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Female Choice and the Evolution of Polygyny in the Marsh Wren (*Cistothorus palustris*)

by

Martha Louise Leonard, B.Sc., M.Sc.

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Department of Biology
University of Ottawa
Ottawa, Canada

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TABLE OF CONTENTS

Page

Chapter 3: Female Settlement: Is it affected by other females?

Chapter 4: Polygyny in marsh wrens: A test of the Polygyny Threshold Model.

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

Several hypotheses have been proposed to explain the evolution and maintenance of polygyny in passerines. One in particular, The Polygyny Threshold Model, has been widely accepted despite limited support. The purpose of this study was to test the major predictions of this model with data from a population of marsh wrens (Cistothorus palustris).

Behavioural and ecological factors influencing female fitness and choice were examined for marsh wrens at two study sites in Delta, Manitoba. Site 2 had significantly denser vegetation and deeper water than Site 1. The proportion of polygynous males and successful nests (nests that fledged at least one young) was higher at Site 2. Despite these differences, males settled at the two sites simultaneously and in numbers expected by chance. Although females settled at both sites simultaneously, there were significantly more females at Site 2 than at Site 1.

With one exception, I could find no measure of male or territory quality that affected female fitness (the number of young fledged/nest) within sites. Females paired with males that helped to feed young fledged significantly more young than females without assistance. However, few males fed young and I could find no relationship between male feeding and physical or behavioural features

suggesting that it may be difficult for females to predict which males would feed.

I could also find no relationship between male and territory quality and male pairing success. This suggests that females do not use the features that I measured (or correlated features) when they select a mate. Also, results of discriminant function analysis showed that these features did not vary significantly among males or territories. These results suggest that male and territory quality did not influence female fitness and were probably of little importance in female choice.

Female settlement may be influenced by male and territory quality and the presence of other females. Therefore, I also assessed the influence of resident females on the settlement patterns of subsequent females. The result of a playback experiment showed that resident females were aggressive to female intruders. Aggression was greatest during the pre-laying stages and decreased during laying and incubation. Females were repulsed in space at both sites and this may have been enforced through aggression on the part of primary females. Overdispersion of females in space may reduce losses from conspecific predation. Second females settled with mated males only after all the bachelor males were chosen.

This settlement pattern appears to be the result of avoidance of settled territories by prospecting females rather than displacement by resident females., Asynchronous settlement may reduce the costs associated with polygyny by reducing the overlap in nestling stages and so reducing competition for resources at this critical stage.

Four of the five predictions of the Polygyny Threshold Model that I tested were not supported. These results suggest that the model may not be the best description for the evolution of polygyny in this population of marsh wrens. I propose an alternative hypothesis that suggests that polygyny is maintained in this population because because females can reduce the costs associated with polygyny by staggering their settlement within territories.

RESUME

Plusieurs modèles ont été formulés pour expliquer l'évolution et la persistence de la polygamie chez les passereaux. L'un d'entre-eux, le modèle du "seuil de la polygamie", est sans aucun doute celui qui a été le plus souvent retenu. Il faut cependant noter qu'en plusieurs occasions le modèle a été retenu malgré que certaines prédictions n'aient été vérifiées. Ainsi, le but de mon étude est de mettre à l'épreuve les plus importantes prédictions du modèle à l'aide de données recueillies au sein d'une population de troglodytes des marais (Cisthotorus palustris).

Mes deux aires d'études étaient situées à Delta au Manitoba. La topographie des deux aires étaient statistiquement différentes. La végétation était plus dense et le marais plus profond à l'Aire 2 qu'à l'Aire 1. En dépit de ces différences, les mâles n'ont démontré aucune préférence et se sont établis simultanément sur les deux aires. De plus, le nombre de mâles sur chaque aire pouvait être décrit par un processus aléatoire. Les femelles se sont elles aussi établies simultanément sur les deux aires bien qu'en nombre toujours statistiquement plus élevé sur l'Aire 2.

J'ai tenté d'établir les facteurs intrinsèques régissant 1)le succès reproducteur des femelles (nombre d'oisillons à quitter le nid) et 2) leur choix de conjoint. Premièrement,

aucune des variables décrivant la qualité du territoire et seulement qu'une décrivant la qualité du mâle fut corrélée avec le succès reproducteur des femelles. Cette variable est l'apport parental du mâle. Le nombre d'oisillons à quitter le nid était statistiquement plus élevé lorsque le mâle participait au nourrissage des oisillons que dans le cas contraire. Les femelles aidées efectuaient également statistiquement moins de randonnée pour trouver de la nourriture que les femelles non-aidées. Il faut cependant noter que 1) seulement quelques mâles ont été observés nourrissant les oisillons et 2) aucune des variables décrivant les caractéristiques physiques du mâle ou son comportement fut corrélée avec son apport parental. Ces résultats suggèrent que les femelles pourraient avoir de la difficulté à déterminer les mâles qui participeront au nourrisage des oisillons.

