in female choice. Relevant information about the reproductive behaviors of both males and females are summarized below.

Male Behavior

Male song. While both male and female zebra finches have a variety of calls in their repertoire, only the male sings. Males sing in two different contexts. Directed song (DSong) is an integral part of all courtship, directed toward the female, and is believed to have an intersexual "attractive" function (Hall, 1962). Song also occurs without orientation to a particular conspecific in situations characterized by low levels of general locomotor activity (Caryl, 1970; Bischof, Böhner, and Sossinka, 1981). This undirected song (USong) is also characterized by the absence of the feather erection found in courtship.

The DSongs and USongs of any individual male sound very similar. Morris (1954) originally proposed that both songs were sexual in function differing only in threshold, USong having a lower threshold.

More recently, Sossinka and Böhner (1980) found that DSong had significantly more introductory notes (an avg. of 6.3 vs. 2.4), more song units (avg. of 3.3 more), and the length of the songs was shorter by an average of 19ms. They concluded that USong and DSong were different intensities of the same song. However, there is no continuum of intensity between the two song types; there was a discrete change in intensity between the types. Similarly, Caryl (1981) found no evidence of a motivational continuum and concluded that the USong was unrelated to a response to sexual stimuli (i. e., it was not sexually motivated). Both songs are hormone dependent, but if a male is castrated USong declines more slowly than DSong (Pröve, 1974; Arnold, 1975). Restoration of singing with androgen replacement reveals the same differences in reverse; USong has a lower threshold and is restored sooner (Pröve, 1978). The length of bouts of DSong, and possibly the tempo, is hormone dependent (Arnold, 1975). In addition, the frequencies of both DSong and USong are related to androgen titers (Pröve, 1974, 1978). It is feasible that females could assess the underlying physiological state of males based on these qualities of their songs (Sossinka and Böhner, 1980). The ability of females to recognize variation between the songs of individual males has already been demonstrated (Miller, 1979a, 1979b).

The Visual Component of Courtship. The visual component, or dance, which is always accompanied by DSong varies in intensity and the specific behavioral patterns incorporated in the display. In its low intensity form, a male assumes a fairly relaxed posture, turns toward the female and sings, fluffing the sexually dimorphic throat feathers, often twisting the head from side to side. In a high intensity dance, the male stands erect, sleeks the feathers on top of his head, fluffs out the sexually dimorphic feathers on cheeks, throat, and flanks. and hops down the perch toward the female, turning 180° with each hop, twisting head and tail toward the female and singing at each turn (Morris, 1954; Harding, et al., 1983). The hormonal specificity of this display is well established. Following castration, the courtship dance decreases in frequency and intensity, and latencies are increased. These effects can be reversed by proper hormone replacement therapy (Arnold, 1975; Harding, et al., 1983). There is a linear relationship between androgen level and courtship frequency (Pröve, 1974, 1978) and the duration of initial courtship bouts is also sensitive to hormone state (Arnold, 1975).

Nestbuilding behavior. In the process of pair formation, following the initial period of interaction, both the male and female solicit for nest sites (Caryl, 1976). The majority of the soliciting is done by the male (personal observation), but the female is though to make the final selection of the nest site (Sargent, 1965). Nest solicitation was first described by Morris (1954) and involves stretching movements sometimes accompanied by drooped wings and a fanned tail. The behavior is usually accompanied by a vocalization best described as a whimpering call (Caryl, 1976). This nest vocalization also appears to occur without the the nest solicitation posture and is more frequent among males. It also closely resembles the introductory notes of a male song (personal observation). The vocalization is emitted in close proximity to the nest site and is usually terminated when the male lands at the nest site. Despite its existence, few researchers have either observed or reported this nest vocalization behavior especially in relation to pair formation. One reason may be that the vocalization, which often is the best indicator of nest soliciting efforts by a male, does not carry well and can only really be heard in a bird room if monitored closely by microphone. There is, therefore, little known of its potential as a male attribute related to female choice, or its dependence on the bird's hormonal status.

Nestbuilding is shared by both the male and female, but usually the male gathers most of the nest material (Caryl, 1976). It is not known if gathering and nestbuilding attract the female or whether pairing occurs first. Harding, et al. (1983) failed to find a relationship between gathering nest material and hormone treatment among isolated pairs, but did find that in a group aviary, high rates of nestbuilding were hormone dependent and that it appeared to be attractive to females (Harding, 1983). Castrated males whose treatments provided estrogenic metabolites had shorter latencies to nestbuilding and more developed nests. Females initially preferred to occupy these nests, sometimes abandoning their original males. Only when the nestbuilding of the other males "caught up" with the estrogen-treated males did females return to their original mates. Implicit in these observations was an "attractive" aspect of the nest and possibly a preference for more efficient nestbuilding by males.

Female behavior

Female preferences for males can be determined using a variety of measures including overall proximity to a male. Critical to an investigation of mate choice, however, is that actual mating preference are measured. Reliable measures of mate choice include: measures of preferences for male nest sites (nest solicitation, nestbuilding, nest-occupancy, and egg-laying) as well as measures of behavioral receptivity (copulation solicitation). In soliciting for copulation, the female crouches on a perch and assumes a rigid horizontal posture with her head lowered. In many cases this posture is accompanied by a rapid vertical vibration of the tail called a tail quiver (Morris, 1954). Almost without exception, males will mount a soliciting female and copulate. Solicitation, though, is selective; it is infrequently observed, especially during initial courting, and successful mating attempts rarely occur without it. For these reasons it appears to be a strong indicator of female choice, at least for copulation, if not for pair formation.

METHOD

Experimental design

The experiment employed a choice paradigm in which females were presented with 2 males, differing in their behavioral attributes, and allowed to freely choose between them. The choice for females was between a behaviorally intact male that could sing (S+), dance (D+), and nestbuild (N+) and a male in which these traits were reduced or eliminated (S- D- N-). Females lived in experimental cages between the two males. Each triad (a female and her two males) was observed in an experimental cage for a period of two weeks, a period normally sufficient for pair formation (Butterfield, 1970). Experimental triads were run in blocks of six. Positions of birds in cages were counterbalanced across experimental treatments as were the order of both morning and evening observations. Three blocks of females were run for a total of 18 females.

Subjects

Zebra finches were obtained from our breeding colony at the American Museum of Natural History. Young birds were removed from the breeding colony at 30 days of age and grouped in a standard flight cage (1.22 x .61 x .61 m) for approximately two weeks until their juvenile molt had progressed sufficiently so they could be sexed by their sexually dimorphic plumage patterns. They were then placed in iso-sexual holding aviaries until approximately 150 days of age. Since white feather coloration has been shown to have some influence on mate choice (Immelmann et al., 1978) only birds with gray or beige wild-type plumage were used in experiments.

All birds were maintained on a 14:10 light:dark cycle and a relative humidity of at least 50% throughout the experiment. Birds were fed a commercial finch mix supplemented with a vitamin-mineral compound (AVIA), water, grit, and cuttlebone, ad libitum. Prior to being placed in experimental cages, fresh orange and chicory was also part of the birds diet.

Both males and females selected for the experiment were sexually naive and at least 150 days of age with an age range of not more than 30 days in each group. All birds had good plumage and no visible signs of illness. Approximately 5-6 weeks before the experiment, males were selected from the holding aviaries. Matched pairs of males were selected at this time based on coloration, age, and weight, in that order of priority. Surgical alterations of the behavioral attributes of males were also conducted at this time. Male pairs were kept in separate flight cages in groups of six until two days prior to the beginning of behavioral observations. The matched pairs were then placed in the experimental cages to insure acclimation to their new environment.

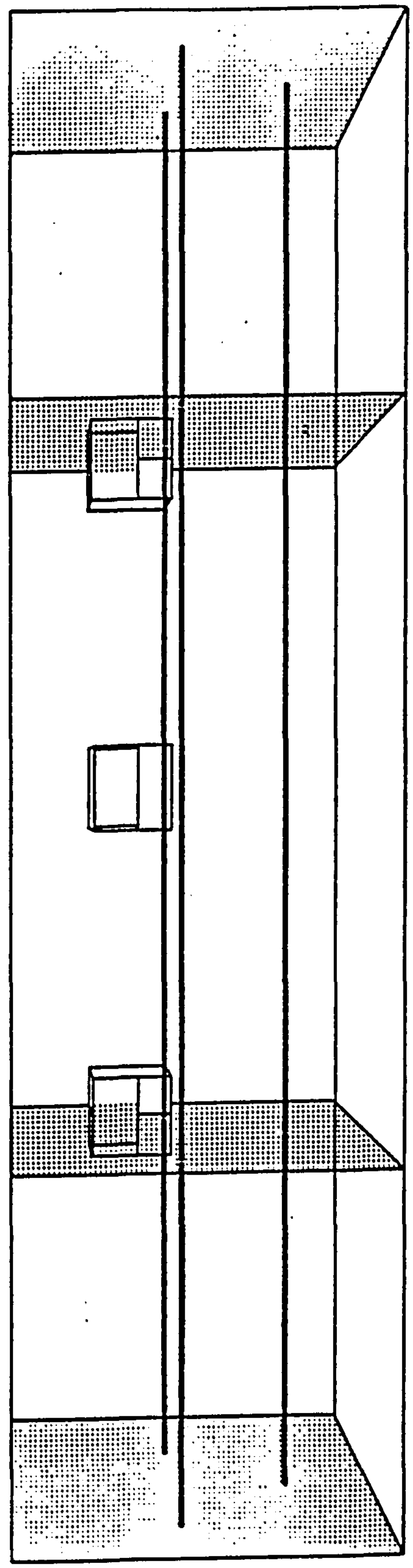
Females were selected 2 days before the beginning of the experiment. Until the morning of the first observation, they were grouped in small flight cages in visual isolation from males. On the morning of the first observations, females were randomly assigned to experimental cages, with the exception that females were never placed in the cages of male siblings.

Apparatus

Behavioral observations of the choice triads (a female and two experimental males) took place in cages (Fig. 1) consisting of a slotted angle frame, a masonite floor, and a covering of 13 mm flexible plastic aviary mesh (Marsh Farms). Each cage was divided into 3 compartments (61 x 61 x 61 cm; 122 x 61 x 61 cm; 61 x 61 x 61 cm; see Figure 1.). The larger central compartment, which housed the female, was separated from the two male compartments by the same flexible mesh material. The pliable mesh allowed virtually complete visual and auditory contact and permitted limited tactile contact. Three perches ran the length of the cage (2.45 m). The two upper perches ran parallel 31 cm apart and 20.4 cm from the top of the cage. A single lower perch ran down the center of the cage 15.3 cm from the floor. Two banks of experimental cages (3 cages each) were built. Each cage was illuminated by fluorescent ceiling fixtures plus a 300 watt flood light to increase illumination and visibility in the nestboxes.

Females had a choice of three nestboxes. Each box was constructed from a square 12.7 cm corrugated cardboard box with the top and front panel replaced with plexiglas to increase visibility into the box. One nestbox was located in the center of the female's compartment equidistant from the male compartments (61 cm) on the upper rear wall of the cage. The other two nestboxes were located at the two mesh partitions. Each was bisected by the mesh, enabling a male and a female to share the nestbox and nest material, and nestbuilding. Pilot experiments demonstrated that males and females did treat these bisected nestboxes as single nestsites. Baskets made

Figure 1. Schematic of experimental cage, front view. Females were housed in the central compartment, males were housed in the two side compartments. Male nestboxes were bisected by the mesh partitions separating their compartments from the female's. See text for further details.



of aviary mesh held loose bundles of nest material (100 pieces of green sport yarn) and were located at the floor on the center rear wall of each male compartment. Baskets for females were located on the center front wall of their compartment.

Food, water, and cuttlebone were placed in "neutral" regions of the compartments: in the central region of the females compartment and at the ends of the two male compartments. Grit was spread across the floor of all three compartments.

Procedure

Independent variables

Three behavioral attributes of male zebra finches (song, dance, and nestbuilding), were abolished or reduced by the following procedures.

Song and Courtship Dance - The frequency of both the visual and song components of courtship were reduced by castration 5-6 weeks before the beginning of the experiment following the procedure outlined in Harding, et al. (1983). This insured a significant decline in the frequency of these hormone-dependent behaviors. At the conclusion of observations, castrated males were sacrificed and autopsied for testicular remnants. Data from males with testicular remnants were discarded.

Song - In order to completely eliminate song, males were muted by bilateral sectioning of the tracheosyringealis branch (cervicalis descendens superior) of the hypoglossal (XXII) nerve using a modification of the procedure of Nottebohm (1971). The procedure was performed two weeks prior to the beginning of the experiment to decrease the possibility of nerve regeneration during the experiment but allow adequate time for surgical recovery. Under Metofane (Pitman-Moore) anesthesia, a small incision was made in the skin of the ventral neck near the midline and 1 cm caudal to the lower limit of the beak to expose a portion of the trachea. A 4 mm section of each branch was dissected free from the tracheo-lateralis muscle and the sides of the trachea, approximately 0.5 cm caudal to the bifurcation of the hypoglossal root, and removed using iris scissors. The incision was closed with 6-0 cardiovascular suture. This procedure eliminated song in males, although a scratchy raspy sound could sometimes be heard during attempts to sing. This sound, however, in no way resembled the song of a normal bird. Nest vocalizations were not eliminated by the muting procedure and, to the ear, these vocalizations sounded normal. One adverse side-effect of the procedure was respiratory distress when birds were startled. If muted birds were frightened, they wheezed for approximately 1-2 minutes. Every effort was made to avoid startling the birds, and the non-singing behaviors of muted birds were indistinquishable from normal birds.

Nestbuilding - Castrated males were prevented from doing any nestbuilding simply by eliminating any nest material from their compartments. Intact males were given bundles of 13 cm long strands of green sport yarn in holders to be gathered and placed in nestboxes.

Behavioral Observations

For each experimental triad, the first observation (am) began immediately after the female was introduced into the experimental cage. Data were collected during 15 m observations twice daily (am - 8:30-11:30; pm - 16:00-19:00) for a two week period with the exception of days 6, and 12 when only afternoon observations were taken, and days 7 and 13 when only morning observations were taken. Birds were left in the cages an additional 2-3 weeks to allow sufficient time for egg-laying. During observations, vocalizations were monitored with the aid of a pair of omnidirectional microphones (Numark) and stereo headphones (Koss HV/LC). Microphones were placed at the ends of the two male experimental cages; males were therefore never more than 0.61 m from their monitoring microphone. This enabled the observer to: 1) isolate the vocalizations of the observed males from males in other cages, 2) identify which of the males was vocalizing, and 3) monitor low amplitude vocalizations such as nest solicitation vocalizations which do not carry well.

Data recording

The behavioral activity of a triad during the 15 m observations was recorded on data sheets divided into 15 s intervals. Behavioral recording emphasized the behavior of males believed to be important for female choice and the behavior of females indicating mating preferences. A secondary effort was made to account for the activity of all 3 birds throughout the observation. The behaviors recorded are listed below.

Behavioral measures

In general, behaviors recorded were of two kinds: for more discrete events, such as courtship or copulation solicitation, frequencies of behaviors were recorded; for more continuous behavioral events, such as time spent at nestboxes, durations to the nearest 15 s interval were recorded. The specific measures for each behavior are listed below.

<u>Behaviors:</u> (M- male, F- female)

Courtship (M): Courtship includes directed song (DSong) plus the visual component, dance.

Intensity of courtship was classified according to the dance component. In a low intensity display (C-LO), the male assumes a stiffened posture, faces the female, and sings while turning his head from side to side and fluffing his dimorphic feathers. In the high intensity display (C-HI), the male stands erect, at a distance from the female, sleeks the feathers on the crown of his head, fluffs out the dimorphic feathers, sings, and approaches the female by hopping down the perch, turning 180^{o} with each hop, always twisting his head and tail towards the female (Harding et al., 1983; Morris, 1954). Courtship dances in which the female was more than 12" away (C-D) were also recorded separately, since in these instances, females often appeared unaware that they were being courted.

S+ D+ N+ male courtship consisted of both the DSong and dance components, but, a result of the experimental manipulations, S- D- N- male courtship consisted of only dance and no DSong. Measure: frequency.

Undirected song (USong) (M): This song is distinguished from DSong by the absence of the visual dance component, feather erection, and lack of orientation to another bird. While singing, the male stands erect with his head up and the feathers around the throat vibrate (Morris, 1954; Caryl, 1976; Harding et al., 1983). S- D-N- males were not able to sing, but their attempts to sing USong were recognizable by a raspy sound as well as their posture and the movement of their throat. Measure: frequency.

Copulation solicitation (F): In response to a male vocalization, a female stands on the perch in a crouched rigid horizontal posture with head bowed. Often this posture is accompanied by a vertical tail quiver in which the tail flutters rapidly. Measure: frequency.

Nest solicitation vocalization (M, F): The behavior most often observed in the process of nest solicitation is the nest vocalization, particularly in males. Described as a whimpering call by Caryl (1976), when monitored by microphone, the vocalizations of some males seemed to resemble the introductory notes of their songs (pers. obs.). The vocalization is accompanied by rapid perch hopping near the nest site and often terminates when the bird enters the nestbox. Measures: frequency, position at the end of vocalization; on the nestbox - VO, at the entrance of the nestbox - VE, in the nestbox - VI, and not at a nest location - V.

Locations at the nestbox (M, F): There were three locations at the nestbox at which birds could be found; on top of the nestbox (ON), at the entrance of the nestbox (EN), and in the nestbox (IN). Measure: duration (15 s intervals).

Eggs (F): location of eggs laid by the female. Measures: date, location.

Position (M,F): location of all three birds at the beginning of each minute during an observation. Measure: frequency.

Additional behaviors

In addition to the behaviors reported here, the following were also recorded during observations: Mandibulating nest material, transporting nest material, nestbuilding activity, pecking the nest, beak wipes, perch hopping (activity level), feeding, pecking cuttlebone, allopreening, heteropreening, clumping, sitting, and sitting with head tucked under wing, but they showed no strong relationship to mate choice.

Data analysis

Non-parametric statistical procedures were used for all analyses (Siegel, 1957). Measures of female preferences were at either the nominal or ordinal level of measurement. When possible ordinal measures of preference were analyzed using the Wilcoxon matched-pairs signed-ranks test. However, when only discrete determinations of choice were possible, i.e., prefer - not prefer, differences were analyzed using the Sign test. Behavioral differences between the two types of males were analyzed, using the Mann-Whitney U test to verify that the experimental manipulations were effective and to determine if additional behaviors were affected by the manipulations. Within each of the male groups, the relationship of the various behavioral measures was assessed using Spearman rank correlations. In order to assess if parameters of male behavior accounted for female preferences, Spearman Rank correlations were used. In an effort to determine how the females made their choices, differences between the males in the frequency of particular behavior patterns were correlated with differences in the frequency with which females directed particular behaviors towards each of the two males. Sign test analyses were one-tailed, all other analyses were two-tailed.

RESULTS

Differences in male behaviors

Experimental manipulation of males had a significant impact on behaviors likely to be important in female choice. Muted castrates (S- D- N-) were unable to sing during courtship, and thus their courtship consisted of only dance. These males showed significant decreases in both total courtship (C-Tot.) and high intensity courtship activity (C-HI) compared to intact males (S+ D+ N+) (Fig. 2). The muting procedure eliminated song in the S- D- N- males, but attempts at USong could be detected by the characteristic singing posture and the rhythmic rasping sound. The frequencies of USong attempts were significantly lower among S- D- N- males (Fig. 2). Castration reduced the frequencies of nest vocalizations most significantly (Fig. 2). However, the vocalization itself was not eliminated by the muting procedure; males continued to make a vocalization at the nest which sounded very similar, if not identical, to normal nest vocalizations. While S- D- N- males spent time at the three nest occupancy locations (ON, EN, and IN), they spent significantly less time IN nestboxes than their behaviorally intact counterparts (Fig. 3).

For the intact males (S+ D+ N+), the frequencies of many male behaviors were positively correlated. The frequency of USong was significantly correlated with total courtship activity ($r = +0.44$, $p < 0.05$) and total durations at the nestbox (ON+EN+IN = N-Tot., $r = +0.45$, $p < 0.05$). Both total courtship and high intensity courtship activity were correlated with total durations at the nestbox (C-Tot., $r = +0.47$, $p < 0.025$; C-HI, $r = +0.44$, $p < 0.05$). High intensity

Figure 2. Differences in mean frequencies (± SEM) of behaviors between S+ D+ N+ males and S- D- N- males. Note: because S- D- N- males were muted, their undirected songs were undirected song attempts, and their courtships consisted of courtship dance alone. The upper graphs show differences in mean total displays, while the lower graphs break down the courtship and nest vocalization data into different types of displays. See text. (Mann-Whitney U, $N_1 = N_2 = 18$; * $p < 0.05$, ** $p < 0.01$).