Deuxièment, je n'ai trouvé aucune corrélation entre la qualité du mâle ou de son territoire et la grosseur de son harem. Une analyse de fonction discriminante a aussi démeontré que la qualité du mâle et du territoire n'étaient pas statistiquement différentes pour les diverses grosseurs de harem. L'ensemble de ces résultats suggèrent que la qualité du mâle ou de son territoire n'influencent pas 1) le succès reproducteur des femelles et 2) leur choix de conjoint.

J'ai ensuite tenté d'établir si la présence de femelles nichant sur un territoire influençait l'établissement de femelles recrues. Pour mettre à l'épreuve l'hypothèse que le comportement aggressif des résidentes empêchent l'établissement de recrues, j'ai fait jouer un enregistrement de femelle troglodyte au centre de chaque territoire mâle. Dans la plupart des cas, les femelles résidentes ont répondu aggresivement à l'écoute. Mes résultats indiquent aussi que la réponse est plus intense lors de la période de pré-ponte et diminue progressivement lors de la ponte et de l'incubation. De plus, les cas de polygamie que j'ai observé sont survenus après que chaque mâle eut attiré une femelle (i.e. lorsqu'il n'y avait plus de célibataire). Je propose ainsi que les femelles préfèrent s'établir avec des mâles célibataires plutôt qu'accouplés et que l'aggression entre résidente et recrue n'influence pas les femelles lorsqu'elles choisissent un conjoint. Il est possible que la nidification asynchrone des femelles d'un même harem est un mécanisme servant à réduire la compétition entre femelle et à minimiser les coûts de la polygamie.

Les résulats de mon étude n'ont vérifié qu'une des cinq prédictions du modèle du "seuil de la polygamie". Ce modèle ne peut donc expliquer l'évolution et la persistence de la polygamie chez le troglodyte des marais. Le modèle que je propose suggère que la polygamie persiste parce qu'elle confère au mâle polygame un plus grand succès reproducteur qu'au mâle monogame et que les femelles peuvent réduire les coûts de la polygamie en nichant de façon asynchrone.

GENERAL INTRODUCTION

Parental investment theory suggests that the sex contributing the most to the reproductive effort should be more selective when choosing a mate (Bateman 1948; Trivers 1972). Females devote more energy to each gamete and, in many vertebrate species, to the rearing of young. Therefore, females are expected to be the more discriminating of the sexes.

Females are limited in reproduction by the number of eggs they can produce and young they can rear, while males are often only limited by the number of females they can inseminate. This difference may favour the evolution of different mating strategies. That is, males should copulate indiscriminately with as many females as possible. Females, on the other hand, should discriminate among males, selecting mates with characteristics that could increase their reproductive output (Searcy 1979). This difference in strategy may lead to conflict between the sexes. For instance, the best strategy for a male is to mate with as many females as possible, while the best strategy for a female is to secure the resources of a single male. Conflict is most likely when males contribute non-shareable resources to the reproductive effort. The mating system in which the potential for conflict is greatest is polygyny, the system in which one male mates simultaneously with more than one female.

Polygyny is usually advantageous to males, so its existence will depend mostly upon the advantages and disadvantages to females (Orians 1969). The costs of polygyny to females include competition for food, male help, and breeding sites, increased attraction to predators, and a possible increase in intraspecific interactions. Thus, for polygyny to evolve and be maintained in a population, the benefits to females should outweigh, or at least balance, the costs.

One of the earliest models proposed to explain the evolution of polygyny suggested that polygyny could be the result of unbalanced sex ratios (Skutch 1935). That is, if sex ratios were skewed toward excess females, then some females are forced to settle with mated males if they are to breed. However, this hypothesis has been rejected as a general explanation, because many polygynous populations have 50:50 sex ratios and females often settle with mated males despite the presence of nearby bachelors (Verner 1964).

Another model suggested that females settle polygynously because they are deceived by males (Alatalo et al. 1981). That is, if later-arriving females are unable to assess male status they may settle with a mated male despite lowered success (Alatalo et al. 1981; Catchpole et al. 1985). If the status of the male affects female success, then females should develop ways to counter male deception. Again, this model is not generally applicable because in most species it is difficult for a male to disguise his status. This is particularly true of species in which the first females to settle are aggressive toward intruding females (Lenington 1980; Yasukawa and Searcy 1981a; LaPrade and Graves 1982; Hannon 1984)

The most widely accepted model proposed to explain the evolution of polygyny suggested that polygyny could evolve if the variance in male and/or territory quality was such that a female mating polygynously in a high quality breeding situation could rear more young by herself than one mating monogamously in a low quality breeding situation (Verner and Willson 1966; Orians 1969). The difference in quality was termed, as was the model, the polygyny threshold. Females would therefore, be compensated for the costs of polygyny by gaining a high quality male or territory..

The Verner-Willson-Orians version of the Polygyny Threshold ~~Model (~~PTM) assumes a strong correlation between male and territory quality. This is because the best males should acquire the best territories. Another version of the PTM suggests that male quality may be more important than territory quality (Weatherhead and Robertson 1979). That is, some males may be better at recruiting females than others and this feature may be independent of their ability to acquire a high quality territory. If the qualities that make males attractive are heritable then their sons would also attract many females. Females may forfeit immediate reproductive success (by settling on a high quality territory) to mate with attractive males and produce "sexy sons" (Weatherhead and Robertson 1979).

The PTM in its original form assumed that females would compete among themselves for critical resources (i.e., the competitive choice model, Altmann et al. 1977; Lenington 1980). Therefore, females choosing to settle with a mated male would have to be compensated for the costs of polygyny. However, if females cooperated in nest defense, vigilance, or foraging, then they could benefit from settling with other females (cooperative choice model, Altmann et al. 1977; Lenington 1980). In this instance, polygyny could evolve because it is advantageous to both males and females.

The PTM is the most widely accepted model for the evolution and maintenance of resource defense polygyny (Emlen and Oring 1977) in passerines (Verner and Willson 1966; Orians 1969, 1980; Altmann et al. 1977; Garson et al. 1981). Polygyny could evolve in territorial birds, because critical resources are distributed so that some males can defend territories containing a larger quantity or better quality resource than others. Second-settling females selecting males with better resources should be compensated for mating polygynously.

Marsh wrens (_Cistothorus_ _palustris_) are polygynous, marsh-nesting passerines (Welter 1935; Verner 1965), common throughout most of North America. This species exhibits low degrees of resource defense polygyny.

Polygyny in marsh wrens is thought to exist because some territories are better than others (Verner 1964; Verner and Engelsen 1970). However, the relationship between territory quality and male pairing success has never been directly tested for this species, nor have the major predictions of the PTM.

The purpose of my study is to determine how female marsh wrens select a breeding situation and how this selection process has shaped the present mating system. This thesis is divided into four chapters. In the first chapter I provide a description of the breeding biology of the study population, including an analysis of mortality factors and their influence on the selection of nesting habitat. In Chapter 2, I determine what features of the male and his territory affect female success and if these features are important in mate selection. In the third chapter, I examine the relationship between co-nesting females, and especially the effect of resident females on the settlement patterns of later-arriving females. Finally, in Chapter 4, I test the major predictions of the PTM, with data from this population of marsh wrens. I also present an alternative model which may be a better explanation for the evolution and maintenance of polygyny in some populations.

CHAPTER 1

NESTING MORTALITY AND HABITAT SELECTION BY MARSH WRENS

INTRODUCTION

Selection of nesting habitat should be partly based on the relative importance of features affecting offspring mortality. Individuals may not always make optimal habitat choices because mortality patterns may be difficult to predict at the time of settlement (Wittenberger 1981a). Thus, the decisions an animal makes may depend on the availability of cues useful in predicting future events.

Predation and starvation are considered the most important sources of egg and nestling mortality in temperate marshes (Orians 1961; Kale 1965; Ricklefs 1965; Willson 1966; Robertson 1972; 1973; Howe 1976; Richter 1984; Bancroft 1986). Thus, high quality nesting habitat for marsh passerines should be safe from predators and contain, or be adjacent to, abundant food resources.

If mortality factors are predictable, then individuals should select habitats where potential nesting losses could be reduced. If individuals are making choices with regard to habitat then i) the best habitat should be settled first by both males and females and ii) there should be more individuals of both sexes in the preferred area.

Marsh wrens (*Cistothorus palustris*) are small, insectivorous passerines found in marshes throughout most of North America. Males, in most populations, are polygynous, although the number of polygynous males per population varies (Verner 1963; Kale 1965). Harems of two or three females are most common. There is no evident sexual dimorphism in plumage and only a slight difference in body size. Both male and female marsh wrens destroy the eggs and nestlings of other marsh-nesting passerines (Orians and Willson 1964; Burt 1970; Picman 1977; Bump 1983), as well as the eggs and nestlings of conspecifics (Picman 1977; Picman and Belles-Isles 1986).

The purpose of this chapter is to examine the habitat preferences of marsh wrens by comparing their breeding success and settlement patterns in two marsh sites.