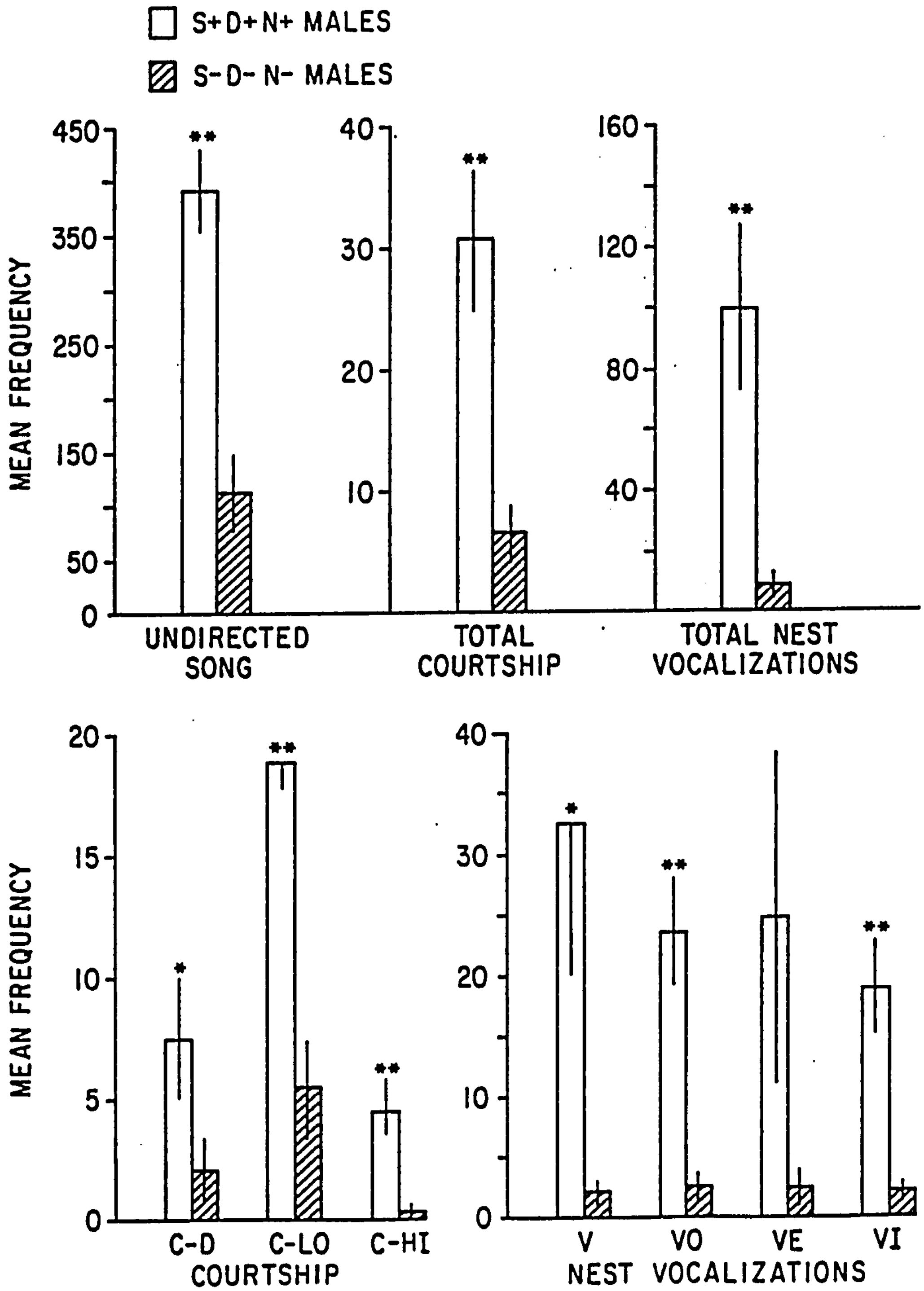
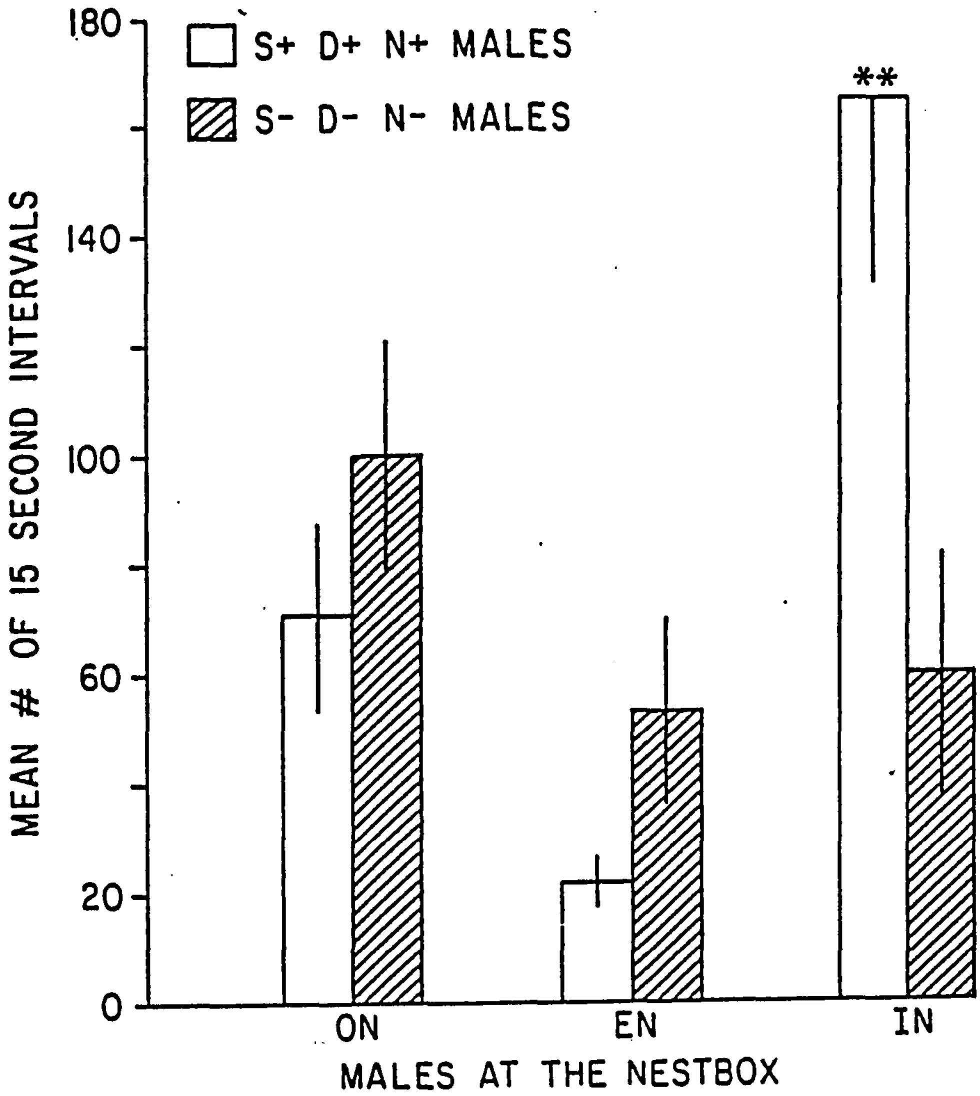

S+D+N+ MALES
S-D- N- MALES
MEAN FREQUENCY
450
350
250
150
50
0
**
UNDIRECTED SONG
40
30
20
10
**
TOTAL COURTSHIP
160
120
80
40
**
TOTAL NEST VOCALIZATIONS
MEAN FREQUENCY
20
15
10
5
0
*
**
**
C-D
C-LO
C-HI
COURTSHIP
40
30
20
10
0
*
**
**
V
VO
VE
VI
NEST VOCALIZATIONS

Figure 3. Differences between males in mean durations (15 sec. intervals, ± SEM) spent at their nestboxes. Nestbox locations: $\overline{O}$N, on top of the nestbox; EN at the entrance of the nestbox; and IN, in the nestbox. (Mann-Whitney U; N1 = N2 = 18; * $p < 0.05$, ** $p < 0.01$).



180
140
100
60
20
0
S+ D+ N+ MALES
S- D- N- MALES
**
MEAN # OF 15 SECOND INTERVALS
ON
EN
IN
MALES AT THE NESTBOX

courtship was correlated with total nest vocalizations (V+VO+VE+VI = V-Tot, $r = +0.54$, $p < 0.01$). Nest vocalizations were differentiated by the nest position occupied by a male immediately (< 1 s) after the vocalization (VO, VE, VI) as well as those in which a male did not occupy the nestbox (V). In addition to VO and VI being correlated with total durations of nestbox occupancy (VO, $r = +0.47$, $p < 0.025$; VI, $r = +0.67$, $p < 0.001$), VO, VE and VI were correlated with durations at the respective nest occupancy locations (VO with ON, $r = +0.71$, $p < 0.001$; VE with EN, $r = +0.49$, $p < 0.025$; VI with IN, $r = +0.59$, $p < 0.01$). Durations at the each of the three locations were not, however, correlated. The nestbuilding behavior of the behaviorally intact males, measured as the amount of nest material gathered by males, appeared to be independent of other male behaviors with the exception of total durations at the nestbox (N-Tot., $r = +0.44$, $p < 0.05$).

The experimental manipulations of muting and castration significantly altered the correlations between male behaviors among the S- D- N- males. The frequency of USong was correlated with C-LO ($r = +0.52$, $p < 0.025$), C-Tot. ($r = +0.46$, $p < 0.05$), and V-Tot. ($r = +0.52$, $p < 0.025$). Courtship activity was not correlated with any of the nest related behaviors, nest vocalizations, or nest occupancy. Nest vocalizations were related to nestbox occupancy (VE with EN, $r = +0.46$, $p < 0.05$; VE with IN, $r = +0.52$, $p < 0.025$; VI with IN, $r = +0.48$, $p < 0.025$). While durations EN and IN nestboxes were correlated ($r = +0.68$, $p < 0.01$), neither of these was correlated with ON nestbox occupancy. In fact, it appeared that ON was primarily a perching site for these males since little soliciting activity occured there.

Preferences of females

Proximity to males: The position of each female and the two males within the experimental cage were recorded at one minute intervals during each 15 minute observation. Position preferences for males were determined from the total number of position recordings in which females were within a region of their cage not more than 0.45 m from the mesh partitions of a male compartment. Females were found significantly more often in the proximity (Prox) of the S+ D+ N+ males (Fig. 4).

In order to determine if these differences indicated a real preference of females, a criterion of preference was established. If a female was found in the proximity of one male at least 20% more often than with the other male, she was scored as showing a preference for that male. This 20% difference criterion was used because, it was sufficient to demonstrate the choices of most females, while being less sensitive to the variablility in position recordings over the two weeks of observations than higher difference percentages. Of the 18 females in the experiment, 12 met this criterion; significantly more females (10) preferred the S+ D+ N+ males to the S- D- N- males (2) (Fig. 5; Sign test, $p < 0.05$).

In order to determine how females were choosing mates, differences between the two males in a triad in the frequencies of each behavior were calculated. A similar score was also calculated for the differences in behavioral responses of females to the two males. These behavioral difference scores were then analyzed for a relationship of choice to male behavior using the Spearman rank

Figure 4. Differences in responses of females to S+ D+ N+ males and S- D- N- males: Mean proximity (± SEM) based on recordings of female position in the cage at one minute intervals during observations (Prox to male), mean durations (+ SEM) at each location at the male nestbox (ON, EN, and IN), mean durations for all nestbox locations (NTOT), and mean durations of simultaneous nestbox occupancy by male and female (Simul IN). (Wilcoxon matched-pairs signed-ranks test; $N1 = N2 = 18$; * $p < 0.05$, ** $p < 0.01$).

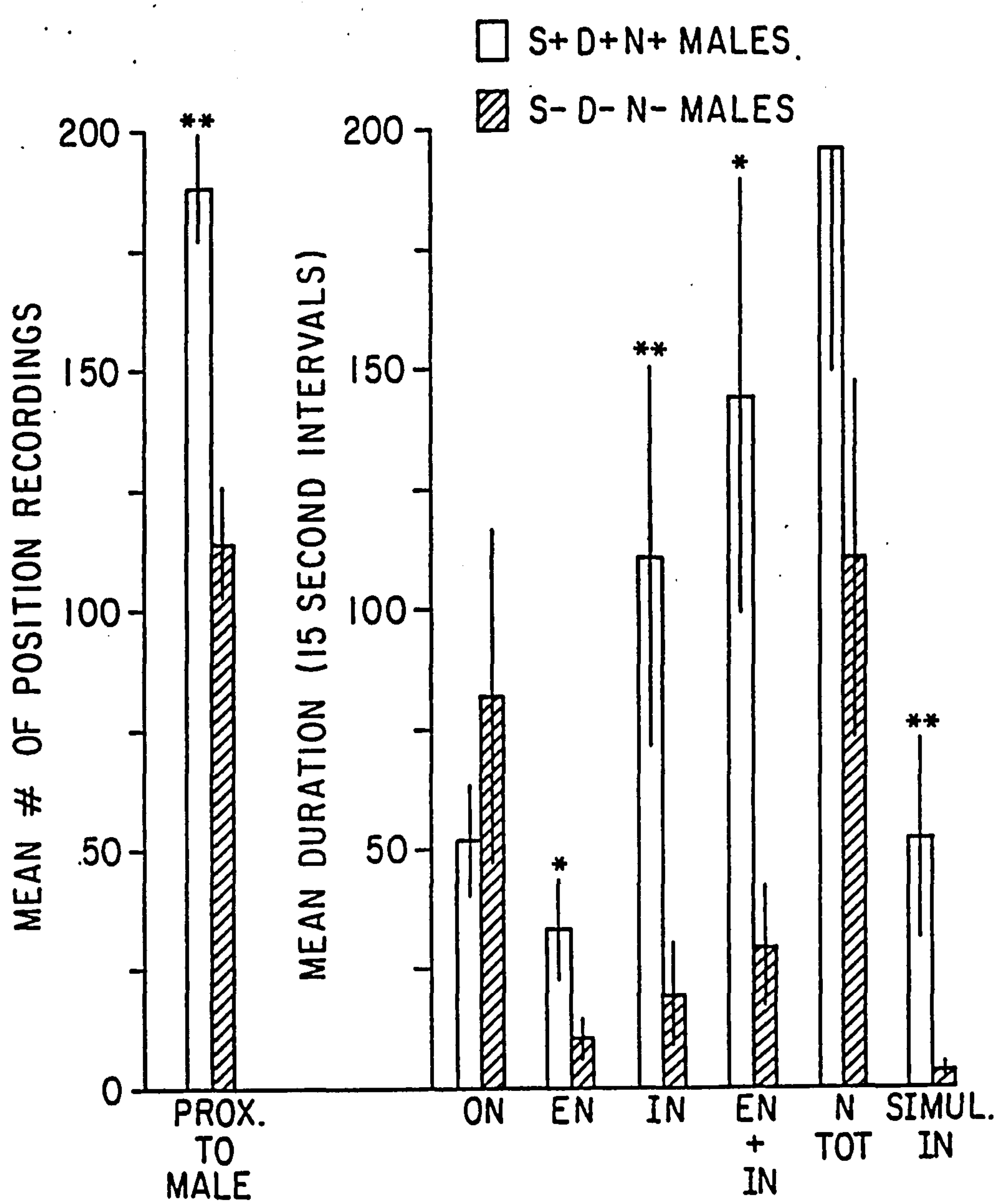
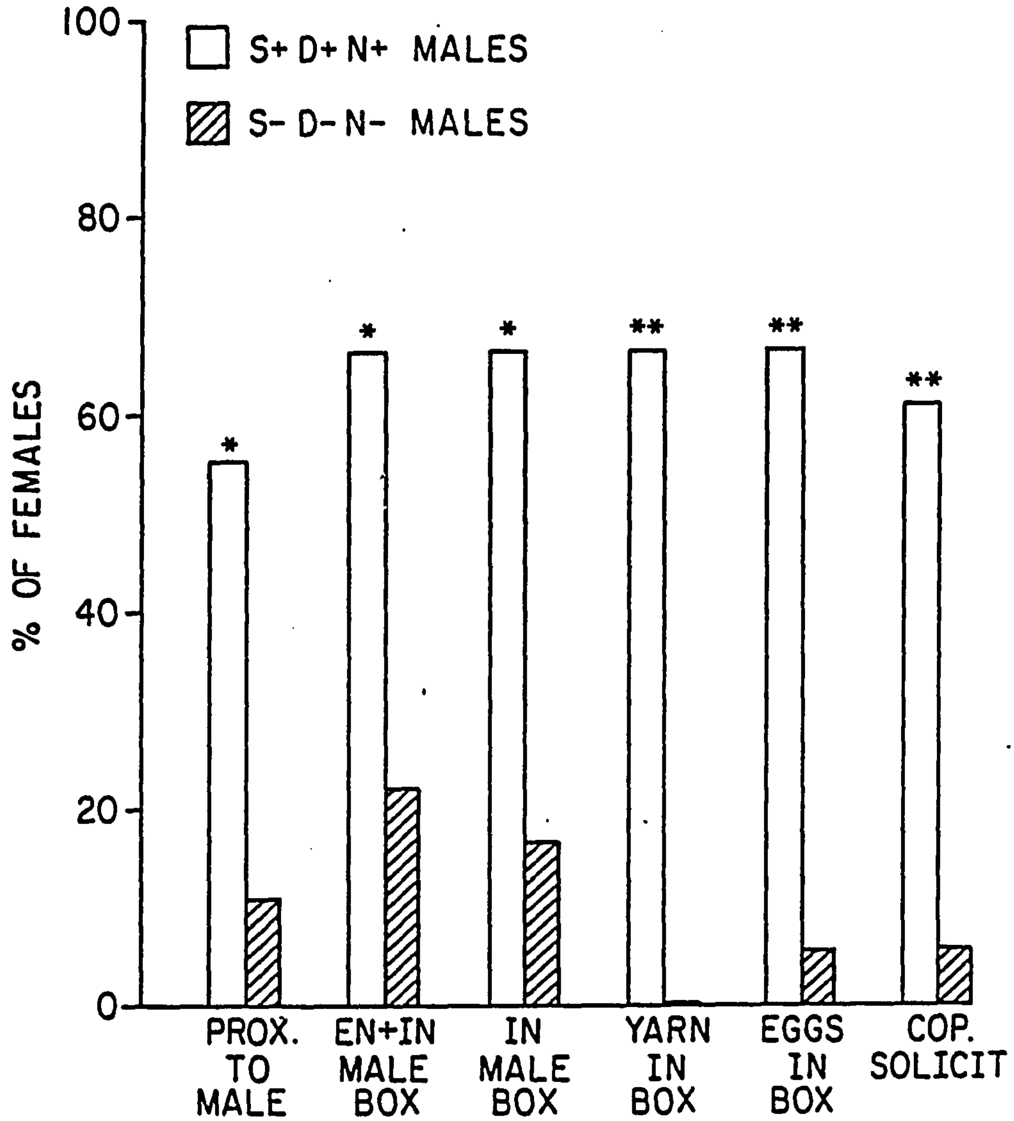

S+D+N+ MALES.
S- D- N- MALES
MEAN # OF POSITION RECORDINGS
MEAN DURATION (15 SECOND INTERVALS)
0
50
100
150
200
PROX. TO MALE
ON
EN
IN
EN + IN
N TOT
SIMUL. IN

Figure 5. Percentage of females choosing S+ D+ N+ males or S- D- N- males. For three behaviors, Prox, EN+IN, and IN, a 20% difference criterion was used to determine female choice (See text). The remaining measures are based on frequency data alone. Percentages were based on all females in the experiment (N = 18), bars reflect only those females that made a choice. (Sign Test; * $p < 0.05$, ** $p < 0.01$).


S+ D+ N+ MALES
S- D- N- MALES
% OF FEMALES
100
80
60
40
20
0
*
*
*
**
**
**
PROX. TO MALE
EN+IN MALE BOX
IN MALE BOX
YARN IN BOX
EGGS IN BOX
COP. SOLICIT

correlation (Table I). For the position recordings, differences in the proximity of females to the males were correlated with differences in the frequency of total courtship. There was also a correlation between the proximity of females to males and the amount of nest material pulled by males from holders.

Copulation Solicitation: The frequency of observing the solicitation posture in response to courtship is usually low. Even in the course of two weeks of observations, the observed frequencies in the experiment were low (mean = 2.92 for females that were observed soliciting). Of the 13 females that solicited in response to courtship, there was a significant preference for the S+ D+ N+ males (Figure 5., Sign Test, $p < .01$). Eleven females solicited the S+ D+ N+ males exclusively and one female, although observed soliciting both males, solicited the S- D- N- male more frequently. The remaining female solicited each of her males once.

Since females solicit for copulation almost exclusively in response to courtship, higher frequencies of courtship by males would increase the probability of observing, the relatively infrequent, copulation solicitations. Thus, any relationship between the frequency of courtship activity and copulation solicitation may not have reflected preference as much as a greater sample of courtships to which females could be observed soliciting. There was, however, no significant correlation between differences in the frequency of the solicitation response and any measure of courtship frequency or any other male behavior (Table I). Low courtship frequencies did not account for triads in which females were not observed soliciting; there were no significant differences in total courtship frequencies

Table I. Correlations of female preferences with male behaviors. Female preference measures are difference scores for behavioral responses to the males within a triad. Male behavior measures are difference scores for male behaviors within a triad. Only significant correlations are listed.

Male Behaviors	Female Behaviors: Prox.	ON	EN	IN	N-Tot.	Simul. IN	Cop. Solicit	Eggs
USong		+.44			+.50 *			
C-D (Courts)	+.50 *	+.47 *	+.69 **		+.51 *			+.44
C-LO	+.54 **		+.44		+.46			
C-HI		+.42	+.46	+.48 *	+.51 *	+.46		
C-Tot.	+.46	+.52 *	+.62 **		+.54 **			+.40
V (nest voc.)		+.50				+.48 *		
VO		+.62 **						
VE								
VI		+.53 *		+.44	+.42	+.47 *		
V-Tot.		+.64 **						
ON (male)		+.49 *						
EN			+.49 *				+.41	
IN				+.47 *	+.42	+.53 *		+.42
N-Tot.		+.43	+.48 *					
Nest material gathered	+.46					+.43		

p <.05
* p <.025
** p <.01

between triads in which females solicited (mean = 25.27, N = 11)and those triads where no solicitations were observed (mean = 22.7, N = 7). In addition, the frequency of courtship of the two S- D- N- males that were solicited by females was lower than the mean for this group of males (2 and 4 vs. a mean of 6.7). The females, therefore, were not soliciting males because they courted more frequently, nor were they more likely to be observed soliciting these males.

Time spent a male nestboxes. Through the two weeks of the experiment, females could occupy any of three possible nestsites; the two male nestboxes bisected by the mesh partitions separating the female from the males, or a nestbox in the neutral center region of the female cage. This third alternative, while occasionally occupied for short periods by females, was never chosen by any female as a nestsite (based on low occupancy durations, an absence of nest material, and the absence of eggs).

ON the male nestbox was never the final nestsite for any of the females, although a few did attempt to build ON at first. There was also no significant preference for males based on this measure (Fig. 4). For both the EN and IN measures of nestbox occupancy, there were significant preferences for the S+ D+ N+ males. Females spent more time at the entrance of the nestboxes and in the nestboxes of the S+ D+ N+ males. Sixteen females met a preference criterion of 20% (see above) more time EN+IN the nestbox of one male, and most preferred the nestboxes of the S+ D+ N+ males (12 vs. 4; Sign test, $p < 0.05$; Fig. 5). The majority of females also preferred to occupy these nestboxes (IN; 12 vs. 3; Sign test, $p < 0.01$).

Female nest site preferences were correlated with differences of several male behaviors within triads. There was a significant correlation between differences in male C-HI and the time females spent at all three nestbox locations (Table I.). Differences in total courtship frequencies were correlated with ON. Differences in male nest vocalization activity were also related to differences in female nestbox occupancy. Nest vocalizations in which males immediately went IN the nestbox (VI) were correlated with female IN nest occupancy. Total nest vocalizations were correlated with combined EN+IN occupancy by females Since males rarely vocalized when females were already either EN or IN, males may very well have been vocalizing to attract females to their nestboxes. Time spent at the various nestbox locations for both males and their females on all three measures (ON, EN, and IN) were correlated, indicating that, even if it was not simultaneous, a male or female was more likely to spend time at the nestsite and occupy a nest if the other member of the pair occupied that site at times.

Nestbuilding In general, although both male and female zebra finches engage in nestbuilding activity, it is the male of the pair that gathers and contributes the majority of nest material. A female had two sources of nest material: a bundle of yarn in the neutral region of her cage and, since fifteen males placed at least 100 pieces of yarn in their nestbox (mean for all males = 372 pieces), the nestbox of the S+ D+ N+ male. If females chose the S- D- N- males for mates, it was necessary for the females to provide all the nest material for the nests. Eleven females removed nest material from their holders. However, 9 of these females placed the nest material exclusively in the nestboxes of the S+ D+ N+ males (Fig. 5; Sign test,

$p < 0.05$). One of the remaining females placed the nest material in the S- D- N- male's nestbox; the other female placed several pieces in both male boxes. A significantly greater number of females also built nests with the S+ D+ N+ male. Of the 14 females for which there was yarn present in the female side of a male nestbox, 12 built nests with the S+ D+ N+ males and the remaining females with the S- D- N- males (Fig.5; Sign test, $p < 0.01$).

Nest material contributed to the nestbox by males was not significantly correlated with nestbox occupancy by females, although females were found in closer proximity to males that gathered more nest material, and simultaneous occupancy IN a nestbox by a pair was correlated with the amount of nest material gathered by the male (Table 1).

Eggs in male nestboxes One of the most important measures of mate choice should be where a female chooses to lay her eggs since it may indicate a choice for males showing greater parental potential. Thirteen females laid eggs, and a significantly greater number of these females laid their eggs in the nests of the S+ D+ N+ males, exclusively (12 vs. 1; Sign test, $p < 0.01$). Only one female laid eggs in the nestboxes of both males and she appeared to prefer the S+ D+ N+ male (5 eggs vs. 1 egg in the S- D- N- male nestbox).

Differences in the number of eggs laid by females were significantly correlated with differences in total courtship activity (Table 1). Low levels of courtship activity, however did not account for triads where females did not lay eggs. There was no significant difference in the courtship activity between males of triads in which females laid eggs (mean = 25.3, N =13) and those triads where no eggs were laid (mean = 21.0, n=5). Additionally, the absence of egg laying was not accounted for by low levels of nestbuilding of the S+ D+ N+ males in these triads. The amount of nest material pulled and placed in nestboxes by the S+ D+ N+ males in triads in which females did not lay (mean = 352, N = 5) was not significantly lower than in triads where eggs were laid (mean = 381.4, N = 12). The presence of males IN the nestbox was correlated with egglaying as were several measures of nest occupancy by the females (Table I).

Simultaneous nest occupancy (Simul IN) by both male and female would seem to be a good indicator of pair formation. Females spent significantly more time IN the nestbox simultaneously with S+ D+ N+ males (Fig. 4). This behavior was correlated with three male activities: C-HI, VI, and IN.