METHODS

Study Sites

This study was conducted between 1 May and 18 August, 1983 and 1 May and 20 July, 1984 and 1985 in two marsh sites in Delta, Manitoba. Site 1 was a homogeneous cattail (Typha spp.) marsh approximately 7.8 ha in area. Site 2 was more heterogeneous with phragmites (Phragmites australis) and cattails along the edges and bulrush (Scirpus acutus) and cattail patches around two central ponds. This study site was 6.1 ha in area in 1983, but was increased to 7.9 ha in 1984 and 1985. However, because of the ponds and the presence of a yellow-headed blackbird (Xanthocephalus xanthocephalus) colony, there were 4.4 ha and 6.2 ha of suitable breeding habitat available at Site 2 in 1983 and 1984 and 1985, respectively. The study sites were separated by 1 km of grassland.

Habitat Characteristics

Each site was divided into a grid of 20 X 20 m squares, marked by 2-m-high wooden stakes. Vegetation quality and water depth were measured throughout the study sites in 1983 and 1984. Point samples, 50 cm in diameter, were made 2 m north of each grid stake before and after the growth of new vegetation. Information on vegetation height, vegetation density, and water depth was collected at each sample point. Vegetation height and water depth were measured using a 2-m-high vertical stake marked in 5 cm intervals. Vegetation density was estimated using a 50 cm long horizontal bar placed 100 cm high on the vertical height stick. The bar was painted with 20 evenly spaced red circles each 1 cm in diameter. A relative measure of vegetation density was estimated by counting the number of dots that were totally clear from a distance of 2 m. Therefore, the higher the density measure the sparser the vegetation.

Breeding Biology

Eighty-nine of the 121 males used in this study were trapped using a method described by Picman (1980a) and individually marked with coloured leg bands. Female wrens were not marked. Territory boundaries were mapped weekly throughout the study period by observing the movements of males during 1-h observation periods in 1983 and 30-min observation periods in 1984 and 1985. Song perches and flight paths were plotted on maps of the study sites. The area of each territory was determined using an Apple Graphics Tablet.

All nests were mapped and checked twice a week and their contents noted. Each nest was marked with a numbered tag that was placed approximately 3 m north of the nest. If clutches were incomplete when found the initiation date was estimated (Kale 1965). A nest was considered depredated by a mammal if the opening was enlarged or the nest dislodged from the supporting vegetation. Depredation by wrens was assumed if eggs were discovered with holes and nest contents were missing but the nest was intact. Nests were considered abandoned if clutches were complete and the eggs in the nest were cold.

When marsh wrens kill older nestlings (> 8 days) they tend to peck the nestling first and then remove it from the nest (Picman 1977; Leonard pers. obs.). I assumed that an older nestling had fallen from a nest (as opposed to having been removed by a marsh wren) if it was found below the nest with no apparent wounds. However, younger nestlings found below the nest were considered to have been killed by marsh wrens. I considered a nestling to have starved if it was found dead in the nest with no apparent injuries. I assumed that nestlings had fledged if they were absent from the nest at 12 or more days of age. If nestlings were gone from the nest before this stage and I was unable to locate them in the general vicinity, I assumed the nest had been depredated. Chick mortality after fledging was not assessed. All nestlings were weighed and banded with Canadian Wildlife Service bands approximately 8 days after hatch.

A territory was considered settled if there was a male present in that area for three consecutive days. Male pairing success was determined by the maximum number of simultaneously active nests within each territory. Female pairing date was estimated from the date of the first egg. This is assumed to be a reliable indicator of pairing date because the interval between female settlement and egg-laying is relatively short and females breed asynchronously (Stutchbury and Robertson in prep). Female reproductive success was measured as the number of young fledged. A nest was considered successful if it fledged at least one young.

RESULTS

Population Size and Habitat Characteristics

Site 1 supported 14 male marsh wrens in 1983, 19 males in 1984, and 28 males in 1985. Site 2 supported 17, 22, and 21 males in 1983, 1984, and 1985, respectively. In addition, Site 2 also supported 67 yellow-headed blackbird territories in 1983 and 63 territories in 1984 and 1985.

Vegetation was significantly denser and higher at Site 2 than at Site 1 early in the season (Figures 1 and 2). In the late season there was no difference in the vegetation density between sites. However, vegetation remained higher at Site 2 late in the season in 1983 (Figure 1). Standing water was consistently deeper at Site 2 than at Site 1 (Figures 1 and 2).

Pairing Success

Harem sizes (number of females/male) were significantly larger at Site 2 when data from the three years were pooled (Table 1). Although not significant, this trend was also evident in each year (Table 2). The operational sex ratio (Emlen and Oring 1977) differed significantly from unity at Site 2 when the three years were pooled (Table 3) and at Site 2 in 1985 (Table 4). There were more females than males at both sites during all three years, although the difference was not statistically significant (Table 4). In addition, only 2 of 14 males that disappeared from the study area early in the season were replaced by new males. This suggests that the overall sex ratio was female-biased.