With the exception of copulation solicitation, all measures of female preference were significantly correlated (Table II.). For the nest occupancy data, durations ON nestboxes were not significantly correlated with the best measures of nest choice, IN occupancy and egg laying, indicating further that time spent ON male nestboxes was probably not related to mating preferences.

Table II. Correlations between measures of female preference: difference scores for behavioral responses of a female to the males within a triad.

	Female Behaviors							
	Prox.	ON	EN	IN	N-Tot.	Simul. IN	Cop. Solicit	Eggs
Proximity	----	+.64 **	+.62 **	+.49 *	+.79 **			+.54 **
ON		----	+.53 *		+.63 **			
EN			----	+.73 **	+.76 **	+.65 **		+.54 **
IN				----	+.81 **	+.92 **		+.49 *
N-Tot.					----	+.89 **		+.50 *
Simul. IN						----		
Cop. Solicit							----	
Eggs								----

p <.05
* p <.025
** p <.01

DISCUSSION

This investigation provides conclusive experimental evidence that female zebra finches utilize aspects of the behavioral repertoire of males in choosing a mate. When given a choice between two behaviorally distinct males, one with the full behavioral repertoire (S+ D+ N+) and another with deficits in song, display, and nestbuilding behaviors (S- D- N-), females choose the S+ D+ N+ males. Previous investigations of mate selection by female zebra finches have emphasized imprinted color morph preferences primarily related to interspecific mate selection (Walter, 1973; Sonneman and Sjölander, 1977; Immelmann, et al., 1978; TenCate and Mug, 1984) although the data of some of these have suggested that male behavior may be important. With the exception of Immelmann et al. (1978), measures of choice have not always included reliable measures of actual mating preference or pair formation. In the present investigation, measures of sexual preference, indicated by copulation solicitation, nest occupancy, and egg laying support the hypothesis that the behaviors of male zebra finches are also criteria for intraspecific mate choice by females.

Consistent with previous reports (Pröve, 1974; Arnold, 1976; Sossinka, Pröve, and Immelmann, 1980; Harding et al., 1983a), the experimental manipulation of male behavior by castration produced significant deficits in the frequency of directed song and dance, and undirected song. The surgical muting procedure effectively eliminated song production when castrated males attempted to sing. Possibly, the muting procedure also contributed to the reduction in song frequencies because of some discomfort or difficulty when males attempted to sing or lack of normal auditory feedback. However, while there is a raspy sound during song attempts, there was no indication that this caused males to abort either courtship or undirected song attempts. In addition, respiratory distress, which often occurs when muted birds are startled, was never observed in muted males following attempts to sing.

The frequency of nest soliciting vocalizations was also significantly reduced by the experimental manipulations. The muting procedure, however, did not eliminate the nest vocalization. S- D- N- males could be heard giving a similar, if not identical, vocalization when they were about to enter the nestbox. There have been no previous reports of the relationship of this vocalization to hormonal condition. However, it is likely that this behavioral deficit was primarily the result of castration. Hormonal condition has been shown to influence nest related behaviors in several other avian species (canary - Hinde and Steel, 1978; ring dove - Martinez and Vargas, 1974). The absence of nest material may have also been a contributing factor, although males are usually not carrying nest material when they vocalize and solicit for a nestsite. Significantly lower levels of nestbox occupancy (IN) in the S- D- N- males may, similarly, have been related to the effects of castration and the absence of nest material.

All the behavioral deficits in the S- D- N- males may have also reflected female responses to these males. Females were found more frequently in proximity to the S+ D+ N+ males. Males rarely court females from a distance, and no male in the experiment courted from greater than two feet away. Thus, low courtship frequencies may have also been partially the result of less frequent visits by females. There was, however, no indication that deprived males attempted to compensate for the limited presence of females by attempting more high intensity courtship; frequencies of it were extremely low.

Patterns of correlations between male reproductive behaviors also distinguished the S+ D+ N+ from the S- D- N- males. While the frequencies of many of the reproductive behaviors of the S+ D+ N+ males were correlated, a similar relationship was not found among the S- D- N- males. In addition to the effects of castration, the lower number of correlations among the behaviors of the S- D- N- males is probably also attributable to the responses of females to these males and their lack of nest material.

Were there specific male behaviors that accounted for female preferences? Correlations are equivocal in demonstrating that specific aspects of male behavior are "attractive" to females or serve as criteria for mate choice. They do, however, suggest behaviors which could account for variations in measures of female preference. One of the consistent proposals about the role of behaviors, particularly courtship song and display, in mate selection is that they "attract" females (Catchpole, 1982). In the present investigation, the significant tendency for females to be found more often in the proximity of the S+ D+ N+ males was significantly correlated with both differences in low intensity and total courtship (DSong + dance) frequencies between the two groups of males. This may indicate that females were attracted by more frequently courting males. Alternatively, however, the S+ D+ N+ males may have courted more frequently because of the close proximity of the females.

The proximity of females to the S+ D+ N+ males was also correlated with the amount of nest material utilized by males. While interpretations similar to those above may account for this relationship, the alternatives themselves may be of importance in assessing the role of nestbuilding as an "attractive" characteristic. If nestbuilding behavior occurs before pair formation, then nestbuilding may be a behavior for "attracting" a female. On the other hand, males may not begin significant nestbuilding activity until they are assured a mate. Females spending time in the proximity of the male may be sufficient assurance. Other investigations have used close proximity as a measure of pair formation in zebra finches (Caryl, 1975; Silcox and Evans, 1982). Female zebra finches have been reported to make the final choice of nest site (Sargent, 1965). Thus, nestbuilding may have been a response to female choice of a site and not an "attractive" trait.

Occupying a male's nestbox and laying eggs in the nestbox should be a reliable indicator of mate choice. We recorded the presence of birds ON, EN, IN nestboxes. Of these only IN was a true indicator of nest choice. Although some pairs initially started to build ON, none completed nests at this location. Females often sat or perched at the entrance of the male nestbox (EN) which, while correlated to actual occupancy (IN), was not itself a nest site. Both ON and EN were basically perching sites and therefore really measures of proximity to a male. Not surprisingly, significant correlations were found between differences in these durations and differences in high intensity and total courtship activity by the two groups of males. Differences in durations ON male nestboxes were also correlated with differences in nest vocalizations by males (V, VO, VI). Presumably, in addition to some solicitations for ON, such close proximity of the females to the actual nestsite (IN) resulted in more active solicitations for the nestsite by males.

Females clearly chose the nestboxes of the S+ D+ N+ males based on IN nest occupancy durations. The differences in time spent IN the nestboxes of the two males were related to differences in their frequencies of high intensity courtship. Males rarely initiated courtship while females were IN the nestbox, and it is therefore more difficult to attribute this relationship solely to proximity. Proximity itself was not correlated with high intensity courtship. Females, however, occasionally responded to higher intensity courtships by jumping into the male's nestbox. High intensity courtship, therefore, may have influenced nest choice.

There was also an indication that the nest vocalizations of males influenced nest choice by females, nest vocalizations terminating with the male IN the nestbox (VI) were correlated with female nestbox occupancy. Again, this can not be attributed simply to proximity, since males did not vocalize and solicit when the females were already in the nestbox. Further evidence of the possible importance of males selecting a nest site may be that male durations IN the nestbox were correlated with the durations females spent IN the nestbox. Time in the nestbox may be another important indicator of a male's choice of a nest site and may be an important influence on female choice; occupancy of a nestbox may be "attractive". However, in the experiment, male occupancy could have been a response to female occupancy since simultaneous nest occupancy was highly correlated with female occupancy of the box.

One of the best indicators of mate choice must be where a female lays her eggs. Not only is it an indication of a preferred nest site, it may also be related to the quality of a male as a mate, particularly as a parent (Searcy, 1979). In the experiment, the preferences of females to lay their eggs with the S+ D+ N+ males was related to total courtship frequencies. This might be interpreted as being the result of the stimulating effects of courtship display on reproductive physiology as has been demonstrated in budgerigars (Brockway, 1965), ring doves (Friedman, 1977), and canaries (Kroodsma, 1976). However, in this experiment, females which did not lay eggs, did not appear to be courted less than females which laid; courtship frequencies in these triads did not differ significantly from courtship frequencies in egg laying triads. It does not necessarily follow that a female will lay her eggs in the nest of the male that contributed the more stimulating effects on her ovarian development, although this could be true. In addition, the presence of a male is not always necessary for ovulation. For example, in canaries the quality of song in playback experiments appears to influence the latency to egglaying and the number of eggs laid, independent of the visual presence of a male (Kroodsma, 1976). Thus, while the behavior of males certainly stimulated females' reproductive states, where the eggs were laid may have been related to the frequency of male courtship activity for reasons other than endocrine stimulation.

Egg laying was also correlated with male nestbox occupancy, although it was not related to gathering nest material. This could indicate that the occupancy of a nest by males is an important criterion for females in choosing a site to lay eggs independent of the quality of the nest that males build. Male nest occupancy could be indicative of later willingness to incubate eggs and be important in the timing of the incubation bouts of the male and female (Ball and Silver, 1983).

Copulation solicitation must also be one of the best predictors of mate choice, since under normal circumstances its occurence, which is infrequent, is usually followed by male mounting and copulation. Females solicited the S+ D+ N+ males more frequently, but solicitation was not related to the frequency of male courtship displays. Although copulation solicitation occurs almost exclusively in response to courtship, females did not solicit more frequently those males that courted more frequently. In addition, low courtship frequencies did not account for triads in which females were not observed soliciting for copulation; there was no significant difference between triads in which females solicited and those in which they did not in low or high intensity courtship frequencies. It appears that solicitation is indeed selective and not any more likely to occur with more frequent courtship. The response must be selective to some other quality of male courtship. Selective copulation solicitation responses to other parameters of courtship song have been reported in other species (swamp sparrows - Searcy and Marler, 1981; cowbirds - West, King, and Eastzer, 1981). In the present study, copulation solicitation was correlated with only one male behavior, durations at the entrance of the nestbox, and this is difficult to interpret. Copulation solicitation appears to be distinct from other measures of female preference. In addition to its lack of significant correlations with the majority of male behaviors, it was not correlated with any other measures of female preference. Thus, even though this measure indicated a strong preference for the S+ D+ N+ males, the response was not related to any of the differences in frequencies of the male behaviors recorded, nor other measures of female preference, possibly because the response is selective for other aspects of male quality. One possibility is that the ability of males to sing had a significant influence on female copulation solicitation in response to courtship.

A measure which suggested not only mate choice by females but also pair formation was simultaneous nest occupancy by both male and female. Silcox and Evans (1982) reported that the maintenance of small individual distances between a male and a female are good indicators of pair formation as well as factors which strengthen the bond. Because of the partition between cages in the present investigation, the typically used indicator of pair formation, clumping, was rarely observed. However, proximity within the confines of the nestbox must also be a measure of pair formation and may in fact be a stronger and more reliable indicator. Simultaneous nest occupancy was correlated with the frequencies of high intensity courtship, VI nest vocalizations, and gathering yarn for nestbuilding. This strongly suggests that these behaviors are important to mate choice and the establishment of a pair bond.

In the experiment, it was not possible to use one criterion of preference to determine the mate choices of females. Various measures of of female responses were all valid indicators of choice, and no single behavioral measure correctly represented the preferences of all females. This was probably due in part to the experimental situation as well as to the differing behavioral interactions of females and males in each triad. For example, while it was possible to determine the choice of one female by the large amount of time she spent exclusively in one male's nestbox nestbuilding, another female was rarely seen in male nestboxes during observations but had clearly made a choice based on her copulation solicitations and the male nestbox in which she laid her eggs. Thus, both females demonstrated a choice, but not on the same measures. However, for the females as a group, most of the measures of preference were correlated, indicating that overall all measures were related to mate choice. The one exception was copulation solicitation which, because of its infrequent occurence, was probably the measure most susceptible to the limited sample of observations (15 min twice a day) and was not observed in frequecies reflecting the strength of the other preferences.

The reproductive behaviors of males, particularly courtship, have always been assumed to "attract" females. The results of this investigation lend support to this view in that aspects of courtship, nest vocalizations, nest occupancy and nestbuilding were related to female preferences. These behaviors, therefore, may be utilized by females in choosing a mate.

What advantage does a female gain by selecting a mate based on the quality of his behavior? It may be an informative predictor of later parental investment. For monogamous avian species, such as the zebra finch, in which males contribute considerably to the raising of the young, choice of a mate with good potential as a parent may be the most critical aspect influencing a female's reproductive success

(Trivers, 1972; Erickson, 1978). The inherent problem in choice for this characteristic is that a female must select her mate based on some pre-mating behavior that predicts later parental involvement. In zebra finches, courtship activity and nest related behaviors are those most likely to fulfill this informative function.

Greig-Smith (1982) reported that in the stonechat, premating song rates in males were correlated with later parental behaviors including nest defense. In the present investigation, zebra finch pairs were not permitted to go through a complete breeding cycle and therefore it was not possible to determine if male courtship behavior was related to measures of parental quality such as incubation and feeding of the young. However, mate choice indicated by nest occupancy and egglaying do suggest that females are selecting a mate on criteria other than just an "attractive" male for copulation. In addition, solicitation in response to courtship is apparently independent of these other behaviors. Whether courtship and nest related male behaviors which correlated with female nest occupancy and egglaying are the criteria used to assess later parental behavior cannot be determined from the present data. Of the male behaviors, those related to the nest would seem to be more likely to be related to the quality of parental behavior, but there are no data demonstrating that male nest box occupancy is related to a later propensity for egg incubation or that males begin selecting a nest site and building a nest prior to females selecting them as a mate, i.e., pair formation. Therefore, while these behaviors may be correlated to female preferences they may not be the behaviors initially assessed by females. For the S+ D+ N+ males, at least, courtship frequencies were related to aspects of nest building possibly suggesting that courtship behavior could be indicative of later nest building and parental behavciors.

Thus, while this investigation demonstrates the importance of behavior in female choice, it also raises a number of questions pertaining to the specific behavioral characteristics that females may use in selecting their mates. The data indicated that female choice is related to three specific male behaviors; directed song, courtship dance, and nesting behavior, but the relative importance of these behaviors is still unclear. Both courtship activity and nest related behaviors may contain the qualities females use as criteria for choice. Courtship itself, contains two components which need not carry redundant information about a male, directed song and dance. By far the most common prediction of the function of avian song is that it "attracts" females (Catchpole, 1982). Various parameters of song have been shown to affect the ability of songs to stimulate ovarian development (Kroodsma, 1976) and the selective copulation responses of females of other species (Searcy and Marler, 1981; West, King and Eastzer, 1981). In many avian species, courtship songs do not occur separate from visual courtship displays, but few studies have investigated the role of the visual displays in "attracting" a female. There is evidence that the visual and vocal components have differential effects on ovarian development (Friedman, 1977; Ficken, vanTienhoven, Ficken and Sibley, 1960). Visual displays may provide females with information about the quality of a male independent of his song. Thus, these two components need to be separated if their relative "attractiveness" is to be determined. Nestbuilding and other nest related behaviors may be indicative of later parental involvement by a male, provided females are able to assess it prior to choosing a mate. These three male behaviors, directed song, the courtship dance and nesting behavior may ultimately provide a means for females to assess the hormonal condition of males. We are currently investigating the relative importance of the directed song, courtship dance, and nest related behaviors of male zebra finches to female choice.

STUDY II.

While the courtship behaviors of the males of many avian species have been described as "attractive" traits (Darwin, 1871; Searcy, 1979), with a presumed role in mate choice, most investigations have examined only the importance of male vocalizations, particularly songs. However, for many avian species, including the zebra finch, the courtship of a male is comprised of both a vocal component and a visual display component. There is evidence that parameters of song are attractive to females (Catchpole, 1982; West King, and Eastzer, 1981; Searcy and Marler, 1981), but evidence for the importance of the visual component of courtship comes primarily from investigations of the physiological and behavioral responses of females to males. In ring doves, only females able to see as well as hear a courting male respond maximally to courtship (Friedman, 1977; Erickson and Lehrman, 1964). Similarly, Bengalese finches will lay eggs with a normal latency only when they can see males and manipulate nest material (Slater, 1969). The behavioral responses of females to males also seem to depend on the presence of both visual and vocal courtship in some species. Female budgerigars solicit for copulation only when both components of courtship are available (Brockway, 1964a, 1964b).

In studies of mate selection, only one published investigation appears to have addressed the importance of a male's visual display. In the European ruff, a lekking species, Shepard (1975) found that female choice was dependent on three characteristics of the male: occupancy of a central territory, the presence of satellite males on the territory, and high visual display rates. High display rates were found to be related to a greater number of female visits and copulation responses to these males.

Male nest related behaviors may also be important to selection of a mate by females. It has been reported that female whydahs and bishop birds assess male nests and nest displays as they move through a potential mate's territory (Emlen, 1957). In village weaverbirds, nest quality (Collias and Victoria, 1978; Jacobs, Collias, and Fujimoto, 1978) or nest displays (Garson, 1979) may determine a female'schoice of a mate. Such behaviors may provide females with a means of assessing and predicting later male reproductive effort which would be especially critical to reproductive success in species in which males share in caring for the young (Searcy, 1979).

In investigations of the behavioral attractiveness of male passerines, visual displays have largely been ignored. While it is certainly important for males to advertize their presence to females with song (Catchpole, 1982), once a female is in close proximity to a male, other behaviors may be important in assessing the quality of a male as a mate. There is no reason to assume that the vocal and visual components of courtship displays carry the same qualitative information for females to utilize in attempting to select the right mate. In addition, females may also assess behaviors other than courtship in making their selection. The purpose of the present investigation was to assess the relative importance of three male behaviors to female choice in an Australian grassfinch, the zebra finch, *Poephila guttata*.

Previous investigations of imprinted sexual preferences among female zebra finches acknowledged the potential importance of male courtship behavior in female choice (Walter, 1973; Sonneman and Sjölander, 1977; tenCate and Mugg, 1984). Our own preliminary work (Sheridan and Harding, 1985) indicated that experimentally induced behavioral deficits made males "unattractive" to females compared to behaviorally intact males. The data suggested that courtship and nestbuilding activity may be crucial for choice, but the specific behaviors were not independently manipulated to determine their relative importance. The purpose of the present investigation was to determine if manipulation of specific behavioral qualities of males would direct female choice in a two choice situation. In the first two experiments, we have investigated the relative importance of the two components of courtship, directed song and dance, and nestbuilding activity in female choice. In the final experiment, we investigated the possibility that variation in these hormone dependent behaviors may be used to detect differences in the reproductive status of males and thereby influence female choice.

EXPERIMENT I.

Method

Experimental design

The experiment employed a choice paradigm in which females were presented with 2 males, differing in their behavioral attributes, and allowed to choose between them. The choice for each female was between a gonadally intact male with the potential for normal levels of courtship dance (D+) and a castrated male with low potential for dance (D-). The two males were equivalent in directed song (DSong) frequencies. Since the frequency of DSong is hormone dependent and would decline as a result of castration, playback of recorded directed songs (PS+) was substituted for actual DSong of both males assuring equivalence in both the duration and frequency parameters of directed song. In addition nest building ability was equated by supplying both males with nest material, and by placing equivalent amounts of nest material in their nestboxes to equate the initial quality of their nests. As a result of these manipulations, females were given a choice between a singing, dancing, and nestbuilding male (PS+, D+, N+) and a singing, nestbuilding but dance deficient male (PS+, D-, N+).

Triads of birds were observed for two weeks in the experimental cages as described previously (Sheridan and Harding, 1985), a female housed between two behaviorally distinct males. Both the order of observations and the positions of males in cages were counterbalanced. Birds were left in the cages for an additional two weeks to allow sufficient time for egg laying.

Subjects

Zebra finches were obtained from our breeding colony at the American Museum of Natural History using the same procedures and criteria as Sheridan and Harding (1985). Both males and females were sexually naive and at least 150 days of age. Half the males were castrated 5-6 weeks before the beginning of observations. All males were muted two weeks before the observations began (See Sheridan and Harding, 1985 for details of the operation). On the morning of the first observation, females were randomly assigned to experimental cages with the exception that females were never placed in the cages of their male siblings. Three groups of six triads were run. The data of one triad was discarded because a castrated male had a testicular remnant, resulting in a total of 17 triads in the experiment.

Apparatus

Triads were housed in the same experimental cages described previously (Sheridan and Harding, 1985). The playback recordings of DSongs, used as substitutes for the songs of the experimental males (see below), were made from the recordings of 4 males individually paired with females in a soundproof chamber (IAC) using a unidirectional microphone (Shure SM-57) and a reel-to-reel tape deck (Sony TC-399) recording at 7 1/2 ips. The DSongs of the four males were used to generate the playback tapes.

The DSong tapes were played back using two stereophonic tape decks (Sony TC-399), two stereophonic amplifiers (Technics SU-Z1, 30 w/channel; Technics SA-203, 30 w/channel). Two speaker switch boxes (Realistic) each enabling playback through 3 pairs of speakers

(Realistic 5" full-range speakers) were used to provide playback to all 6 experimental cages concurrently. Speakers were located on the exterior end of each male's compartment, a distance of two feet from the mesh partition separating the male from the female. Using this playback arrangement, the four playback tapes (A, B, C, D), each consisting of the directed songs of a different male, could be paired in six non-redundant combinations: A-B, A-C, A-D, B-C, B-D, and C-D. In each block of birds tested, each female was therefore presented with a unique combination of two playback recordings. Directed songs were played back for 13 of the 14 hours of daily light at frequencies approximating normal courtship activity during the initial days of pairing; details of the contents of the tapes are presented below. Tapes were broadcast at an amplitude of 65 db measured from two feet (at the mesh partition) using a General Radio sound pressure level meter set at scale A, fast.

Procedure

Independent variables

Estimates of normal courtship frequencies were made by recording the courtship songs of 5 sexually naive males during the first two days of pairing with a female. Typically, males courted four times per hour with the exception of two peak periods of courtship activity ($\geq$ 10 songs/hr.), one hour after the lights came on in the morning, and again in the late afternoon. Frequencies of courtship song on the playback tapes reflected these frequencies. During 11 of the 13 hours of playback, songs were played at the rate of 4/hr at 15 m intervals. Songs within each hour consisted of two short duration songs (1-3 song units) (Price, 1979) and two intermediate duration songs (4-8 song units) in random order. There were two hours of peak song. One during the second hour of playback, and the other during the ninth hour. These two periods consisted of 10 courtship songs 6 minutes apart, of three different durations, 3 short (1-3 song units), 4 intermediate (4-8 song units), and 3 long (>8 song units), in random order. To avoid the continuous occurrence of simultaneous playback of the courtship songs of both males in any experimental cage, intervals between songs on the tapes were offset by $\pm$ 15 s, and the tape decks were started 5-10 s apart.

All males were provided with bundles of 100 13 cm strands of green sport yarn in holders for use in building nests. Supplies of nest material were replenished daily during the two weeks of observations. To insure initial equivalence in the quality of male nests, each male's nestbox also contained a loosely wound and dished ball of yarn (14 g) simulating a rudimentary nest.

Behavioral observations and data recording followed the same procedures and methods as described previously. The behaviors recorded were also the same as those reported previously. Specific measures for each behavior are listed below.

<u>Behaviors:</u> (M- male,F- female)

Courtship (M): In courtship there is both a song component, DSong, and visual component, the dance. Since in this experiment both males were muted, directed song was not part of courtship; courtship consisted of only the dance component. Playback of DSong did not occur simultaneously with the dance. Thus, for all males courtship consisted of the dance component alone.

Intensity of courtship was classified according to the dance component. C-LO: In low intensity courtship dances, the male assumes a stiffened posture, faces the female, and sings while turning his head from side to side and fluffing the dimorphic feathers around the throat. C-HI: In high intensity courtship dances, the male stands erect at some distance from the female, sleeks the feathers on the crown of his head, fluffs out the dimorphic feathers, sings, and approaches the female by hopping down the perch, turning 180° with each hop, always twisting his head and tail towards the female. (Morris, 1954; Harding, Sheridan and Walters, 1983). C-D, courtship dances >12" from a female were recorded separately because females in these instances appeared often unaware they were being courted. Measure: frequency.

Undirected song attempts (USong) (M): While muting effectively eliminates male song, USongs attempts were easily detected by the characteristic erect posture and a low amplitude and rhythmic raspy sound when the male attempted to sing. Measure: frequency.

Copulation solicitation (F): Measure: frequency.

Nest solicitation vocalization (M, F): Measure: frequency, position at the end of vocalization; on the nestbox - VO, at the entrance of the nestbox - VE, in the nestbox - VI, not at a nest location - V.

Locations at nestboxes (M, F): On top of the nestbox (ON), at the entrance of the nestbox (EN), and in the nestbox (IN). Measure: duration (15 s intervals).

Nest material (M, F): amount of nest material removed from holders each day for nestbuilding. Measure: pieces removed/day.

Eggs (F): Measures: date, location.

Position (M,F): Recorded at one minute intervals during observations. Measure: frequency.

Additional behaviors

In addition to the behaviors above, the following were also recorded during observations: female responses to playback songs, mandibulating nest material, transporting nest material, nestbuilding activity, nest pecking, beak wipes, perch hopping (activity level), feeding, pecking cuttlebone, allopreening, heteropreening, clumping, sitting, and sitting with head tucked under wing, but proved to have not strong relationship to mate choice.

Data analysis

For all analyses, two-tailed non-parametric statistical procedures were used (Siegel, 1957). Measures of female preferences were at either the nominal or ordinal level of measurement. When possible, ordinal measures of preference were analyzed using the Wilcoxon matched-pairs signed-ranks test. However, when only discrete determinations of choice were possible, i.e., prefer - not prefer, differences were analyzed using the Sign test.

Behavioral differences between the two male groups were analyzed using the Mann-Whitney U test (MWU) to verify that the experimental manipulations were effective and to determine if additional behaviors were affected by the manipulations. Relationships between behaviors in both groups of males and in females were assessed using Spearman rank correlations.

In order to assess if parameters of male behavior accounted for female preferences, Spearman Rank correlations were used. In an effort to determine how the females made their choices, differences in the frequency of behaviors between the two males of a triad were correlated with differences in the frequency of behaviors directed toward each of the two males by females. Sign test analyses were one-tailed, all other analyses were two-tailed.

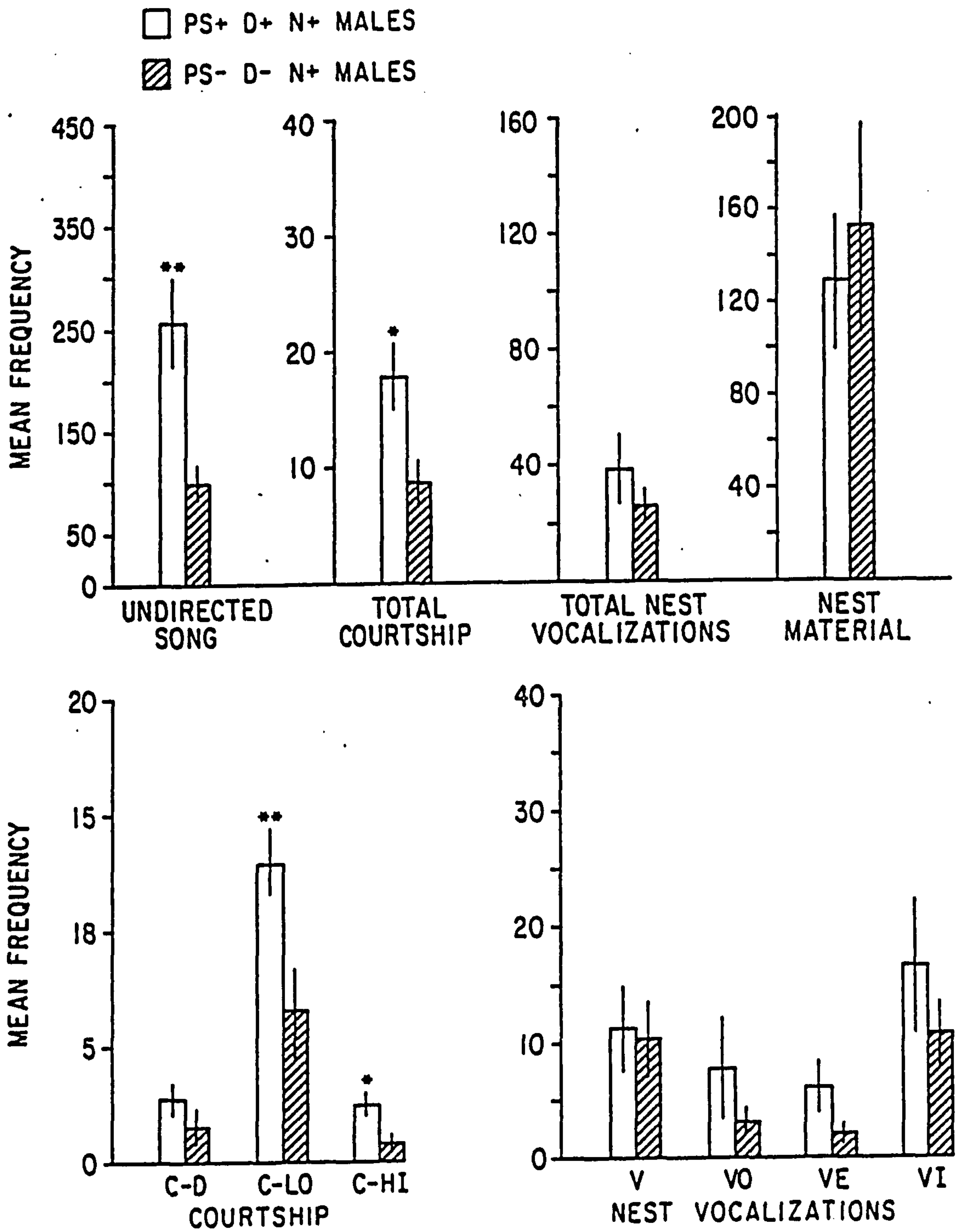
Results

Differences in male behaviors

As anticipated, overall there were significant deficits in the frequencies of all courtship dance activity as well as in two types of dance activity, C-LO and C-HI, among the D- (PS+ D- N+) males (Fig. 1). While neither these males nor the D+ (PS+ D+ N+) males could actually sing, there was a significant difference in the frequency of their attempts to sing USong. Nest vocalizations, while less frequent among the D- males, were not significantly different from the levels seen in the D+ males. There was a trend, again not significant, for the D- males to spend more time at their nestboxes (See, Fig. 2). The two groups of males did not differ in nestbuilding activity based on the amount of nest material gathered for nestbuilding. Females, therefore, had a choice between males that differed primarily in the visual component of courtship, dance, and USong activity.

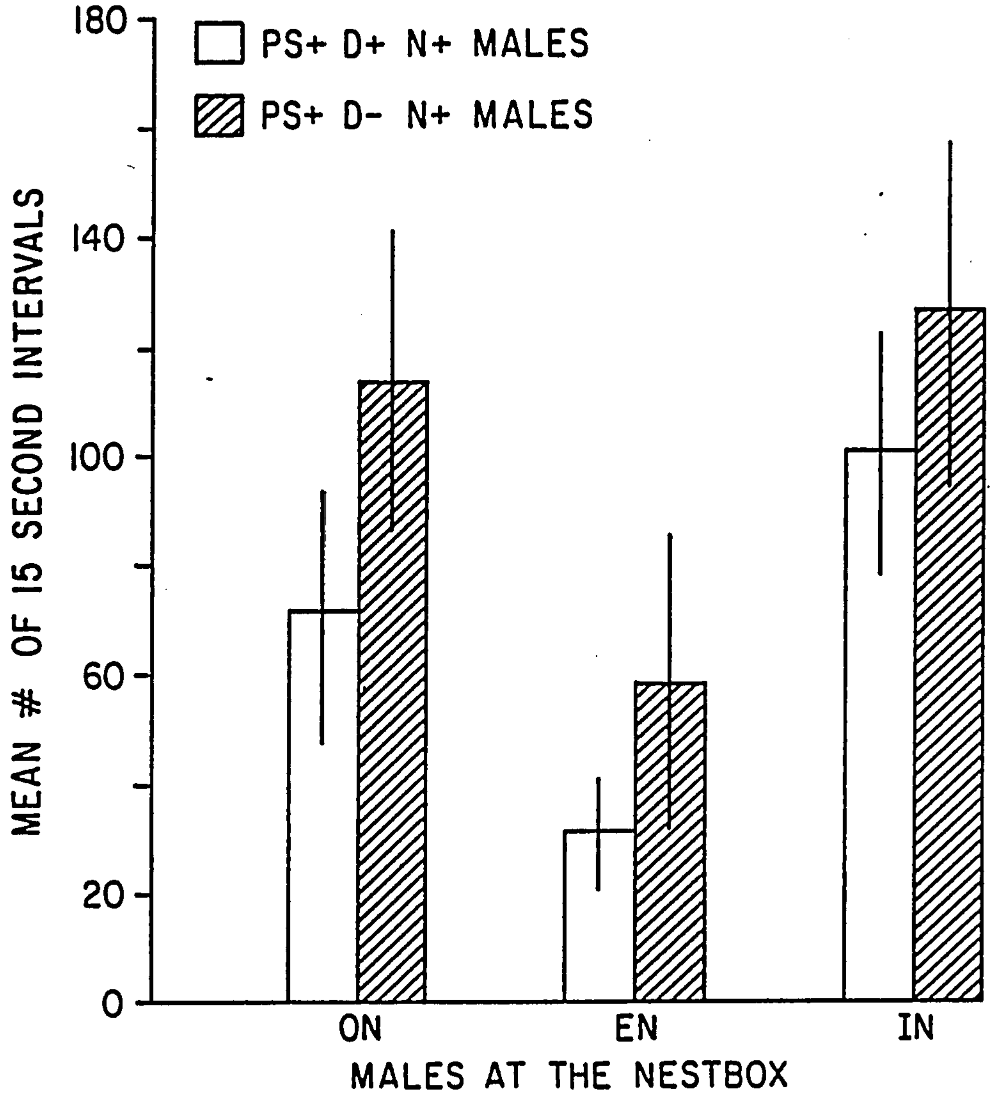
For the gonadally intact D+ males, many aspects of their behavior were correlated. USong attempts were correlated to all types of nest vocalization activity (V, $r = +0.52$, $p < 0.02$; VO, $r = +0.52$, $p < 0.02$; VE, $r = +0.68$, $p < 0.001$; VI $r = +0.69$, $p < 0.001$), but were unrelated to measures of dance activity. Only high intensity dance (C-HI) was correlated with nest vocalizations (V, $r = +0.42$, $p < 0.05$; VO, $r = +0.47$, $p < 0.05$; VE, $r = +0.51$, $p < 0.025$; VI, $r = +0.48$, $p < 0.05$) and time spent at two of the nestbox locations (EN, $r = +0.58$, $p < 0.01$; EN+IN, $r = +0.46$, $p < 0.05$). Nest vocalizations were correlated with the time spent at all nestbox locations except ON (VE with EN, r $+0.56$, $p < 0.01$; VI with IN, $r = +0.65$, $p < 0.002$); V-Tot. with EN, $r = +0.59$, $p < 0.01$; V-Tot. with IN, $r = +0.65$, $p < 0.002$). Similarly,

Figure 1. Differences in mean frequencies (± SEM) of behaviors between PS+ D+ N+ males and PS+ D- N+ males. Note: because both of these groups of males were muted, their undirected songs were undirected song attempts and their courtships consisted of courtship dance alone. The upper graphs show differences in mean total behaviors, while the lower graphs break down the courtship and nest vocalization data into different types of displays. See text. (Mann-Whitney U; $N1 = N2 = 17$; * $p < 0.05$, ** $p < 0.01$).



PS+ D+ N+ MALES
PS- D- N+ MALES
MEAN FREQUENCY
450
350
250
150
50
0
UNDIRECTED SONG
40
30
20
10
TOTAL COURTSHIP
160
120
80
40
TOTAL NEST VOCALIZATIONS
200
160
120
80
40
NEST MATERIAL
MEAN FREQUENCY
20
15
18
5
0
C-D
C-LO
C-HI
COURTSHIP
40
30
20
10
0
V
VO
VE
VI
NEST VOCALIZATIONS

Figure 2. Differences between males in mean durations (15 sec. intervals, $\pm$ SEM) spent at their nestboxes. Nestbox locations: ON, on top of the nestbox; EN at the entrance of the nestbox; and IN, in the nestbox. (Mann-Whitney U; $N1 = N2 = 17$; * $p < 0.05$, ** $p < 0.01$).



PS+ D+ N+ MALES
PS+ D- N+ MALES
MEAN # OF 15 SECOND INTERVALS
180
140
100
60
20
0
ON
EN
IN
MALES AT THE NESTBOX

gathering nest material was correlated with measures of nest vocalizations with the exception of those ending ON the nest box (VO) (VE, r = +0.61, p <0.004; VI, r = +0.71, p <0.001), and time spent at the nestboxes (EN, r = +0.49, p <0.025); IN, r = +0.64, p <0.003). Time spent ON the nestbox was not correlated with either EN or IN, although EN and IN were correlated (r = +0.59, p <0.006).

As a consequence of castration, the number of correlations among the behaviors of the D- males was decreased; especially in relation to dance activity. USong was positively correlated with total dance activity (C-Tot., r = +0.54, p <0.013), but negatively correlated with time ON nestboxes (r = -0.42, p <0.05). Low intensity dance (C-LO) was correlated with time at only one nestbox location (EN, r = +0.48, p <0.025). Total dance activity correlated with both VE and VI nest vocalizations (VE, r + +0.55, p <0.01; VI, r = +.44, p <.04). Total nest vocalization activity was correlated with the time males spent at two of the nest locations with the notable distinction that with ON the correlation was negative (ON, r = -0.46, p <0.04; IN, r = +0.72, p <0.001). Only VI was correlated with time spent at that nest location (IN, r = +0.69, p <0.001). Gathering nest material was correlated with the three nest oriented vocalizations (VO, r = +0.73, p <0.001; VE, r + +0.57, p <0.01; VI, r = +0.73, p <0.001). In addition, gathering nest material was correlated with time at two nestbox locations; there was a positive correlation with IN (r = +0.48, p <0.03), but a negative correlaton with EN (r = -0.52, p <0.02). The durations at each of the three nestbox locations were not correlated for these males.

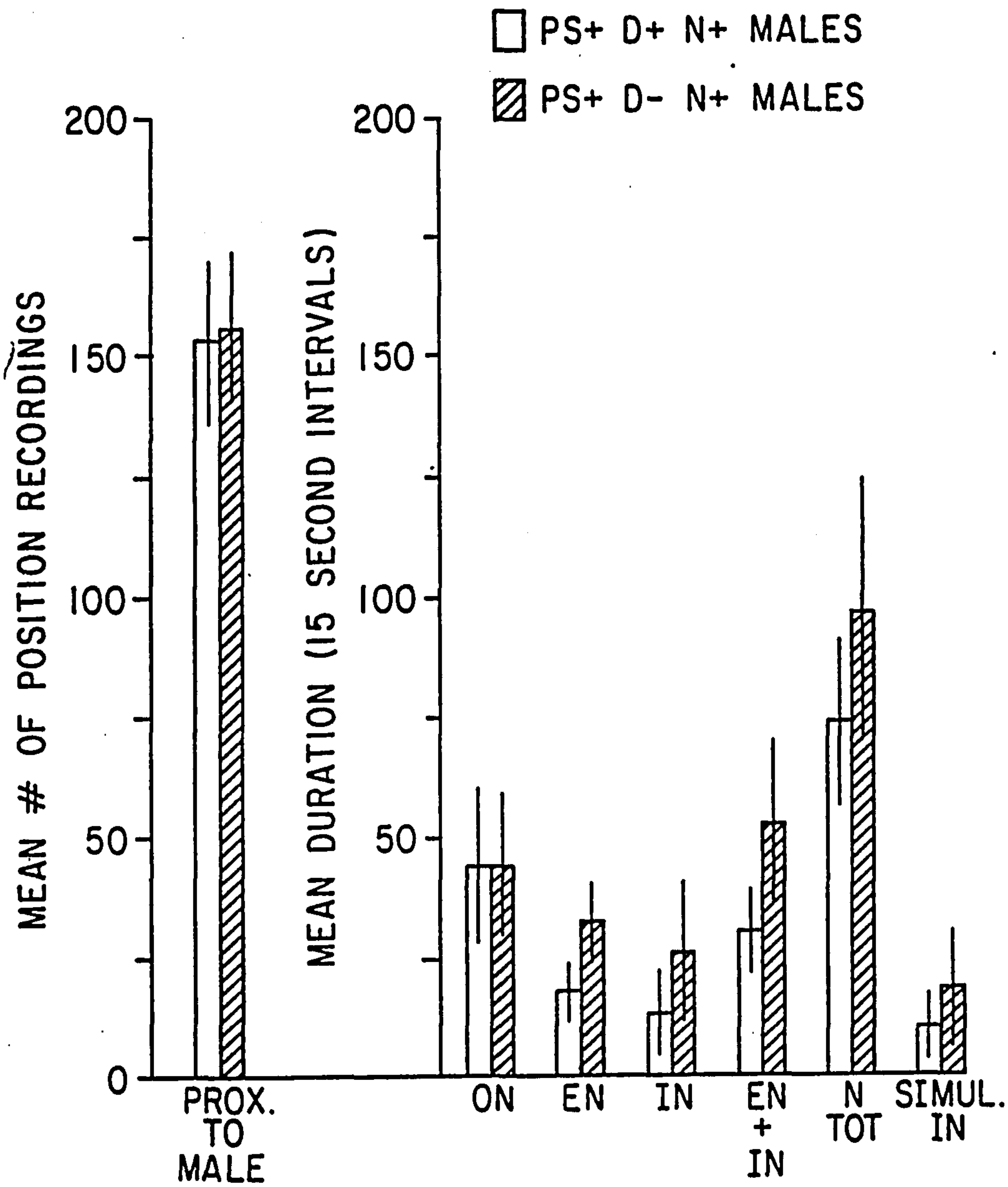
Preferences of Females

Proximity to males. As can be seen in Fig. 3, overall females were just as likely to be found with either of their two males; there was no significant preference based on position recordings (Prox). In order to determine the individual preferences of females, a criterion of choice based on being found at least 20% more frequently with one male than the other was used. This 20% difference criterion was used because, it was sufficient to indicate the choices of most females, while being less sensitive to the variability found in the position recordings over the two weeks of observations than higher difference percentages (See Sheridan and Harding, 1985). Based on this measure, 11 of the 17 females in the experiment appeared to prefere one male. However, there was no preference for a particular type of male; 5 chose the D+ male and 6 preferred their D- male (Fig. 4). Although overall females did not prefer D+ males that danced more frequently, their differential proximity response to their two choices were positively correlated with differences in dance activity between males (Table I).

Copulation solicitation. During the two weeks of observations, ten females were observed soliciting a male for copulation. There were no females which solicited both of their males. Of those that solicited, 7 solicited the D+ male and 2 the D- male. The difference, however, was not significant using the Sign test.

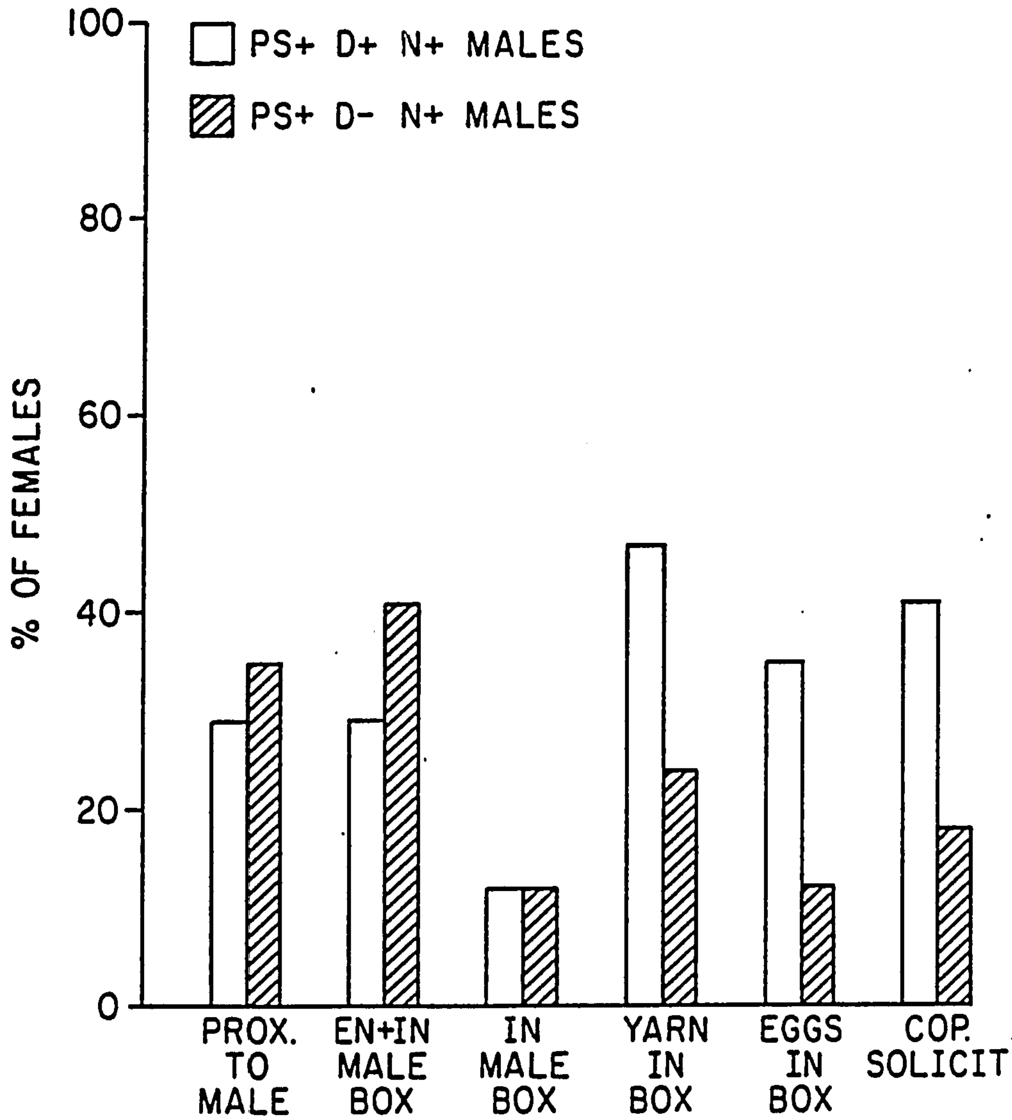
Copulation solicitation preferences were not correlated to any differences in the behavior of the two male choices. This included differences in dance activity. A comparison of the differential dance activity of males (D+ - D-) in triads where females solicited the D+

Figure 3. Differences in responses of females to PS+ D+ N+ males and PS+ D- N+ males: Mean proximity (± SEM) based on recordings of female position in the cage at one minute intervals during observations (Prox to male), mean durations (± SEM) at each location at the male nestbox (ON, EN, and IN), mean durations for all nestbox locations (NTOT), and mean durations of simultaneous nestbox occupancy by male and female (Simul IN). (Wilcoxon matched-pairs signed-ranks test; N1 = N2 = 17).



PS+ D+ N+ MALES
PS+ D- N+ MALES
MEAN # OF POSITION RECORDINGS
MEAN DURATION (15 SECOND INTERVALS)
200
150
100
50
0
PROX. TO MALE
ON
EN
IN
EN + IN
N TOT
SIMUL. IN

Figure 4. Percentage of females choosing PS+ D+ N+ males or S- D- N- males. For three behaviors, Prox, EN+IN, and IN, a 20% difference criterion was used to determine female choice (See text). The remaining measures are based on frequency data alone. Percentages were based on all females in the experiment (N = 17), bars reflect only those females that made a choice. (Sign Test).