Reproductive Success

There were no significant differences in clutch size between Site 1 and Site 2 (Table 5) when all years were pooled and when each year was considered separately (Table 6). However, when successful (nests that fledged at least one young) and unsuccessful nests were considered, significantly more eggs hatched and more young fledged at Site 2 than at Site 1, for all years combined (Table 5). Although these trends were evident each year, they were not significant (Table 6). These results presumably follow from the fact that there were significantly more successful nests at Site 2 than at Site 1 when the three years were combined ($X^2=21.1$, df=1, $P<0.005$). This difference was also significant in 1984 ($X^2=5.27$, df=1, $P<0.025$) and 1985 ($X^2=4.91$, df=1, $P<0.05$) but not in 1983 ($X^2=2.97$, df=1, $P>0.05$). However, when only successful nests were considered, there were more young fledged/nest at Site 1 than at Site 2 (Table 5). This difference was also significant in 1985 ($t=2.22$, df=25, $P=0.03$). In summary, there were more successful nests at Site 2 than at Site 1. However, there were more young fledged from successful nests at Site 1.

Mortality Factors

Total Nest Losses

Over the three years of this study 68% (49/72) of all unsuccessful nests were destroyed by predators. Forty-four percent of these nests were assumed to be lost to mammals (32/72) and 23.8% (17/72) to marsh wrens. A heavy wind storm in 1985 was responsible for 11.1% (8/72) of nest losses and 8.3% (6/72) of nests were abandoned by the resident female. In 12.5% (9/72) of cases the cause of the nest loss was unknown.

Mammalian predation accounted for 65.3% (32/49) of complete clutches lost to predation for both sites over the three year period. Seventy-three percent (24/33) of nests at Site 1 and 50.0% (8/16) of nests at Site 2 were lost to mammalian predators. I have no direct evidence on the species of mammals depredating nests. However, I observed minks (Mustela vision) and skunks (Mephitis mephitis) in the marshes during the three years. Marsh wrens destroyed 34.6% (17/49) of depredated nests during the three years. Twenty-seven percent (9/33) and 50.0% (8/16) of complete clutches lost at Site 1 and Site 2, respectively, were depredated by marsh wrens.

Most (79.5%) mortality occurred during the egg stage (Table 7). Egg predation accounted for 50.4% (188/373) of all egg mortality and 40.2% (188/468) of the total egg and nestling mortality (Table 7). Depredation at the nestling stage accounted for 84.2% (80/95) of nestling mortality and 15.5% (80/468) of total mortality (Table 7). Other egg and nestling losses were attributed to unhatched and abandoned eggs, eggs lost to weather and nestlings falling from nests (Table 7).

Partial Losses

Fifty-five percent (61/110) of successful nests suffered some partial brood loss (Table 8). There were more nests with partial losses at Site 2 than at Site 1. Most losses, at both sites, were because of unhatched eggs (86.8%, 53/61). Twenty-six percent (15/61) of partial losses were attributed to marsh wrens (Table 8).

Male and Female Settlement

The first male marsh wrens were observed in the study area on 10 May, 7 May and 1 May, 1983, 1984, and 1985, respectively. In all three years the first female wrens arrived approximately one week after the arrival of the first male. In all three years males and females settled within 25 days of the first arrivals. With one exception, there was no significant difference in the rate at which males and females settled at Site 1 and at Site 2 (Table 9). With the exception of 1983, male wrens settled at the two sites in densities expected by chance (Table 10). Females however, settled at Site 2 more often than expected by chance during the three year period (Table 10).

Return rates of adult males and yearlings was low. Ten percent (2/19) and 9% (2/22) of marked males returned to Site 1 and Site 2, respectively, in 1984. In 1985 there was a 7% (2/28) return rate at Site 1, while at Site 2 no marked males were observed on the study area. With one exception, returning males settled—either on or within 100 m of their previous territory. Return rates of yearlings were extremely low. Only one of 540 banded nestlings was observed in the study area. This yearling male held two different territories in succession, at Site 2 in the 1985 season. The first was approximately 140 m from his natal territory and the second was within 40 m.

DISCUSSION

Male marsh wrens at Site 2 had higher pairing success than males at Site 1. Female wrens at Site 2 had a greater probability of having a successful nest and subsequently in fledging more young per nesting attempt than their counterparts at Site 1. However, females at Site 2 suffered greater partial losses and so fledged fewer young per successful nest.