PS+ D+ N+ MALES
PS+ D- N+ MALES
% OF FEMALES
100
80
60
40
20
0
PROX. TO MALE
EN+IN MALE BOX
IN MALE BOX
YARN IN BOX
EGGS IN BOX
COP. SOLICIT

Table I. Correlations of female preferences with male behaviors in Experiment I. Female preference measures are difference scores for behavioral responses to the males within a triad. Male behavior measuress are difference scores of male behaviors within a triad. Only significant correlations are listed.

	Female Behaviors							
Male Behaviors	Prox.	ON	EN	IN	N-Tot.	Simul. IN	Cop. Solicit	Eggs
USong								
C-D (courts)			+.55 *	+.62 **	+.58 **	+.46		
C-LO	+.55 *			+.49 *	+.44	+.46		+.44
C-HI								
C-Tot.	+.58 **			+.50 *	+.62 **			+.43
V (nest voc.)								
VO			-.58 **					
VE								
VI								
V-Tot.								
ON (male)								
EN								
IN				+.42		+.49 *		
N-Tot.				+.43				
Nest material gathered								

p <.05
* p <.025
** p <.01

male (mean = 14.57, N = 7) and those in which the D- males were solicited (mean = -4.67, N = 3) did not reveal any significant difference in courtship dance activity. The means themselves, however, suggested a trend of females to choose the D- male when the difference between the males in a triad was minimal and the castrated males danced slightly more frequently as indicated by the negative mean frequency.

Time spent at the male nestbox. While females had the opportunity to occupy a nestbox in the neutral (central) region of their cage, none chose to do so. Time spent at the three locations at the males' nestboxes (ON, EN, and IN) revealed a surprising result. Durations ON the nestboxes of both males were essentially equivalent, which is not surprising since this was typically a perching site. However, females appeared to spend more time EN and IN the nestboxes of the D- males, although not significantly more (Fig. 3). Overall mean nestbox occupancy durations were low, and occupancy IN the two male nestboxes was equivalent for 11 females. Thus, the majority of females never showed a preference for a male nestbox. Using a 20% difference criterion of nestbox occupancy for choice, only four females showed a preference for one male's nestbox over the other's. Two chose the nestbox of the D+ male, and two chose that of the D- male (Fig. 4).

Differences in nestbox occupancy (IN) were correlated with differences in male dance activity (C-D and C-LO, Table I). This reflected the fact that of the two females that spent more time IN the nestboxes of their D- male, the D- males actually danced more frequently than the D+ males. Thus, these females occupied the nestbox of the male that danced relatively more frequently. Female nestbox occupancy was also correlated with increased nestbox occupancy by that male relative to the other male and the overall presence of males at the nestbox (N-Tot., Table I). This, also reflected a difference in nestbox occupancy durations in some triads in which the D- males spent more time at their nestbox than their D+ counterparts.

Durations of simultaneous occupancy (Simul. IN) in a nestbox by both a male and the female were probably a good indicator of pair formation, but did not reveal a significant trend for pairing with D+ D- males (Fig.3). This measure was postively correlated with differences in dance activity by males, however (C-D and C-LO, Table I.).

Nestbuilding. In the experiment, females had access to nest material from either the nestboxes of the two males or their own supply of nest material. Only 5 females took yarn from their holders. Four of these took less than 11 pieces, and one female took 258 pieces and placed them in her D+ male's nestbox. Nest material was found on the female side of a male nestbox in 12 triads. In the majority of cases (8 vs. 4) the yarn was found in the D+ male's box, but the difference was not significant (Fig. 4). Only 6 females had put enough nest material in the male nestbox to cover the floor of the box. Here, again, the trend favored the D+ males (4 vs. 2). The quantity of nest material contributed by males to a nestbox was not correlated with any indication of preference by females.

Eggs in male nestboxes. Egg-laying in the experiment was limited. Of the 8 females that laid eggs (47%), 6 females laid more eggs in the nestboxes of the D+ males (2 of these laid in both male boxes), and 2 females laid more in the nestboxes of the D- males. One of these laid eggs in both male boxes, and the other laid eggs exclusively in the D- male's nestbox (This D- male also danced more frequently than his D+ counterpart).

Egg-laying preferences were correlated with differences in low intensity dances and total dance activity between males (Table I.). However, lower frequencies of dancing were not found to account for triads in which females did not lay eggs. Differences in mean dance activity in triads where no eggs were laid were lower (C-Tot. mean = 2.33, N = 9) than in the triads where females laid eggs (mean = 18.25, N = 9), but not significantly. This suggested that in triads where no eggs were laid there was less of a difference in dance activity between males.

A few of the measures of female preferences were correlated (Table II.), but there was not a great degree of consistency among them. Females tended to lay eggs in the nestboxes of the males they were observed soliciting for copulation, but neither of these measure was correlated with the time females spent in male nestboxes (IN) or in close proximity to a male.

Table II. Correlations between measures of female preference in Experiment I.: difference scores for behavioral responses of a female to the males within a triad. Only significant correlations are listed.

Female Behaviors

	Prox.	ON	EN	IN	N-Tot.	Simul. IN	Cop. Solicit	Eggs
Proximity	----				+.42			
ON		----			+.76 **			
EN			----		+.47			
IN				----	+.75 **			
N-Tot.					----			
Simul. IN						----		
Cop. Solicit							----	+.56 *
Eggs								----

p <.05
* p <.025
** p <.01

Discussion

Previously, we reported that the behavior of male zebra finches is utilized by females in their selection of a mate. The results of the present experiment indicate that when males differ in their frequency of courtship dance, independent of the frequency of directed song, females do not show a significant preference for the behaviors of either male.

Females as a group spent more time on the average EN and IN the nestboxes of the D- males than in the D+ male nestboxes, although the trend was not significant. This, however, did not mean that the majority of females preferred the the nestboxes of the D- males. Using the 20% difference criterion for time spent IN the nestboxes to indicate preference, only four females made a choice and their choices were evenly split between the two types of males. Thus, while there was a tendency for females to spend more time in the nestboxes of the D- males, few females actually demonstrated a choice of mate based on this measure and those that did had no preference for one type of male. Durations in male nestboxes were correlated with courtship dance activity. Interestingly, in the two triads in which females spent more time IN the nestboxes of the D- males, the D- males danced more frequently than their gonadally intact counterparts. Whether this relationship was due to the "attractiveness" of more frequent courtship dances or was simply a result of females being in close enough proximity for males to initiate courtship is difficult to determine. Possibly, courtship dance activity correlated with female proximity for the same reason, especially since females did not demonstrate a real preference based on this measure. Male nestbox occupancy was also related to nestbox occupancy by females, especially in the four triads in which females met the preference criterion. Nest occupancy durations (IN) of the males they chose were the highest durations within their respective groups. While a willingness to occupy a nest may be an "attractive" quality of a male, males may have occupied their nestboxes only after some assurance of acceptance by females, possibly female occupancy of the nestbox.

Time spent in the nestbox by both a male and female (Simul IN) should be a good indicator of pair formation. Not only did females fail to indicate a preference for one type of male on this measure, but time spent simultaneously IN nestboxes was low. This indicates that few pairs were actually formed in the experiment which may been due to the fact that neither male could sing while courting. Simultaneous nestbox occupancy was, however, correlated with courtship dance frequencies suggesting that in those triads where pairs were formed, courtship dance may have been a determining factor.

Although there were no other measures that indicated a significant preference by females, trends in copulation solicitation, female nestbuilding, and egg laying, favored the dance (D+) males). Copulation solicitations were not correlated with courtship dance activity, but there was some indication that in the two triads where females preferred to solicit the D- males the difference in total courtship dance activity between the males was lower, although it did not favor the D- males.

Only 47% of the females in the experiment laid eggs, and while most of them laid the majority of their eggs in the D+ male's nestbox, the trend was not significant. Differences in courtship activity were correlated with egg laying, however, and appeared to account for one of the females that laid her eggs with the D- male. In this triad the D- male was observed dancing more frequently than the D+ male. Inexplicably, the other female that preferred to lay her eggs in the D- male's nestbox, did so with a male that was never observed courting and did not gather any nest material for a nest. Although not a significant trend, in the triads where no eggs were laid there was less of a difference in courtship dance activity between the two males. For the most part, this was due to lower frequencies among the gonadally intact males, and it may suggest that females did not lay eggs because frequencies of courtship dance were too low to stimulate ovulation.

One of the shortcomings of substituting recorded playback of directed song for actual directed song in the experiment was that, unlike normal DSong, P-DSong was not coincident with male courtship dances. There was no guarantee that females would associate the P-DSong from the speaker with the male himself. In an attempt to determine if an association with the playback song was established, female responses to these songs were monitored. Females were never observed clearly responding to the P-DSongs. There was no incidence of a female approaching a male, entering a nestbox, or soliciting for copulation in response to the recorded songs, behaviors one would expect to see in response to a normal male's singing. The parsimonious conclusion is that females did not associate the P-DSong recordings with the males and were choosing between two non-singing males. This may account for the failure of females to indicate a choice on several of the measures of preference. Compared to our previous investigation, involving a choice between intact males and castrated, muted males, a much smaller percentage of females (24% vs. 83%) occupied male nestboxes for a duration sufficient to indicate choice. In addition, fewer females laid eggs (47%) than in our previous investigation (72%). Both are interesting findings, since all males in the current experiment had nests, access to nest materials and, presumably, vocalized at the same levels. We might have expected more variability in female choices, but not fewer females choosing, since both males in the present experiment appear qualitatively better than the behavior reduced males (S-D-N-) of the previous investigation (Sheridan and Harding, 1985). Perhaps DSong paired with courtship dance, or maybe more importantly paired with a male, is essential for a female to select a site for laying her eggs. An important factor in the experiment may have been that males could not interact with females via song, e.g., males could not adjust their singing to the females' behavior.

The playback of male song, without the presence of a male has been shown to be sufficient to produce ovulation in several species (budgerigar, Brockway, 1964a,b; canary, Kroodsma, 1976). And the visual-behavioral presence of a male is adequate for stimulation in the ring dove (Friedman, 1977), although the combination of visual and vocal components produces optimal stimulation. In the present investigation, both the visual and vocal components were present, although they occurred independently. It is not known if vocalizations alone are sufficient for for ovulation in zebra finches. Our data minimally demonstrate that DSong and the courtship dance must be integrated for maximal reproductive stimulation. However, the lack of DSong when males were courting may have also affected the ability of females to select a mate from their choices, i.e., without song males may not be "attractive."

Regardless of whether females associated playback of DSongs with a male, the males were equivalent in their singing ability. The results indicate that the courtship dance is not sufficiently "attractive" to direct female choice independent of DSong. While their was some tendency for females to accept the D+ males, it did not appear that this hormone dependent behavior provided females with those male qualities assessed when choosing a mate. The dance itself, however, may have stimulated female reproduction because differences in total courtship dances were correlated with eggs laid.

In addition to the equivalence in singing, males were also equivalent in nestbuilding. The quality of a male as a mate might be indicated by his nestbuilding behavior and the nest produced, and females might assess these parameters. There was little indication of this in our data, since preferences were not correlated with the gathering of nest material, a good indicator of nestbuilding. Of course the song deficits of both male choices may have disrupted the influence that nestbuilding may have had. The next experiment addressed the relative importance of nestbuilding and song to female choice.

EXPERIMENT II.

Method

Experimental design

As in the previous experiment, this experiment employed a choice paradigm in which females were presented with two males, differing in their behavioral attributes, and allowed to choose between them. The choice for females was between a vocally and gonadally intact male deprived of nest material (S+ D+ N-), and a muted gonadally intact male provided with nest material (S- D+ N+). Thus, females were given a choice between two males equivalent in their courtship dance potential, but differing in their abilities to sing and to build nests.

As in the previous experiment, triads of birds were observed for two weeks in the experimental cages, a female housed between her two behaviorally distinct males, and left in the cages for an additional two weeks for egg laying. Triads were run in blocks of six, and the order of observations and the position of males were counterbalanced.

Subjects

Zebra finches were obtained from our breeding colony at the American Museum of Natural History using the same procedures and criteria as described previously. Half of the males (S- D+ N+) were muted two weeks before the observations began. On the morning of the first observation, females were randomly assigned to experimental cages with the exception that females were never placed in the cages of their male siblings. Three blocks of triads were run in the experiment. One male died 4 days into the observations and this triad's data was deleted from the analysis; 17 triads completed the experiment.

Procedure

Song and nestbuilding were manipulated as described previously. S+ D+ N- males were not given any nest material (yarn) to gather for nestbuilding, and any nest material contributed to their nestboxes by females was removed daily. The muted S-D+N+ males were given free access to nest material. In addition these males had loosely wound and dished balls of yarn (14 g) placed in their nestboxes at the beginning of the experiment to simulate rudimentary nests. Behavioral observations, data recording, and data analysis followed the same procedures as the previous experiment.

Behavioral measures

The behaviors recorded during the two weeks of morning and late afternoon observations were the same as in previous experiments. Specific behaviors were: Undirected song (USong) or USong attempts in the case of muted males; Courtship, C-D, C-LO, and C-HI (Courtship dance alone in the case of muted males); Copulation solicitation; Nest solicitation vocalization, V, VO, VE, and VI; Locations at nestbox, ON, EN, and IN; Eggs; and the positions of birds in the cage recorded at one minute intervals.

Results

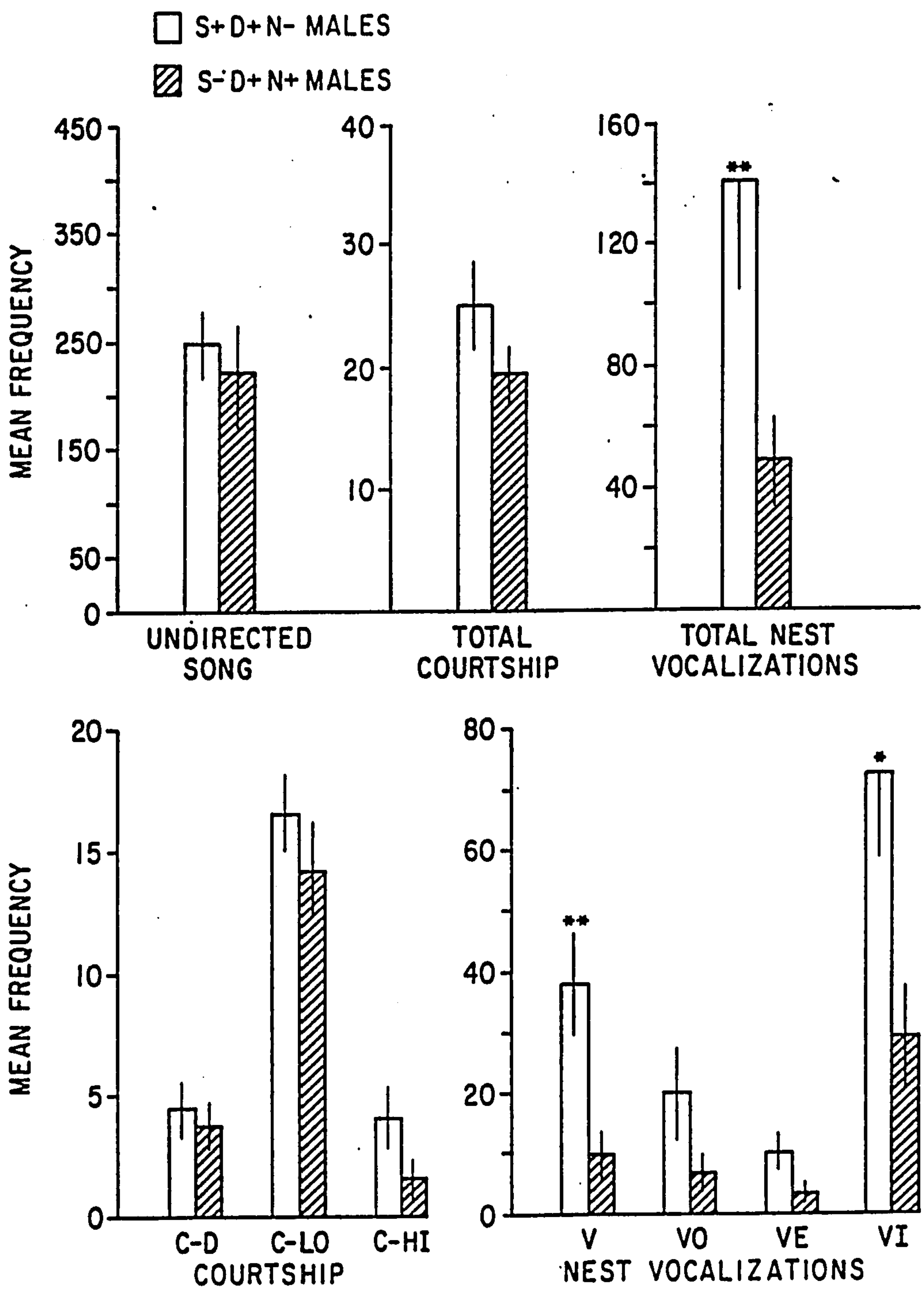
Differences in male behaviors

Differences in the behaviors of the males of the two groups are presented in Figure 5. For the graph of total undirected song (or undirected song attempts), courtship (or courtship dance alone), and nest vocalization activity, y axis scales are consistent with previous experiments for ease of comparison. Even though the Nest males (S- D+ N+) were muted, USong attempts and courtship dance frequencies were not significantly lower than those of the Song males (S+ D+ N-). The time males spent at their nestboxes also did not differ between the two groups (Fig. 6). The two types of males did differ, however, in the frequencies of nest vocalizations, particularly V and VI; S- D+ N+ males vocalized at significantly lower levels. However, changes in the quality of this vocalization as a result of muting were not apparent; their nest vocalizations sounded similar to those of vocally intact S+ males.

USong activity among the S+ D+ N- males was negatively correlated with some types of nest vocalizations (V, $r = -0.46$, $p < 0.03$; VE, $r = -0.60$, $p < 0.01$). Nest vocalizations that did not terminate at the nestbox (V) were positively correlated with USong attempts (V, $r = +0.41$, $p < .037$) among the S- D+ N+ males. USong was also correlated with gathering nest material ($r = +0.71$, $p < 0.01$) in the S- D+ N+ male group.

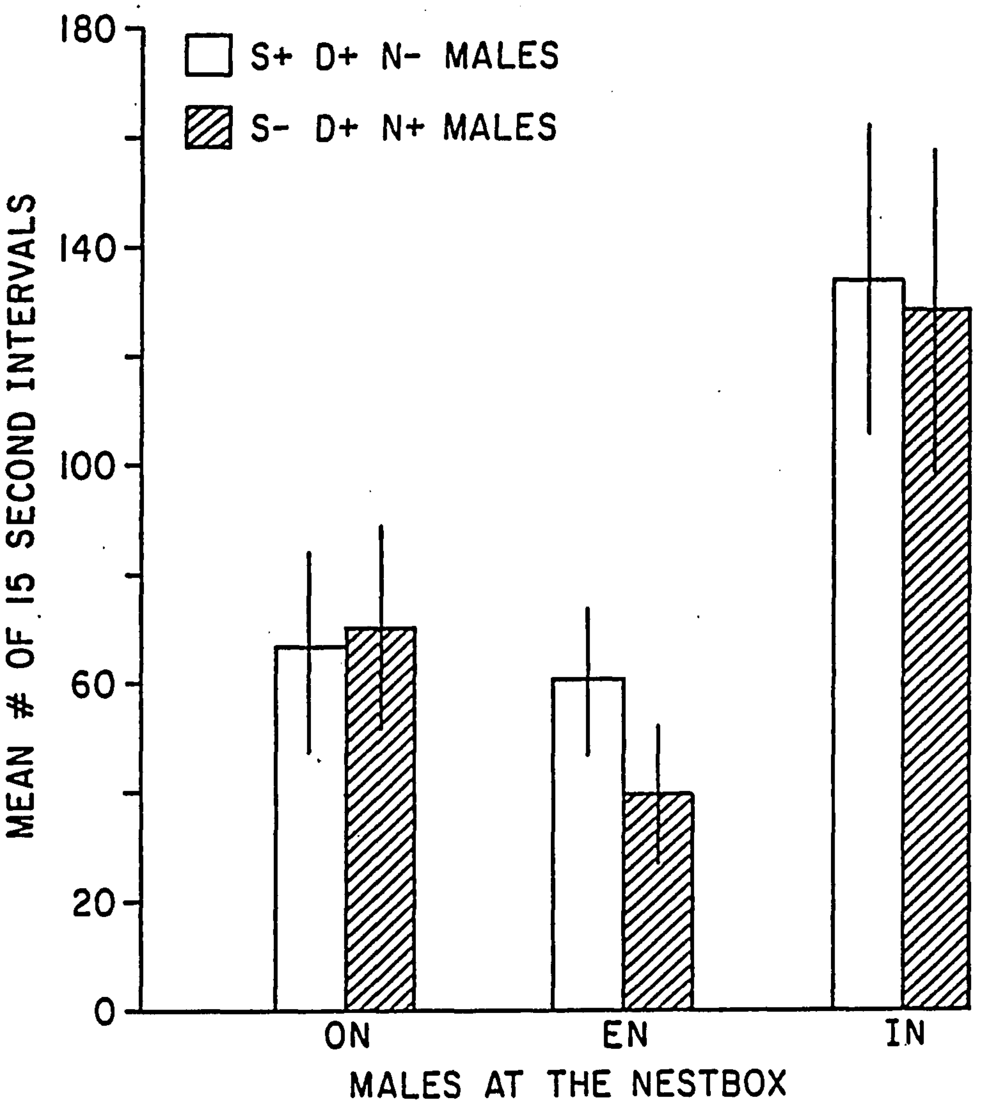
Among the S+ D+ N- males, only one measure of courtship (C-D) was correlated with the other male behaviors, and the relationship was negative (C-D with EN, $r = -0.48$, $p < 0.025$). Total courtship

Figure 5. Differences in mean frequencies (± SEM) of behaviors between S+ D+ N- males and S- D+ $\overline{\text{N}}$+ males. Note: because S- D+ N+ males were muted, their undirected songs were undirected song attempts and their courtships attempts consisted of courtship dance alone. The upper graphs show differences in mean total displays, while the lower graphs break down the courtship and nest vocalization data into different types of displays. See text. (Mann-Whitney U; N1 = N2 = 17; * $p < 0.05$, ** $p < 0.01$).



S+D+N- MALES
S-D+N+ MALES
MEAN FREQUENCY
450
350
250
150
50
0
UNDIRECTED SONG
40
30
20
10
TOTAL COURTSHIP
160
120
80
40
**
TOTAL NEST VOCALIZATIONS
MEAN FREQUENCY
20
15
10
5
0
C-D
C-LO
C-HI
COURTSHIP
80
60
40
20
0
**
*
V
VO
VE
VI
NEST VOCALIZATIONS

Figure 6. Differences between males in mean durations (15 sec. intervals, $\pm$ SEM) spent at their nestboxes. Nestbox locations: ON, on top of the nestbox; EN at the entrance of the nestbox; and IN, in the nestbox. (Mann-Whitney U; $N1 = N2 = 17$; * $p < 0.05$, ** $p < 0.01$).



180
140
100
60
20
0
MEAN # OF 15 SECOND INTERVALS
S+ D+ N- MALES
S- D+ N+ MALES
ON
EN
IN
MALES AT THE NESTBOX

frequencies were also negatively correlated with the time S+ D+ N- males spent at the entrance of their nestboxes (C-Tot with EN, $r = -0.48$, $p < .025$). Among the S- D+ N+ males, low intensity dance (C-LO) was correlated with gathering nest material (Yarn) ($r = +0.42$, $p < 0.048$), all measures of nest vocalizations (V, $r = +0.49$, $p < 0.023$; VO, $r = +0.56$, $p < 0.01$; VE, $r = +0.49$, $p < 0.021$; and VI, $r = +0.57$, $p < 0.008$), and the combined time the males spent at the entrance and in their nestboxes (EN+IN, $r = +0.47$, $p < 0.03$). Courtship dances from a distance (C-D) were correlated with only two types of nest vocalizations (V, $r = +0.54$, $p < 0.013$; VE, $r = +0.60$, $p < 0.005$) and C-Tot. with EN ($r = +0.48$, $p < 0.025$). Only one measure of nest vocalizations was correlated with time spent at the nestbox by the S- D+ N+ males (VO with EN, $r = +0.60$, $p < 0.006$). Times spent at the three nestbox locations (ON, EN, and IN) were not correlated.

Preferences of Females

Proximity to males.

During the two weeks of the experiment, females were observed significantly more often in closer proximity to the S+D+N- males (Prox., Fig. 7). Using a 20% difference criterion (see Exp. I.), all the females indicating a preference (11) preferred the S+ D+ N- males (Fig. 8). Correlations did not reveal any significant relationship between differences in the behavior of the pairs of males and female proximity to them (Table III).

Copulation Solicitation.

Thirteen of the 17 females solicited the S+ D+ N- males exclusively (13 vs. 1, Sign test, $p < 0.01$; Fig.8). One female preferred to solicit her S- D+ N+ male, but she also solicited her S+

Figure 7. Differences in responses of females to S+ D+ N- males and S- D+ N+ males: Mean proximity (± SEM) based on recordings of female position in thecage at one minute intervals during observations (Prox to male), mean durations (± SEM) at each location at the male nestbox (ON, EN, and IN), mean durations for all nestbox locations (NTOT), and mean durations of simultaneous nestbox occupancy by male and female (Simul IN). (Wilcoxon matched-pairs signed-ranks test; N1 = N2 = 17; * $p < 0.05$, ** $p < 0.01$).

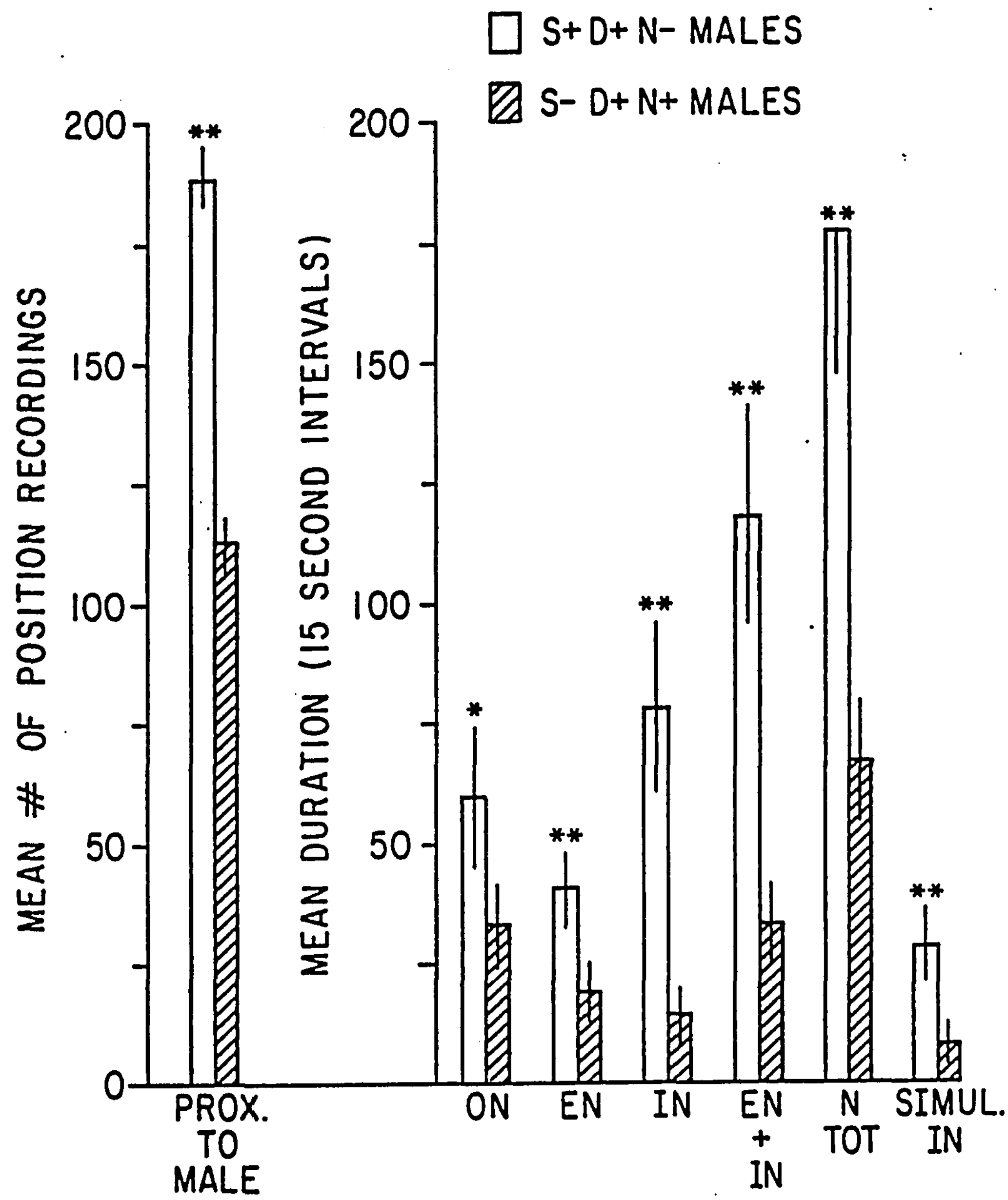

S+ D+ N- MALES
S- D+ N+ MALES
MEAN # OF POSITION RECORDINGS
MEAN DURATION (15 SECOND INTERVALS)
200
150
100
50
0
**
*
PROX. TO MALE
ON
EN
IN
EN + IN
N TOT
SIMUL. IN

Figure 8. Percentage of females choosing S+ D+ N- males or S- D+ N+ males. For three behaviors, Prox, EN+IN, and IN, a 20% difference criterion was used to determine female choice (See text). The remaining measures are based on frequency data alone. Percentages were based on all females in the experiment (N = 17), bars reflect only those females that made a choice. (Sign Test; * $p < 0.05$, ** $p < 0.01$).

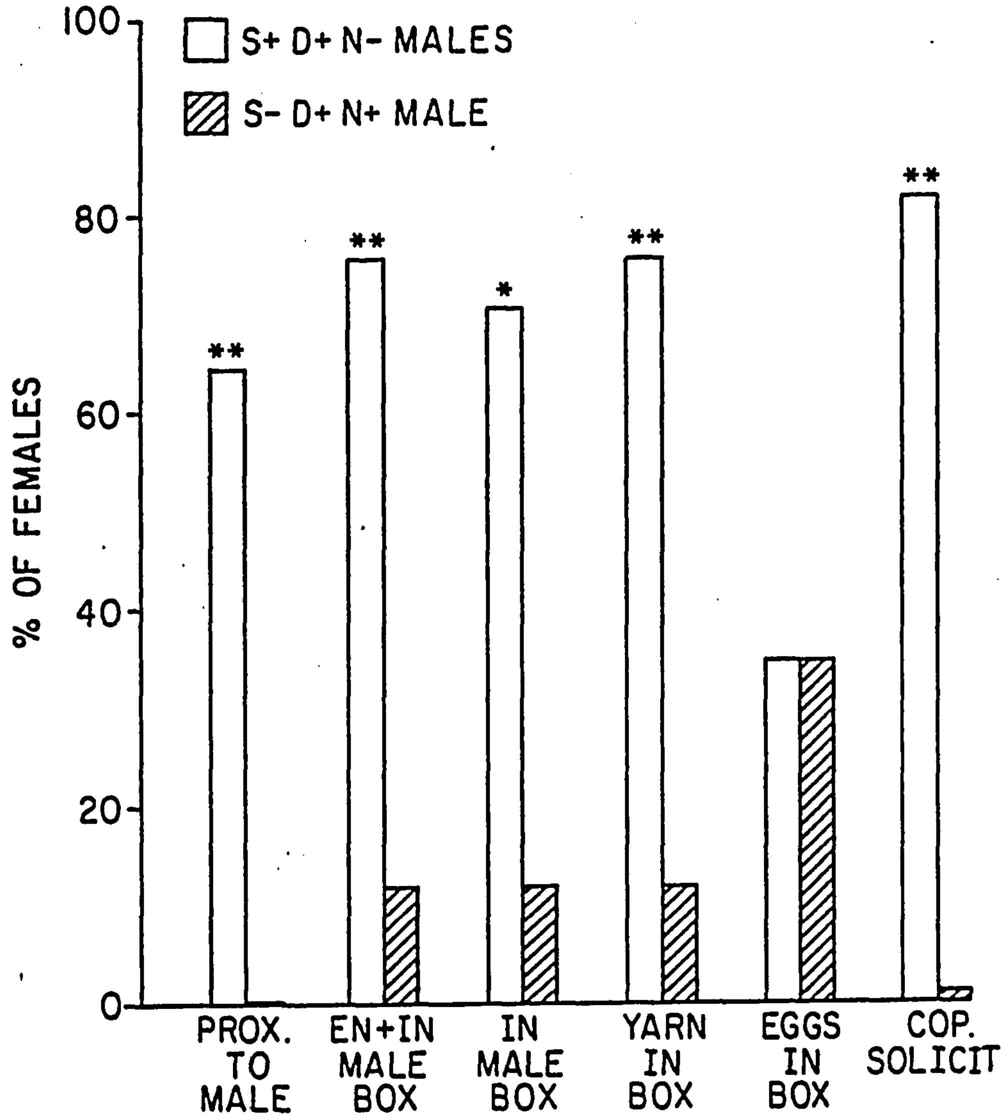

S+ D+ N- MALES
S- D+ N+ MALE
% OF FEMALES
100
80
60
40
20
0
**
**
*
**
**
PROX. TO MALE
EN+IN MALE BOX
IN MALE BOX
YARN IN BOX
EGGS IN BOX
COP. SOLICIT

Table III. Correlations of female preferences with male behaviors in Experiment II. Female preference measures are difference scores for behavioral responses to the males within a triad. Male behavior measures are difference scores of male behaviors within a triad. Only significant correlations are listed.

Male Behaviors	Female Behaviors							
	Prox.	ON	EN	IN	N-Tot.	Simul. IN	Cop. Solicit	Eggs
USong				-.42				
C-D (courts)								
C-LO								
C-HI			+.43					
C-Tot.								
V (nest voc.)						+.54 *		
VO			+.49 *		+.46	+.50 *		
VE								
VI								
V-Tot.						+.52 *		
ON (male)								
EN					+.47			
IN						+.60 **		
N-Tot.						+.68 **		
Nest material gathered								

p <.05
* p <.025
** p <.01

D+ N- male.

There was no correlation between differences in courtship dance frequencies and female copulation solicitation preferences (Table III.). Female copulation solicitation responses were also independent of the frequencies of all other male behaviors recorded. In contrast to previous experiments, where solicitation responses were independent of other measures, the copulation solicitation preferences of females were correlated with time spent at the nestboxes of the males and egg laying location preferences.

Time spent at male nestboxes.

No female chose the nestbox located in the neutral region of her cage as a nest site. Overall, females spent significantly more time at all three sites (ON, EN, IN) at the S+ D+ N- males' nestboxes (Fig. 7). ON was never actually a nestsite for any pair of birds, and this distinction from EN and IN was evident from the failure of the ON preference to be correlated with EN and IN preferences; EN and IN were correlated. The preference for the nestboxes of the S+ D+ N- males was reflected in the number of females that met the 20% criterion for nestbox preference. For both IN and EN+IN combined, a significantly greater percentage of females that met the criterion chose the S+ D+ N- nestboxes (IN, N=14, 12 vs. 2, Sign test, $p < 0.01$; EN+IN, N=15, 13 vs. 2, Sign test, $p < 0.01$; Fig. 8).

Differences in the amount of time females spent at the nestboxes of the two males were correlated with differences in several male behaviors (Table III.). High intensity courtship dances and nest vocalizations terminating at ON were correlated with durations at EN by the females. The differences in USong and USong attempts between the two groups of males were not significantly different, but were negatively correlated with the time females spent IN the nestboxes of males. The greater the difference in USong activity between males, the less time females appeared to spend IN the S+ D+ N- males' nestboxes. This appeared to be independent of the fact that the S- D+ N+ males could not actually sing, since the majority of females occupied S+ D+ N- males' nestbox. The time males spent at the entrance of their nestbox was correlated with the total time females spent at male nestboxes indicating that the presence of either the male or the female at these locations influenced the other bird's presence.

A likely indicator of pair formation, simultaneous occupancy of a male nestbox by a male and a female occurred significantly more often with the S+ D+ N- males (Fig. 7), and was correlated with the differences in nest vocalization activity between males (Table III.).

Nest building by females

Each female had two potential sources of nest material for building a nest. All but three of the S- D+ N+ males placed nest material in their nestbox, and 10 put a minimum of 50 pieces in their nestbox. The majority of females, therefore, could have used these male's nestboxes as a source of nest material in addition to the bundles of material provided for them on their cages. Ten females took nest material from these bundles, and a majority (6) placed it exclusively in the nestbox of S+ D+ N- males. Only one female put nest material exclusively in the nestbox of the S- D+ N+ male. This difference was not significant (Sign test, Fig. 8). The remaining three females either put equivalent amounts of nest material in both male nestboxes, or left the nest material on the floor of their cages. At the conclusion of observations, nest material was found in male nestboxes (the female side of the box) of 15 triads. For a significantly greater number of triads, nest material was in the S+ D+ N- male's nestbox (13 vs. 2, Sign test, $p < 0.01$). Apparently, females compensated for the fact that S+ D+ N- males were not provided with nest material by taking yarn, not only from own supply, but from the nestbox of the S- D+ N+ male and putting it in the S+ D+ N- male's nestbox. Consistent with this preference, the gathering of nest material by the S- D+ N+ males was not significantly correlated with nestbox occupancy by females.

Eggs in male nestboxes.

Twelve females laid eggs in male nestboxes, but they did not reliably distinguish between the two types of males in selecting a site for laying. Five females laid their eggs exclusively in the S+ D+ N- male's nestboxes, six laid their eggs exclusively in the S- D+ N+ male's nestboxes, and one female laid the majority of her eggs in the S+ D+ N- male's nestbox. Even though many of the females put nest material in the nestboxes of the S+ D+ N- males, when the males pulled the nest material to their side of the box it was removed so that they could not engage in nestbuilding. As a result, only one S+ D+ N- nestbox had sufficient nest material to cover the floor (all others had three to 4 pieces), and this female did not lay eggs. Consequently, females that laid eggs in S+ D+ N- male nestboxes did so in empty nestboxes. Interestingly, the amount of nest material gathered by S- D+ N+ males in the triads where no eggs were laid was significantly lower than the egg laying triads (Eggs, N = 12, mean =

183.58 pieces; No Eggs, N = 5, mean = 16.4 pieces; MWU, $U = p < 0.05$).

In general, the various measures of preference were correlated (Table IV.). Proximity, Simul. IN, Copulation solicitation, and Eggs were all correlated with the total amount of time spent at male nestboxes. The copulation solicitation preferences of females were correlated with the male nestboxes chosen as the site for egg laying.

Table IV. Correlations between measures of female preference in Experiment II.: difference scores for behavioral responses of a female to the males within a triad. Only significant correlations are listed.

Female Behaviors

	Prox.	ON	EN	IN	N-Tot.	Simul. IN	Cop. Solicit	Eggs
Proximity	----				+.45			
ON		----			+.59 **			+.79 **
EN			----	+.51 **	+.56 **		+.48	
IN				----	+.77 **	+.62 **		
N-Tot.					----	+.51 *	+.58 **	+.50 *
Simul. IN						----		
Cop. Solicit							----	+.67 **
Eggs								----

p <.05
* p <.025
** p <.01

Discussion

In this experiment, muting males did not produce significant deficits in USong attempts or the frequency of attempted courtship without song. The frequencies of nest vocalizations did differ from those of the unmuted (S+ D+ N-) males, however. Interestingly, muting did not appear to alter the quality of these vocalizations; to the ear they sounded no different than those of intact males. It appears, therefore, that the muting procedure itself did not produce the decreases in nest vocalizations among the S- D+ N+ males. Female responses to these males, particularly their proximity to them, may have been an important factor. Males usually only vocalized and entered the nestbox when the female was nearby. Thus, the strong preferences of females for the S+ D+ N- males decreased the opportunity for the S- D+ N+ to solicit the females at their nestbox. Time spent at nestboxes by the two types of males did not differ. Females in the experiment, therefore, had a choice between males differing primarily in their ability to sing and nestbuild as a result of the experimental manipulations. With the exception of these two behaviors and nest vocalizations, the two groups of males behaved similarly on all other behaviors recorded.

On most of the measures of preference, female responses indicated that song was a relatively more important factor for mate choice than nest building or the presence of a nest. Females preferred to be in closer proximity to the S+ D+ N- males. Their preferences on this measure, however, were independent of the frequencies of all of the male behaviors recorded. Since half of the males could not sing during courtship dances or when attempting undirected song, the qualitative differences in the ability to sing between the males most likely accounted for females spending more time near the S+ D+ N- males and interacting with them.

Female solicitations for copulation were observed in most triads exclusively in response to S+ D+ N- male courtship. Even though females solicited exclusively to courtship, the reason for this preference was not an increased likelihood of observing solicitation with more frequent courting. The two groups of males did not differ significantly in courtship dance activity (although of course the S- D+ N+ males lacked the vocal component), nor were the solicitation preferences correlated with differences in courtship dance activity within triads. In addition, copulation preferences were not correlated with the frequencies of any other male behavior. The selectivity of the female preference, then, was apparently due to the ability of S+ D+ N- males to sing during courtship. The criterion for solicitation was probably some quality of song.

Even though we might have predicted that females would spend more time near S+ D+ N- males and solicit them more frequently because of some "attractive" quality of song, the choice of nestsites would have seemed more likely to be dependent on the quality of some nest related behavior. Since S+ D+ N- males were not able to build nests, the nestboxes of S- D+ N+ males would appear to be the better nest site. The S- D+ N+ males did add to the nests they were given, 10 males put at least 50 pieces of nest material in their nestbox, but females spent more time at the nestboxes of the S+ D+ N- males. This included occupancy (IN) of nestboxes which in almost all cases contained almost no nest material. Females seemed to compensate for the S+ D+ N- males lack of nest material by taking nest material from the S- D+ N+ males' nestboxes and their own supply and putting it in the deprived males' nestboxes. Females did not find male nestbuilding or nests attractive; interest in the nestboxes of the S- D+ N+ males was not correlated with nestbuilding activity by these males. The two types of males did not differ in the time they spent IN their nestboxes so it would be difficult to attribute preferences to the attractiveness of nestbox occupancy. The ability to sing, or some other quality associated with it, was far more important to the females even though they had to build nests themselves and their nestbuilding efforts were usually stymied by removal of nest material once it was pulled to the males' side of the box. Simultaneous nestbox occupancy also significantly favored the singing males indicating that pair formation occured more often with these males. Its relationship with nest vocalization activity may have been due to male efforts to get females to accept their nest site, the more effort (frequency) the more likely that a female would accept the site. It seemed unlikely that vocalization activity was indirectly related to simultaneous occupancy because higher nest vocalization activity resulted in more time being spent by males in the nestbox; vocalization activity and male nestbox occupancy were not correlated for either group of males. Thus, male interest in the nest site may have enhanced pair formation as indicated by simultaneous nestbox occupancy.

Nestbuilding activity or the quality of a nest may not actually be a criterion for female choice. The S- D+ N+ males did gather nest material and build nests, but appeared to do much less gathering than the normal males in a previous experiment (Sheridan and Harding, 1985; means 149 vs. 372 pieces, respectively). The males in the present experiment may not have gathered as much because they were provided with a rudimentary nest (loose ball of yarn) in order to give them an initial nest advantage over the singing males. However, it is possible that the males built little because male zebra finches do not actively build to attract a mate, but only after they are assured a mate. Although it was not possible to directly determine if low levels of nestbuilding were the result of female preferences for the other male, the mean latency to gather at least 100 pieces of nest material (an amount probably indicative of active nestbuilding) was significantly longer in the present experiment than previously found (Sheridan and Harding, 1985; 12 days vs. 8 days, respectively; MWU, $p < 0.02$). This may reflect the fact that nestbuilding males in the present experiment (S- D+ N+) were not preferred by females and as a consequence active nestbuilding was delayed, although the presence of some initial nest material may have also affected the latency to active nestbuilding.

In this experiment, the majority of females laid eggs. Although most females showed a clear preference to spend time in and around the nestbox of the S+ D+ N- male, they showed no clear preference for this site when it came to egg laying. However, it is interesting that some females chose to lay their eggs in the empty nestboxes of the S+ D+ N- males. In at least 4 triads, some eggs laid in S+ D+ N- male nestboxes were broken, and it is possible that other eggs were laid, broken and consumed before they could be recorded. Clearly, even with such negative consequences for reproductive success, the quality of the nest was not absolutely critical to the choice of a site to lay eggs. The quality of the males themselves was important. Nest building activity was not related to egglaying preferences, although it may account for triads where no eggs were laid; the S- D+ N+ males in the triads that had no eggs gathered significantly less nest material than males in the other triads. Possibly the stimulation of male nestbuilding is also an important stimulus for ovulation. Some females chose to lay their eggs in the nestbox of the S- D+ N+ male that did more nest building even though, based on the other measures, they clearly preferred the S+ D+ N- males. This could indicate that females, will switch their preferences if their mate fails to contribute an essential ingredient necessary for reproductive success, nestbuilding in this case, once the reproductive sequence has begun. Mate choice need not be an all or none decision; a female may be better off finding a better mate than completing the reproductive effort with a male that has revealed himself to be a poor mate. Another possible explanation is that some females laid eggs in the S- D+ N+ males' simply because they were better nests, essentially dumping their eggs in a nestbox in which the eggs were more likely to survive. Of those triads where females laid eggs in the S- D+ N+ males' nestbox, all the males had put some nest material in the nestbox; although in only 3 of these 6 triads did the female side of the nestbox have nest material in it. It is not possible to determine how the females viewed these bisected male nestboxes with differing amounts of nestmaterial on either side of the mesh partition, but they did have nest material in them. This may have been sufficient for some females to have preferred to lay their eggs in these nestboxes.

In our breeding aviary and in some experiments we have also found evidence that females sometimes dump eggs in the nests of other pairs. Thus, females may not have switched their choice of mate, but laid their eggs in a qualitatively superior nest.

Probably reflecting the strong overall preferences for the S+ D+ N- males, most behavioral measures of preference were correlated among the females. This included copulation solicitation which was correlated with overall time at the male nestbox and egg laying. Egg laying was also correlated with time spent at male nestboxes. Since egg laying did not reveal a preference for a particular type of male, positive correlations between egg laying choices and the other measures must be attributable to females with the strongest preferences on the other measures laying their eggs with the S+ D+ N- males, while other females laid their eggs with the S- D+ N+ males. This may indicate that, when the preferences of females were not that strong, they switched their allegiance when they laid their eggs because of the failure of their S+ D+ N- males to build a nest.

EXPERIMENT III.

Method

Experimental design

Using the same paradigm as the previous experiments, females were given a choice between males differing in their hormonal status; both males were gonadally intact, but one male received an implant of a potent androgen, androstenedione (AE). Previous research (Harding, Sheridan, and Walters, 1983) demonstrated that implants of this hormone were most effective in increasing the frequencies of reproductive behaviors, particularly courtship, above the levels seen in normal males. In the present investigation, both males were able to sing and were provided with material for building nests. The choice for females was, therefore, between males with normal and enhanced hormone levels.

Subjects

All birds were selected and maintained as in the previous experiments. Two blocks of 6 triads were run, N = 12.