Predation was the main source of nest mortality for this population of marsh wrens (68% of nest losses). Mammals were the most important predators and their impact was greatest at Site 1. Losses to mammals at Site 2 were the same as losses to marsh wrens at both sites. Predation is considered one of the most important mortality factors for marsh-nesting passerines (Orians 1961; Willson 1966; Ricklefs 1965; Robertson 1972, 1973; Holm 1973; Caccamise 1976; Clark and Wilson 1981; Bancroft 1986) including marsh wrens (Welter 1935; Kale 1965). Thus, there should be selection on these species to reduce nesting losses from predators. Colonial nesting, common in many marsh-nesting icterids (e.g. Orians 1961; Willson 1966; Bancroft 1986) may reduce predation through group vigilance and mobbing. However, because marsh wrens destroy the eggs and nestlings of conspecifics (Picman 1977) the costs associated with female clumping may be greater than the benefits of group living. The best strategy for marsh wrens may be to select a habitat that is relatively safe from predators.

Tall, dense vegetation and deep water provide protection from mammalian predators (Goddard and Board 1967; Holm 1973; Hoogland and Sherman 1976; Richter 1984; Collias and Collias 1984). In my study area there were more successful nests at Site 2, the site with denser vegetation and deeper water. Also, successful nests were in significantly denser vegetation and deeper water than unsuccessful nests (Chapter 2). In addition, nests at both sites were always placed in significantly denser vegetation than what was generally available (Chapter 2), again suggesting that marsh wrens may be attempting to protect their nests against mammalian predation.

Marsh wrens at Site 2 may also suffer fewer losses because yellow-headed blackbirds may buffer them from predators. In Delta, wrens and blackbirds are spatially segregated (Leonard and Picman 1986). Predators may locate blackbird nests more readily because they nest at higher densities. Therefore, they may find wren nests only by chance. It is difficult to separate the buffer effects of the blackbirds from the effects of the habitat. However, either or both of these features may make Site 2 a safer nesting habitat.

Both male pairing success and female reproductive success were enhanced by selection of a predator-reduced habitat. Fifty-four percent of males at Site 2 were polygynous versus 42% at Site 1. In addition, 7 of 9 cases of trigamy were at Site 2 while, 7 of 10 bachelors were at Site 1. Females at Site 2 fledged more young and had a greater probability of having a successful nest. Presumably, there should be strong selective pressure on male marsh wrens to acquire territories at Site 2 and for females to select nest sites within these territories. However, males and females settled at both sites simultaneously, although, more females settled at Site 2 than would be predicted by chance. This suggests that only the later-arriving females showed some preference for the predator-safe habitat. These results are consistent with the idea that males and the first females to arrive may make poor choices because they cannot adequately assess the differences between the sites (see for example, Wittenberger 1981a) early in the season. Vegetation density may become easier to evaluate as the season progresses and new vegetation appears.

CHAPTER 2

BEHAVIOURAL AND ECOLOGICAL CORRELATES OF POLYGYNY

INTRODUCTION

Many recent studies have tried to identify the characteristics that female passerines use when selecting a mate (Verner 1964; Willson 1966; Zimmerman 1966; Holm 1973; Martin 1974; Carey and Nolan 1975; Wittenberger 1976; Pleszczynska 1978; Searcy 1979; Weatherhead and Robertson 1979; Picman 1980b; Yasukawa 1981). The available evidence suggests that females choose males based on parental quality, genetic quality, and/or territory quality (Searcy 1982). However, before females can use these characteristics as a basis for selection the following three criteria must be met (Searcy 1979). First, the characteristics should have some effect on female fitness. This is because selection should favour choices that maximize a female's inclusive fitness. Second, the characteristics should vary among males. Females should be selected to discriminate among males if the variation in quality is great enough to increase female fitness above what it would be for a random choice. Finally, females should be able to evaluate the quality of the characteristic. That is, characteristics must be assessable by females or correlated with features that are.

Male parental care may have a direct effect on female fitness (Searcy and Yasukawa 1983). However, it may be difficult for a female to predict the eventual contribution of the male at the time that she settles (Wittenberger 1981a). Thus, she must base her choice on features that are reliable predictors of male help. For example, in red-winged blackbirds (Agelaius phoeniceus), male experience is positively correlated with the contribution of the male to feeding (Yasukawa 1981). Courtship intensity, repertoire size, and physical size all vary with age and so could be predictors used by females to determine male experience (Yasukawa et al. 1980; Searcy and Yasukawa 1983). Therefore, females may use behavioural or physical correlates of parental quality to choose a mate.

Male genetic quality can influence female success if highly fit males produce highly fit offspring (Bateson 1983; Partridge 1983; Searcy and Yasukawa 1983). Genetic quality includes features of the male that affect female fitness in the present and future. For instance, male size may affect a female's success in the present breeding season if larger males have larger offspring. This is because post-fledging survival has been correlated with fledging weight (Perrins 1965; Lack 1966). "Sexiness" (Weatherhead and Robertson 1979), the ability to attract many females, may affect future fitness because sexy males may have sexy sons that attract several mates. Genetic quality may be correlated with age (Weatherhead 1984), courtship intensity, competitive ability, or behavioural markers, such as multiple nests in wrens (Verner and Engelsen 1970; Garson 1980) or the decorative bowers of bower birds (Ptilonorhynchus violaceus, Borgia 1985). Male vigour and age may also be correlated with morphological features such as size and physical condition. Females should be able to assess male size directly, but it may be difficult to assess other types of male genetic quality.

Territory quality could directly affect female reproductive success because a territory provides food, nest sites and protection from predators. Again, females may not be able to assess important features of territory quality when they settle (Wittenberger 1981a). For instance, it may be difficult for a female to predict the quantity of food that will be available when she has nestlings. Thus females may have to rely on predictors of future quality (e.g. the length of emergent vegetation may be a good predictor of insect abundance, Verner 1964).

If male and territory quality affect female fitness, then a male that can sequester high quality resources or who is himself a high quality resource should be more attractive to females than a lower quality male. Thus, females settling with an already-mated male may be compensated for the potential costs of polygyny by selecting a high quality breeding situation (Verner 1965;

Verner and Willson 1966; Orians 1969).

The purpose of this chapter is to identify the behavioural and ecological correlates of polygyny in marsh wrens (<u>Cistothorus palustris</u>) by determining whether male and territory features i) affect female success, ii) can be evaluated by females, and iii) are the basis by which females select mates.

METHODS

Study Sites

Descriptive information on male and territory quality were collected from 1 May to 20 July 1983 and 1984. See Chapter 1 for a description of the study sites.

Male Quality

Parental Care

I made observations at breeding nests during the nestling stage to determine the relative contribution of males to the care of offspring. Nest watches were conducted between 09:00 and 12:00, when nestlings were 3-4 days old and again when they were 8 days old. Observation periods were 30 min long and began after the adult(s) resumed feeding. Male and female feeding rates were recorded. To test the relative contribution of the male to nest defense, I recorded the amount of time that the male spent in nest defense beginning with my arrival in the nesting area. I assumed that wrens responded to me as they would to a predator. I considered alarm calls (Welter 1935) and continued circling of the observer by the male to be behaviours associated with nest defense. Nestlings were weighed and banded after the last observation period, at 8 days.

Physical Correlates of Male Quality

Fifty-six of 64 males were trapped using a method described by Picman (1980a) and individually marked with coloured leg bands. Weight, flattened wing chord, and tarsus length were measured at this time. A relative measure of physical condition (weight/wing length^3, Searcy 1979) was then determined for each of the banded males.

Behavioural Correlates of Male Quality

Detailed behavioural observations were made on each male to calculate their time budgets. Observation periods were 1 h long in 1983 and 30 min long in 1984. They were conducted between 05:30 and 09:30, corresponding to the marsh wren's most active period. An effort was made to monitor the same individual at least once a week. The following activities were noted every 10 s on coded check sheets: singing, wren-wren interactions, wren-yellow-head interactions, nest building, moving low in the vegetation (presumed feeding, Verner 1965), perching up, and preening.

Time budgets provided the following behavioural measures of male quality: proportion of time/sample period spent at each behaviour and song rates. Male marsh wrens build multiple nests ("courtship nests") few of which are used by females for breeding (Welter 1935; Verner and Engelsen 1970). The number of nests used by the male may be correlated with male quality. Thus, the number of courtship nests built by each male was recorded at each nest check. Behavioural measures and nest number were calculated for the period before pairing and for the entire season.

Courtship intensity experiment

I conducted a playback experiment during May 1985, to directly test whether male courtship intensity was correlated with female reproductive success and female choice (i.e., harem size). Before pairing, I presented 18 males at Site 1 and 10 males at Site 2 with a recording of a female "kek kek" call (Welter 1935) recorded outside the study area. The order of presentation among males within a site was random. Presentations were made between 07:00 and 11:30 and between 18:00 and 20:00.

I placed a General Electric 3-5091A cassette tape recorder with built-in speaker on a 0.5-m-high stool in the centre of each male's territory. The volume of the recorder had previously been adjusted by ear to natural sound levels. I began the tape and then moved 10 m to the west of the recorder. A trial consisted of a pre-playback followed by a playback period, each 2 min long. The pre-playback period began 10 min after the equipment was in place. During the pre-playback a blank tape was played.

The resident male was considered to respond if he moved toward the speaker, flew directly to the speaker, or perched up in the vegetation and displayed. Observations provided the following measures of response: 1) the time (s) between the beginning of the tape and the first obvious response (= time to first response); 2) the time (s) between the first response and the closest approach to the speaker (= time to closest approach); 3) the time (s) at closest approach and 4) an estimate of the distance (m) at closest approach to the speaker (= distance at closest approach).