Procedure

Half of the males received implants of crystalline androstenedione (Sigma) in silastic tubing placed subdermally on the upper back four days before observations began. The first six males to receive implants received 2.5 mm of AE in silastic tubing (0.76 mm id. 1.65 mm od.). These implants failed to increase the frequencies of courtship activity above normal levels. The second block of AE males received 5.0 mm implants of hormone in tubing. Again there was no significant increase in courtship activity. Comparisons of the behaviors of AE males in the two blocks of triads did not reveal any significant differences between them. Data from the two blocks were therefore pooled for analysis. All other aspects of the procedure, behavior recording, and data analysis were identical to the previous experiments.

Results

Differences in male behaviors

Contrary to prediction, AE treatment did not significantly increase the levels of courtship or other male behaviors above the frequencies of normal males (Fig. 9). In addition, the frequencies of courtship, nest vocalizations, and nest occupancy (Fig. 10) of both groups of males appeared to be lower than those of gonadally intact males in previous experiments.

For the most part, the relationship among the behaviors within each of the two groups of males were similar. For the AE males, USong was correlated with gathering nest material ($r = +0.65$, $p < 0.01$), nest vocalizations terminating IN nestboxes (VI, $r = +0.60$, $p < 0.02$), and the time spent IN the nestboxes themselves ($r = +0.78$, $p < 0.01$). For the Normal males, USong was also correlated with gathering nest material, VI, and IN ($r = +0.60$, $p < 0.02$; $r = +0.69$, $p < 0.007$; $r = +0.55$, $p < .03$, respectively), and, in addition, VE and EN (VE, $r = +0.72$, $p < 0.004$; EN, $r = +0.87$, $p < 0.001$).

The relationship of courtship activity with other male behaviors also revealed some distinctions between the two male groups. Courts from a distance (C-D, from greater than 12 inches) and low intensity courtships (C-LO) were negatively correlated with gathering nest material in the AE males (C-D, $r = -0.51$, $p < 0.05$; C-LO, $r = -0.59$, $p < 0.021$). In the normal males, only C-LO was related to nest material gathering and the correlation was positive ($r = +0.51$, $p < 0.05$). C-LO was also correlated with some nest vocalization activity among the normal males (V, $r = +.54$, $p < 0.034$; VE, $r = +0.63$, $p < 0.014$). High intensity courtships (C-HI, directed song plus high intensity dance)

Figure 9. Differences in mean frequencies (± SEM) of behaviors between androstenedione (AE) males and normal males. The upper graphs show differences in mean total behaviors, while the lower graphs break down the courtship and nest vocalization data into different types of displays. See text. (Mann-Whitney U; N1 = N2 = 12).

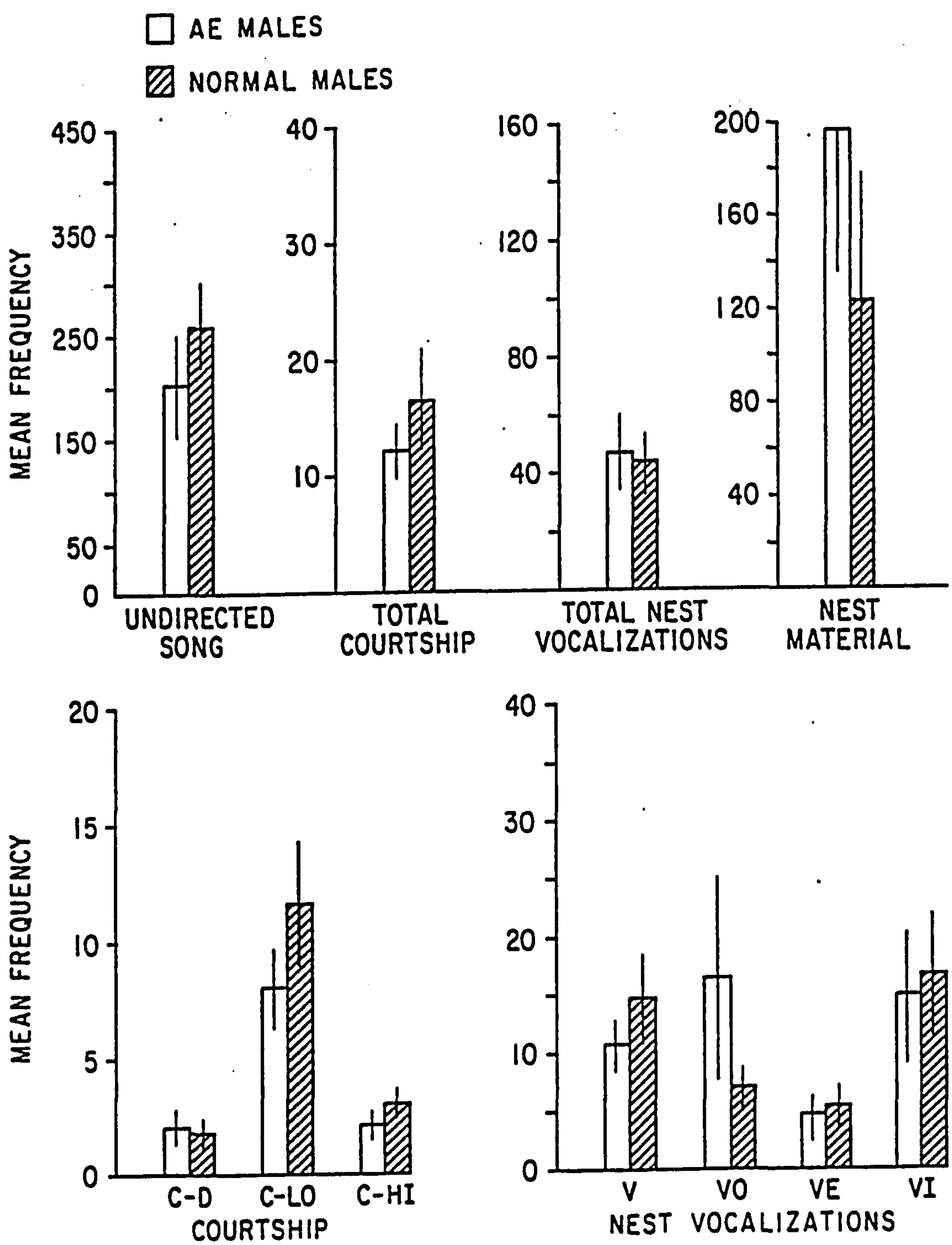
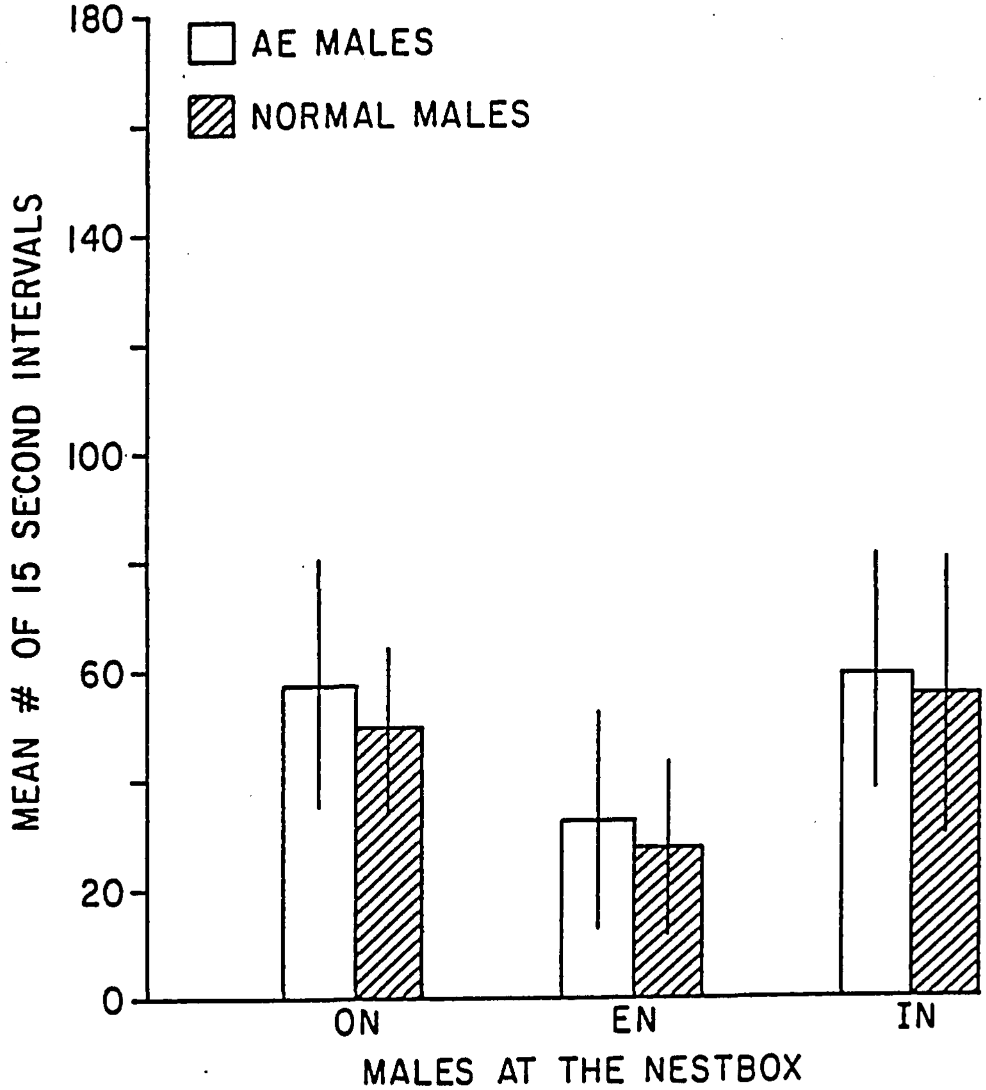

AE MALES
NORMAL MALES
MEAN FREQUENCY
450
350
250
150
50
0
UNDIRECTED SONG
40
30
20
10
TOTAL COURTSHIP
160
120
80
40
TOTAL NEST VOCALIZATIONS
200
160
120
80
40
NEST MATERIAL
MEAN FREQUENCY
20
15
10
5
0
C-D
C-LO
C-HI
COURTSHIP
40
30
20
10
0
V
VO
VE
VI
NEST VOCALIZATIONS

Figure 10. Differences between males in mean durations (15 sec. intervals, ± SEM) spent at their nestboxes. Nestbox locations: ON, on top of the nestbox; EN at the entrance of the nestbox; and IN, in the nestbox. (Mann-Whitney U; N1 = N2 = 12).


180
140
100
60
20
0
AE MALES
NORMAL MALES
MEAN # OF 15 SECOND INTERVALS
ON
EN
IN
MALES AT THE NESTBOX

were correlated with nest related behaviors only among the AE males (V, r = +0.65, p <0.01; VI, r = +0.54, p <0.021; EN, r = +0.70, p <0.005; IN, r = +0.59, p <0.02). However, in the normal males, total courtship (C-Tot.) was correlated with VI (R = +0.52, p <0.039) and IN (r = +0.54, p <0.035).

Nest vocalizations terminating at ON were correlated with time spent ON the nestbox only among the normal males (VO with ON, r = +0.77, p <0.001), but in both groups, the time spent at EN and IN were independent of time spent ON. In both groups, time at EN and IN were correlated (AE males, r = +0.82, p <0.001; normal males, r = +0.68, p <0.008), and nest vocalization activity terminating at these two locations was associated with time spent at the nestbox (AE males; VE with EN, r = +0.76, p <0.02; VE with IN, r = +0.62, p <0.016; VI with EN, r = +0.88, p <0.001; VI with IN, r = +0.82, p <0.001. Normal males; VE with EN, r = +0.65, p <0.01; VE with IN, r = +0.66, p <0.009; VI with EN, r = +0.61, p <0.018; VI with IN, r = +0.79, p <0.001).

For both groups the gathering of nest material was correlated with nest occupancy (IN) and the nest vocalizations at this location (AE males; IN, r = +0.72, p <0.004; VI, r = +0.55, p <0.033. Normal males; IN, r = +0.90, p <0.01; VI, r = +0.82, p <0.001). However, among the normal males, gathering nest material was also associated with VE and EN (VE, r = +0.72, p <0.004; EN, r = +0.70, p <0.005).

Preferences of females

Proximity to males.

Overall, females were found more frequently with the AE males, based on position recordings at one minute intervals during observations, but the trend was not significant (Fig. 11). Similarly, while the majority of females that met the 20% difference criterion for proximity preference chose the AE males (5 vs. 1) not enough females made a choice to attain significance (Fig. 12). The trends in the proximity responses were not correlated with any differences in the frequencies of male behaviors (Table V).

Copulation Solicitation.

During the two weeks of observations, copulation solicitation was observed in 8 triads (67%). A significant majority of females (7 vs. 1, Sign test, $p < 0.05$, Fig. 12) solicited the AE male, 5 of them exclusively. The remaining female solicited her normal male once. Copulation solicitation preferences were not related to the male courtship rates. Overall, mean frequencies of courtship activity between the two types of males were not significantly different (Fig. 9), and no measure of courtship activity was correlated with the copulation solicitation responses of the females. Copulation solicitations were correlated with differences in male nestbox occupancy although mean durations of nestbox occupancy between the two male groups were not significantly different. Solicitations were also positively correlated with differences in the frequencies of nest vocalizations terminating in the nestbox.

Comparisons of differential courtship activity and total courtship within triads (AE + normal male courtship) did not account

Figure 11. Differences in responses of females to AE males and normal males: Mean proximity (± SEM) based on recordings of female position in the cage at one minute intervals during observations (Prox to male), mean durations (± SEM) at each location at the male nestbox (ON, EN, and IN), mean durations for all nestbox locations (NTOT), and mean durations of simultaneous nestbox occupancy by male and female (Simul IN). (Wilcoxon matched-pairs signed-ranks test; N1 = N2 = 12; * $p < 0.05$, ** $p < 0.01$).

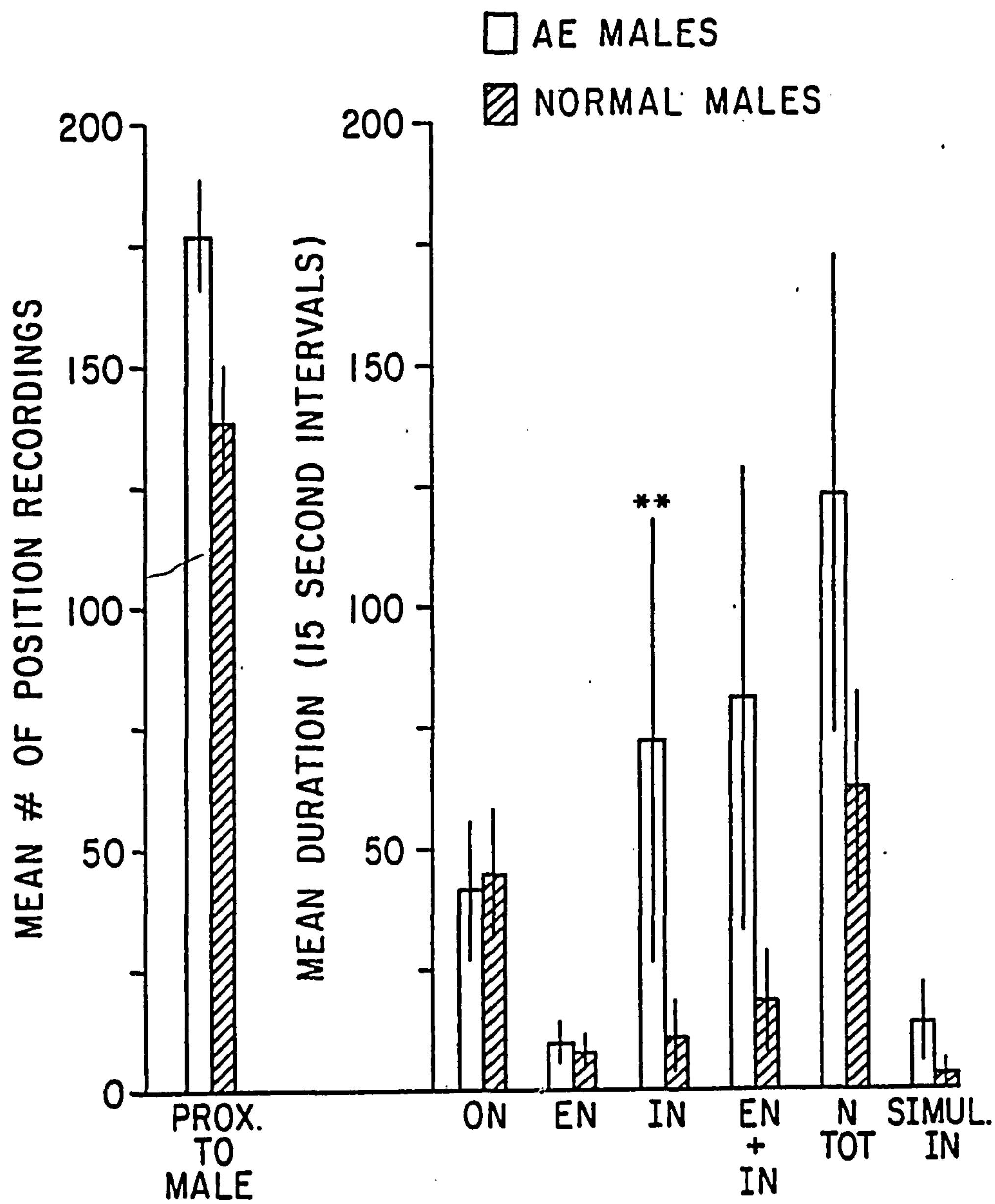
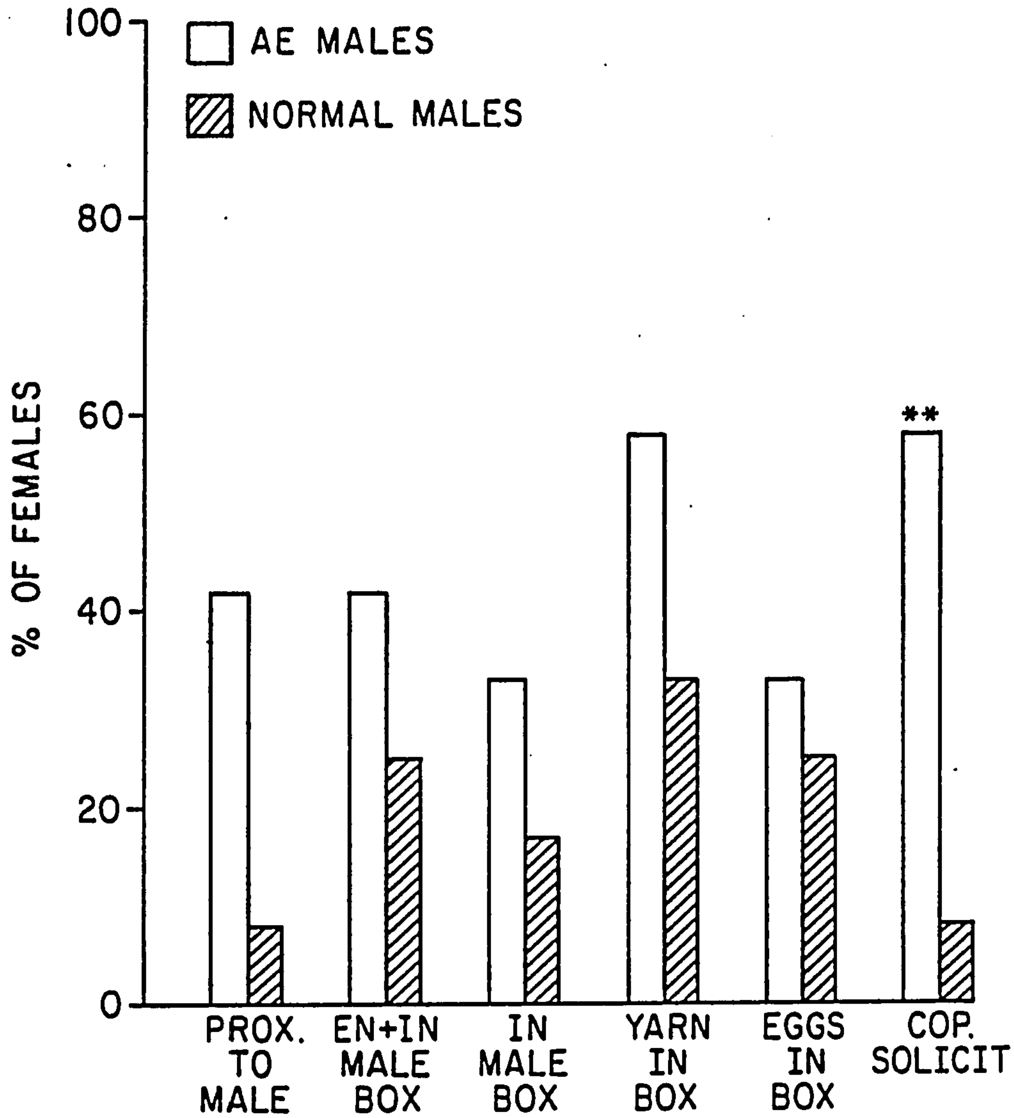

AE MALES
NORMAL MALES
MEAN # OF POSITION RECORDINGS
MEAN DURATION (15 SECOND INTERVALS)
0
50
100
150
200
PROX. TO MALE
ON
EN
IN
EN + IN
N TOT
SIMUL. IN
**

Figure 12. Percentage of females choosing AE males or normal males. For three behaviors, Prox, EN+IN, and IN, a 20% difference criterion was used to determine female choice (See text). The remaining measures are based on frequency data alone. Percentages were based on all females in the experiment (N = 12), bars reflect only those females that made a choice. (Sign Test; * $p < 0.05$, ** $p < 0.01$).



100
80
60
40
20
0
% OF FEMALES
AE MALES
NORMAL MALES
**
PROX. TO MALE
EN+IN MALE BOX
IN MALE BOX
YARN IN BOX
EGGS IN BOX
COP. SOLICIT

Table V. Correlations of female preferences with male behaviors in Experiment III. Female preference measures are difference scores for behavioral responses to the males within a triad. Male behavior measures are difference scores of male behaviors within a triad. Only significant correlations are listed.

Male Behaviors	Female Behaviors							
	Prox.	ON	EN	IN	N-Tot.	Simul. IN	Cop. Solicit	Eggs
USong								
C-D (courts)								
C-LO		+.56						
C-HI								
C-Tot.								
V (nest voc.)								-.64 *
VO								-.64 **
VE								
VI							+.59 *	
V-Tot.								
ON (male)								
EN								
IN			+.76	+.54			+.61 *	
N-Tot.								
Nest material gathered					+.71 **			+.58 *

p <.05
* p <.025
** p <.01

for triads in which females were not observed soliciting for copulation. Mean differences in courtship for those triads in which soliciting was observed (mean = .625, N = 8) were were not significantly higher than those in the non-soliciting triads (mean = -14.00, N = 4). Similarly, the means of total frequencies of courtships within triads did not significantly differ between triads in which females solicited (mean = 24.88, N = 8) and those in which they did not (mean = 36.5, N = 4).

Time spent at male nestboxes.

As in previous experiments, no female chose the nestbox located in the central region of her cage as a nest site. Overall, females spent equivalent periods of time ON the nestboxes of both types of males (Fig. 11). Time spent at the entrance of male nestboxes was also virtually equivalent, and, in addition, it was low compared with the previous experiments. Nestbox occupancy, a good indicator of nest choice, indicated a significant preference for the AE males (Fig. 12). Ten females met the 20% difference criterion for preference based on the time spent IN male nestboxes, but there was no significant trend of preference for either type of male; 6 chose the AE male, and 4 the normal male (Fig.12).

Preference to spend more time in a male nestbox was correlated with only one male behavior, male nestbox occupancy. However, simultaneous nestbox occupancy was not correlated with the time spent in the nestbox by either the male or the female. Thus, the presence of either bird in the nestbox was related to overall occupancy, but it did not have a significant influence on occupancy by the other bird. Simultaneous nestbox occupancy was correlated with male nest vocalizations terminating IN.

Nestbuilding.

In 7 triads, at least one of the males gathered more than 100 pieces of nest material and placed them in the nestbox. The females in these triads, then, had the option of taking nest material from the males' nestbox or the bundle provided them in their cage. Six females took nest material from their supply with a trend to place it in the nestboxes of AE males (4 vs. 1, 1 female did not put it in a nestbox, Sign test, NS). At the end of the experiment, nest material was found in the female side of male nestboxes in 11 triads. In the majority of these triads (7) most of the nest material was found in the AE male's nestbox, but the trend was not significant.

Eggs in male nestboxes.

Seven females laid eggs. Four females laid their eggs exclusively in the nestbox of the AE male, and 3 exclusively in the nestbox of the normal male. Egg laying preferences were correlated with differences in the amount of nest material gathered by males within triads ($R = +0.58$, $p < .025$). Yet, the amount of nest material gathered was not found to account for triads in which females did not lay eggs. More nest material was gathered in triads with eggs (mean = 357.86, N = 7), but it was not significantly greater than in triads in which no eggs were found (mean = 290.20, N = 5). Differences in the amount of nest material gathered by males within triads revealed an interesting but non-significant trend. In triads with eggs, the AE males gathered more nest material (mean difference = 119.857, N = 7) than those in triads without eggs (mean difference = 8.2, N = 5). Courtship activity also did not appear to account for triads with no eggs. Mean differences in courtship were similar in the egg triads (mean differences = -3.4, N = 7) and no eggs triads (mean differences = -5.4, N = 5; negative numbers indicate that normal males tended to court more, see Fig. 9). Differences in total courtship activity within triads did not significantly differ between triads in which eggs were laid (mean C-Tot. = 24.29, N = 7) and those in which no eggs were laid (mean C-Tot. = 35.00, N = 5).

In general, the number of female behaviors that were correlated was somewhat lower than in previous experiments (Table VI), however, some of the more important relationships remained. Nest occupancy by females was correlated with the trends in proximity and egglaying. IN was also correlated with the other behavior in which a preference was found, copulation solicitation. Nest occupancy preferences were correlated with time spent around the nestbox, but with ON the correlation was negative. Egg laying was correlated with proximity and EN.

Table VI. Correlations between measures of female preference in Experiment III; difference scores for behavior responses of a female to the males within a triad. Only significant correlations are listed.

	Female Behaviors							
	Prox.	ON	EN	IN	N-Tot.	Simul. IN	Cop. Solicit	Eggs
Proximity	----			+.56	+.78 **			+.57
ON		----	-.58 *					
EN			----	+.80 **	+.54			+.55
IN				----	+.71 **		+.54	+.52
N-Tot.					----			+.79 **
Simul. IN						----		
Cop. Solicit							----	
Eggs								----

$p < .05$
* $p < .025$
** $p < .01$

Discussion

AE and normal males, did not differ significantly on any of the behavioral measures. In addition, the relationship among behaviors in the two groups were similar, and any distinctions may have been the result of female responses to the males. Nonetheless, there were significant trends among females indicating a preference for the AE males on two measures of female behavior. The majority of females that solicited males for copulation preferred to respond to the courtship of the AE males. This preference, however, was not due to the frequency with which these males courted. In fact, for both low and high intensity courtship there was a trend for the normal males to court more frequently. In addition, low courtship frequencies within triads did not account for females that were not observed soliciting for copulation. Clearly, the frequency of courtship was not a parameter which influenced this measure of preference. It is also unlikely that the intensity of courtship, as measured by changes in the posture and the movement patterns of the visual dance component of courtship, was related to solicitation. High intensity courtships were not correlated with copulation solicitation, and there was no suggestion that females were more likely to respond to courtship dances of greater intensity. Thus, while females solicited almost exclusively in response to courtship, neither the frequency nor the visual intensity of the behavior appear to influence the occurence of this behavioral measure of receptivity. Some other parameter, must direct the occurence of this hightly selective behavior. Some of the more likely parameters are probably contained in the song itself. Specific parameters of male song have been shown to have differential effects on the copulation solicitation responses in sparrows (Searcy and Marler, 1981) and cowbirds (West, King and Eastzer, 1981). While specific parameters of song were not examined in the present experiment, it is possible that the AE implants produced changes in some parameter making songs more "attractive" to females. The susceptibility of song, independent of frequency, to changes in androgen levels has been suggested by the work of Arnold (1975) who found that the tempo and duration of songs decreased following castration. Thus, females may have been responding to changes in the song of males reflecting their altered hormonal state.

Nestbox occupancy by males was correlated with the copulation solicitation preferences of females. Females did not directly respond to nestbox occupancy by soliciting, but interest in a nestbox by males may have been a factor influencing female receptivity. Alternatively, however, male occupancy of the nestbox may have been a male response to female acceptance of them as indicated by copulation solicitation.

There was a significant preference for the AE males based on the overall time spent by females IN their nestboxes. However, this preference did not carry over into the choices of individual females. Of the ten females meeting the choice criterion, a majority preferred the AE male nestbox (6 vs. 4), but the trend was not significant. The difference in overall mean durations in occupancy of nestboxes appeared to be the result of females that chose the AE males spending much more time in their nestboxes than those females that chose the normal males. Thus, while the AE males were not unequivocally "attractive", the females that chose them may have been showing a stronger preference than the other females that made a choice.

Time spent IN the nestbox by males was correlated with female nestbox preferences (EN and IN) suggesting that pairs were formed. However, simultaneous nestbox occupancy was not correlated with the amount of time either males or females spent IN the nestboxes. This was probably because nestbox occupancy and simultaneous nestbox occupancy durations were generally low, and suggests that while occupancy of the nestbox by one member of a pair influenced the other, they were not likely to be found IN the nestbox together.

Differences in the total time females spent at the three nestbox locations (ON, EN, IN) of the two males were correlated with gathering nest material. Although neither the amount of nest material gathered by the two types of males nor total time females spent at the two male nestboxes differed significantly, both trends favored the AE males. Although this may suggest that females found the AE male nestboxes more "attractive" because of the amount of nest material contained in them, or the amount of nestbuilding activity, males may not build until females indicate an interest in a nest site. The correct alternative is difficult to ascertain.

Although no other female behaviors indicated a significant preference for one group of males, the trends for proximity, nestbuilding, and egg laying all favored the AE males. Both the proximity and egg laying data were correlated with the significant difference in nestbox occupancy. In addition, egglaying was correlated with the gathering of nest material by males. This may indicate that nestbuilding activity has some "attractive" influence on female choice or that nestbuilding stimulates ovarian development. Egg laying was also negatively correlated with differences in two types of male nest vocalizations (V, VO). It is difficult to explain this relationship, except that it may mean that females did not choose the male that was soliciting primarily for a nest ON top of the nestbox or away from the nestbox.

The relationship of the various measures of female preference revealed a consistency in choices overall. Including the two measures including significant preferences, copulation solicitations and time spent IN male nestboxes, most measures that favored the AE males were correlated. IN was also correlated with measures with trends favoring the AE males, female proximity and egg lating. These relationships suggested a reliable tendency to prefer the AE males as mates.

Given a choice between two active males, it is somewhat surprising that more females did not indicate a choice of a mate. In previous experiments, at least one male was deficient in some behavioral quality. In the present experiment, females should have found at least one of the males adequate for mating. Yet, a lower percentage of females met the choice criterion on the various behaviors, except female nestbuilding, in this experiment than in the other experiments. Perhaps it was a result of the choice paradigm or the difficulty of choosing between similar males. Nevertheless, for a significant number of females that indicated a choice by copulation solicitation preferences the males receiving a supplementary hormone were found more "attractive". Those females that chose the AE males, spent significantly more time in the nestbox, than females that chose the normal males.

GENERAL DISCUSSION

The purpose of our investigation of mate selection in zebra finches was to determine the importance of various behavioral characteristics of males to female choice. A previous report (Sheridan and Harding, 1985), demonstrated that the quality of male behavior can direct a female's choice of mate. When females were given the choice between behaviorally intact males and males whose song, courtship dance, and nestbuilding behaviors were reduced or eliminated, they reliably chose males with the full behavioral repertoire. The preferences found were not simply a measure of approach or affiliation, but more reliable measures of mate choice; copulation solicitation, nestbox occupancy, and the chosen site for egg laying. In the present series of experiments, we have sought to determine the relative importance of qualitative differences in the three behavioral attributes which were manipulated concurrently in the previous study. We were also interested in determining whether hormone dependent parameters of these behaviors were critical to choice.

Male singing behavior appeared to be the most important characteristic to females in assessing males and choosing a mate. Males that were unable to sing were least "attractive" to females. When females were given a choice between males who could sing and dance but not nestbuild vs. males who could not sing but could dance and build nests, they overwhelmingly chose those that could sing . When playback of recorded courtship songs were substituted for the songs of muted males, females did not appear to associate the playback songs with the males themselves. There was no clear preference for either muted male even though they differed in visual courtship display activity. Using the more reliable measures of mate choice, copulation solicitation, nestbox occupancy, and egg laying, less than 50% of the females actually selected a mate. In the second and third experiments, where females could choose a singing male, preferences were not related to the frequency of male songs. In each of these experiments, the frequencies of some types of directed songs used in particular courtship displays (C-HI) were correlated with the total time females spent at the nestbox, but not with nestbox occupancy (IN). Thus, these correlations were probably due more to the proximity of females increasing male courtship rates than to a female preference for high rates of singing. Interestingly, in the second experiment in which the singing males were preferred, differences in USong frequencies were negatively correlated with differences in the time females spent in the two male nestboxes. This meant that within a triad, a male's USong frequencies were higher when the female was in the other male's nestbox. This tends to support the view that USong increases in the absence of the female (Sossinka and Böhner, 1980; Caryl, 1981), especially since a female in the nestbox of one male was out of view of the other. In the third experiment, half of the males received hormone implants in an attempt to increase the frequency of male reproductive behaviors above normal levels. These AE treated males did not significantly differ from normal males in their frequencies Usong, courtship, or any other behavior recorded, but these males may have differed in other aspects of their behaviors as a result of the hormone implants. It is not clear what male characteristics caused females to show significant preferences for AE males as demonstrated by their copulation solicitation and nestbox occupancy. Because copulation solicitation is usually a direct response to song, it has been used as a behavioral means of assessing the quality of male songs in several species. In the song sparrow, both temporal pattern and syllabic structure are parameters of importance to the response (Searcy and Marler, 1981). In the cowbird, the presence of a specific phrase element in the song is necessary for the receptivity response (West, King, Eastzer, 1981). It is therefore possible that female zebra finches were more receptive to the courtship songs of the hormone treated males because of a change in some hormone dependent parameter of song other than frequency. In addition to an effect on song frequency, Arnold (1975) found that the duration of song and the tempo of song are both reduced in male zebra finches following castration. More recently, Sossinka and Böhner (1981) have reported that tempo is a parameter of song which distinguishes USong from DSong. The females in the third experiment, then, may have found the males more attractive because of a change of tempo or some other hormone dependent parameter of song. Thus, they may have been able to detect the hormonal condition of males through their songs.

Somewhat surprisingly, the visual component of zebra finch courtship, the dance, was relatively ineffective in directing female choice. If song was eliminated, as it was for some males in the first two experiments, the ability to dance was not sufficient to "attract" females. In the second experiment, females seemed to ignore muted males even though they danced at normal levels and appeared normal in all other respects. In the first experiment, both males were muted and differed significantly in the quantity and quality of their courtship dance. Yet, few females found the differences in courtship dances sufficient to select a mate. Song was apparently necessary. Even though the alternative was a behaviorally deficient male, females did not find the male that danced more normally significantly more "attractive." Trends in the data as well as the correlations of differences between males in the frequency of dances with nestbox occupancy and egg laying suggested that the differences between males may have been detected, and that dance alone may have had have some stimulating effect on female reproduction. However, aside from the frequency of these courtship dances, other parameters, such as intensity, did not seem to be of much importance. High intensity courtships, which were distinguished from low intensity courtship based on differences in posture and more elaborate dance patterns, were not correlated with female behavioral responses. More elaborate courtship dances were then not any more attractive to females than low intensity courtship displays. Apparently, if the physiological condition of a male is important to female choice, the visual components of male courtship were not the primary criteria.

Our data, then, indicate that whatever "attractiveness" courtship behavior might have for females, it is primarily a result of the vocal component and the various parameters within it. This is not to say that the quality of a male's song is the sole criterion on which females make their selection of a mate. Nor is it likely that the courtship dance of the male is unimportant. Our data only show that song is more important. It was not possible to produce a male capable of singing without the concommitant dance component of courtship and still present females with an otherwise normal male. If such a manipulation were possible, it would likely indicate that the dance does contribute to the "attractiveness" of directed song. The presence of both components may be qualitatively more "attractive" than either alone. In budgerigars, the occurence of copulation solicitation by a female depends upon both the visual and vocal components of courtship (Brockway, 1964b). In ring doves, maximal physiological reproductive stimulation only occurs when both components are present (Friedman, 1977). Female sparrows do solicit for copulation in response to song alone, but the disposition to solicit must be artificially induced by hormone treatments. Thus, while song seems critical to choice in zebra finches, it may not be sufficient in the complete absence of the courtship dance for behavioral receptivity and the optimal integration of the physiological and behavioral changes in the reproductive sequence.

In addition to courtship activity, other behaviors of the male may be critical to female choice, especially in species where males play an active role in caring for the young (Searcy, 1979, Halliday, 1983). Behaviors associated with the selection and building of nests may be important to females in choosing a good mate and/or parent if they are an early part of a male's reproductive repertoire. In the present series of experiments, male behaviors associated with nesting were manipulated to determine the role of nest vocalizations, gathering nest material, nestbuilding, nestbox occupancy, and the nest itself in female choice. In the second experiment, the ability to build a nest proved to be of less than primary importance for female choice; females chose males that could sing over those that could nestbuild. Female preferences included occupancy of the singing males' nestbox even though in almost all cases the nestbox contained no nest material. In addition, there was no indication that the nestbuilding activity of the males with nest material had any influence on female preferences; gathering nest material was not correlated with any measure of female preference. Females actually seemed to compensate for the singing males' lack of nest material by gathering some nest material themselves. More females contributed nest material to male nestboxes in this experiment than in any of the other experiments.

In our previous report (Sheridan and Harding, 1985), gathering nest material by normal males was correlated with the proximity preferences of females and their simultaneous nestbox occupancy. While some attractive feature of this behavior may have indeed resulted in the relationship, the manipulations of males in that experiment meant that singing, dancing, and nestbuilding covaried. Thus, the relationship may have been an artifact of the overall preference for the behaviorally intact males. In the present study, both groups of experimental males in the first and third experiments were provided with nest material. In the first, differences in gathering nest material between males were not correlated with any measure of female preference. Nestbuilding activity did not compensate for the males' inability to sing. In the third experiment, gathering nest material was correlated with both the total time females spent at male nestboxes and their egg laying preferences. On both of these measures the trends favored hormone-treated males who, on the average, gathered more nest material. Possibly, this indicates that when the choice is between two basically normal males (the frequencies of their behaviors did not differ) attributes such as nestbuilding become important to female choice. However, there is an alternative explanation for these correlations. A male may only begin actively building a nest once a female indicates either a.) her acceptance of him as a mate or b.) a preference for the site he has chosen. There was some suggestion of this in the second experiment, females did not choose the males able to build nests and the latency to active nest building was significantly longer than that of the behaviorally intact males who had nest material in the previous study. The mean amount of nest material gathered in the second experiment was 1/2 that of the males in the previous report. In fact, the amount of nest material gathered by males in our initial study (Sheridan and Harding, 1985) was close to twice that gathered by any other group of males that had access to nest material in the present study. While the fact that in the present experiments males able to build nests were given rudimentary nests may account for some of the reduction in nestbuilding, another factor that distinguishes the males of the first study from the others is that females showed a strong preference for them. All the others were only partially preferred at best; the strongest preferences were for the AE males, and they gathered the most nest material of any group in the present investigation. While it is important to note that the nestboxes of males in the present series of experiments were not empty, and their rudimentary nests may have reduced nest building, a failure of females to choose or accept a male or his nest site may have been a contributing factor to lower nestbuilding activity by males.

In some other avian species, males only begin nestbuilding after being assured a mate. Male ring doves, for example, only begin after a female indicates her acceptance of the nest site. Initially a female follows a soliciting male to the nest site but leaves when he does, eventually she will remain at the nest site and solicit. Only at this point does the male begin gathering nest material (Martinez-Vargas and Erickson, 1973). Nestbuilding is primarily a result of a change in physiological state, males do not begin to nestbuild until the reproductive sequence has begun. In zebra finches, females are believed to make the final choice of nest site (Sargent, 1965) and, although it has not been demonstrated that males gather only after nest site acceptance by females, our data are in line with this interpretation.

Zebra finches solicit for nest sites using a characteristic vocalization often coupled with a particular display posture. In our experiments, the posture was seen infrequently, possibly because of the limited area available to each bird at the nestbox to turn while soliciting. Nest vocalization activity was far more frequent. These vocalizations have received only limited interest in the literature, presumably because of their low amplitude in a typical bird room; they are only consistently heard when monitored with microphone and head phones. They are, however, a reliable part of most males' nesting behavior.

From our data, it was difficult to determine if these vocalizations were hormone dependent. The mean frequencies of the vocalizations among the various groups of males implied that the muting and castration procedures, as well as the responses of females, all contributed to decreases in their occurence. By far the greatest frequencies were among the male groups that were most strongly preferred by females. Were the vocalizations functioning to attract females or were they simply the result of females being in closer proximity to a male and his nest site? In our previous study (Sheridan and Harding, 1985), nest vocalizations were not related to general proximity but were, in general, related to nestbox occupancy by females. This was especially true of those vocalizations terminating in the nestbox. This suggested that they did function to attract females to the nest site. In the present study, females in Experiment II. strongly preferred to occupy the nestboxes of the singing males and these males vocalized significantly more often in relation to this nestbox location (VI). However, there was only a limited relationship between vocalization frequency and female responses that might indicate that these vocalizations were attractive; total nest vocalization activity was correlated with simultaneous nestbox occupancy. This measure was probably a good indicator of female nest site acceptance as well as pair formation, but it was puzzling why female nestbox occupancy (IN), independent of the male's presence, was not also correlated with vocalizations if they did actually attract females to the nestbox. The relationship, then, may have been a coincidence of males that vocalized more often tending to occupy the nestbox more often especially when the female was present. From our observations, it was clear that males used these vocalizations in an attempt to get females to enter the nestbox. However, it was not clear if these vocalizations are attractive in themselves or whether they are only involved in the determination of the nest site.

Even if females make the final choice of a nest site, the males' solicitations and occupancy of the site prior to choice may be a critical attribute of their premating behavior. In species where males actively participate in raising the young, activity at the nest could be indicative of later parental involvement such as time contributed to incubating eggs. While no evidence exists to confirm that interest in the nest has a relationship with later parental behavior, the importance of synchronized incubation of eggs by a male and female for reproductive success has been demonstrated in the ring dove (Ball and Silver, 1983). Male nestbox occupancy was correlated with several female behaviors in the experiments, but there was no strong indication that the relationships were due to an attractive quality of nest occupancy; male nestbox occupancy could have been in response to female occupancy or pair formation.

Mate choice is unlikely to be an all-or-none phenomenon based solely on some initial attractive quality, although in most instances the qualities used in choice are probably predictive of later behaviors which are also attractive to females. When the integrated sequence of behaviors in reproduction are disrupted by some shortcoming in the male's behavior, it may be of greater advantage to a female's reproductive success to leave and find a new mate. In the second experiment, females clearly preferred the S+ D+ N- males as mates up until they laid their eggs; half of the females that laid eggs chose the nestbox of the nest males (S- D+ N+) as the site for laying their eggs. When faced with the possibility of laying eggs in the empty nestboxes of the song males that would have a detrimental effect on reproductive success, females appeared to switch mates. While the situation females were presented with in the experiment was extreme, it demonstrated that female choice is not some static assessment of male quality early in the reproductive sequence which is immutable; males must continue to meet the criteria of a quality mate for the pairing to be maintained.

In general, it appeared that behaviors of the male associated with the nest were not critical to female choice. Females did not require males to build a nest in order to mate with them, but some aspects of nestbuilding may have been attractive when males were similar. It is likely, however, that nestbuilding follows mate choice and is an indication of pairing. Nest vocalizations certainly were used by males to attract females to a nest site, but if some parameter of these vocalizations indicates male quality, it was not readily apparent in our data. Males may enter the nestbox in efforts to attract the female to it, but the majority of male nestbox occupancy probably follows pairing.

Most previous investigations of mate selection in zebra finches have emphasized the role of imprinted preferences in female choice (Immelmann, 1972, Walter, 1973; Sonneman, and Sjölander, 1977; Immelmann et al., 1978). More recently it has been recognized that the behavioral attributes of males are important to choice. Ten Cate and Mug (1984) found that courtship activity of males partially accounted for the preferences of females. Our previous investigation (Sheridan and Harding, 1985), found that disruption of the reproductive behaviors of males altered their attractiveness as potential mates.

In the present investigation, it was evident that song was clearly a quality of males essential for female choice. Males able to courtship dance were not preferred as mates if they could not sing. When both males were unable to sing, females were reluctant to choose a mate and did not prefer males dancing at normal levels over males showing deficits in the dance displays. Trends in the data, as well as correlations with courtship activity, did, however, suggest that these differences were detected. Evidence for the importance of behaviors associated with the nest were somewhat equivocal. While it was clear that the ability to sing took precedent over nestbuilding, it was not apparent if the male's nest related behavioral repertoire could attract females as mates. Nest vocalizations appeared to function in male attempts to attract the female to the nest site, but it was unclear if this behavior and the others associated with the nest, nestbuilding and nest occupancy, preceded initial mate choice and pair formation.

One of our contentions about female choice in zebra finches was that male behavior would provide females with characteristics indicative of the quality of a male as a mate. Also, male premating displays may be indicative of later parental behavior because of its assumed importance in determining reproductive success (Orians, 1969, Trivers, 1972). Our results indicated that if qualitative assessments are made, courtship and more specifically the song component is most likely to be the feature of male behavior utilized in choosing a male. A specific parameter of song related to choice could not be discerned from our data. In our previous report, courtship frequencies differed between the two male groups as a result of castration, and females preferred gonadally intact males courting at normal frequencies. In our final experiment we attempted to increase courtship frequencies using androgen (androstenedione) implants. This manipulation failed to produce significant changes in courtship frequency as measured here. Interestingly, the hormone-treated males were still somewhat preferred to normal males, especially in terms of copulation solicitations by females which occur directly in response to directed song and the courtship dance. Female preferences were not correlated with differences in courtship frequencies within triads. Since in the absence of song females did not show strong preferences for either of the behaviorally distinct males, it was likely that some parameter of song accounted for solicitation preferences in the final experiment. Thus, it appeared that hormone treatment altered song in such a way to make it more attractive for copulation solicitation. Of course, the frequency with which a male sings may still be an important parameter in female preference, but our data suggest that small differences in frequency are relatively unimportant.

Our contention that females may be able to detect the physiological condition of males was also partially supported by our results. Hormone-treated males were more attractive as mates and this appeared to be related to parameters of song, since females did not show any strong preference for either a gonadally intact male or a castrate when both males were unable to sing. It is known that the frequency of song, particularly directed song, is related to androgen titers (Pröve, 1978; Sossinka, et al., 1980). There is also data suggesting that the tempo and duration of song are also hormone sensitive (Arnold, 1975; Sossinka and Böhner, 1980). Females zebra finches have been shown to be able to distinguish the songs of individual males (Miller, 1979a; 1979b). Females may be able to use song to assess some underlying physiological state indicative of the quality of a male as a mate. Song rates during pairing have been shown to predict later parental behavior in the stonechat (Greig-Smith, 1982).

Our investigations of mate selection in zebra finches have demonstrated the importance of behavior in female choice. Consistent with previous theories and research (Marler, 1959; Searcy, 1979; Catchpole, 1982), the song of males appears to be the primary characteristic of male behavior critical to initial female choice. Because of its dependence on hormone titers, the behavior of male zebra finches may enable a female to select a mate based on qualities critical to maximizing her reproductive success.

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