Territory defense experiment

I also conducted a playback experiment during June 1984, to test whether the vigour with which males responded to territorial intruders was correlated with female reproductive success and choice. I presented 18 males from Site 1 and seven males from Site 2 with taped songs of a marsh wren recorded outside the study area. The order of presentation among males within a site was random. All males, except for bachelors, had females that were laying or starting to incubate. Presentations were made between 18:00 and 21:00.

I placed a Radio Shack unidirectional speaker on a 2-m-high stake in the centre of each male's territory. The speaker was placed facing north and I stood approximately 10 m to the west of the speaker. A tape loop of the singing male was played on a General Electric 3-5091A cassette tape recorder. The volume of the recorder was set to natural levels by ear. A trial consisted of a pre-playback and a playback period, each 60 s long. The pre-playback period began 10 min after the equipment was in place. The tape recorder was not played during the pre-playback period. Response levels were the same as those used in the courtship study.

Territory Quality

Size

Territory boundaries were mapped weekly by recording the movement of males during time budgets and noting the position of song perches, courtship nests, and flight paths. Territory areas were calculated by the minimum convex polygon method using an Apple Graphics tablet. The average territory size before pairing and maximum territory size were determined for each male.

Vegetation

The proportion of open water, cattail (_Typha_ sp.), bulrush (_Scirpus_ _acutus_), phragmites (_Phragmites_ _australis_), and mixed patches of vegetation was determined for each territory. The area of each was calculated using an Apple Graphics Tablet. Vegetation density and water depth on each territory were determined from measurements made at the six grid stakes closest to, or within each territory (see Chapter 1).

Because yellow-headed blackbirds (_Xanthocephalus_ _xanthocephalus_) chase marsh wrens (e.g. Verner 1975; Leonard and Picman 1986), territory quality may be affected by the distance between marsh wren and yellow-head nesting areas. The distance between active wren nests and the closest active yellow-head nest was determined at Site 2 during the time when yellow-heads were most active (see Leonard and Picman 1986).

Food Availability

Because female marsh wrens feed on male territories (Verner 1964) insects were sampled from 25 May to 27 July 1983, using sticky plates. To reduce interference between wrens and sticky traps I sampled outside male territory boundaries, but within suitable nesting habitat. Five, 2-m-high stakes were placed in three patches each of cattail, phragmites and mixed patches of bulrush and cattail. Each stake had a 20 X 20 cm plate placed at 50, 100, and 150 cm above the ground. Plates were exposed from 06:00 to 19:00 once a week. Each plate was sprayed with a layer of the insect adhesive, Tanglefoot prior to every exposure. Insects were collected from each plate counted, measured, and identified to family.

Nest Sites

In addition to their number, the quality of courtship nests may affect female choice. That is, a male with many low quality nest sites may not attract as many females as a male with few high quality sites. Therefore, measures of nest site quality were collected for both courtship and breeding nests. The density of vegetation supporting courtship and breeding nests was determined by placing a 50 X 4 cm dotted stick (identical to the bar used to measure vegetation density at the study sites, Chapter 1) on the top of each nest, facing north. The number of complete dots visible at a distance of 2 m was used as a relative measure of vegetation density. Water depth, height of the majority of supporting stems, height of the tallest stem, and the height of the nest above the substrate were determined using a 2-m-high stick, marked in 5 cm intervals.

Arbitrary Territories

If females are choosing a breeding situation based on territory quality, then the number of females settling and the order in which females choose territories should be consistent between years. Because there were no apparent changes in the habitat between years, I tried to test this prediction. To control for the influence of male quality, the study area was divided into 40 X 40 m areas (i.e., "arbitrary territories") that were independent of actual territory boundaries (Searcy 1979), but included areas defended by males. I did not use the north end of Site 2 in 1983, so I could compare female settlement patterns between 1984 and 1985 only.

Vegetation Density Experiment

This study was conducted from 10 May to 15 June 1985 at Site 1 and was initiated because of the results of the multivariate study. Vegetation was removed from the north side of each new courtship nest in eleven experimental territories, so that 10 complete dots could be read from a distance of 2 m. The mean number of dots visible in unmanipulated nests is approximately 4.5/20 (Leonard unpublished). Vegetation density at each nest was measured in the manner described above. Vegetation density was also measured in eleven control territories as each new nest was discovered. All nests were tagged and checked twice weekly. Because this experiment was conducted before the growth of new vegetation, the density of experimental nests was not checked after the initial manipulation.

Measures of Reproductive Success

All courtship and breeding nests were checked and mapped twice a week and their contents noted. If clutches were incomplete when found, the initiation date was estimated, assuming that females laid one egg a day (Kale 1965). Female pairing date was considered to be the day that the first egg was laid. The maximum pairing success of each male was taken as the number of simultaneously active nests present on his territory. Reproductive success was considered to be the number of young fledged. A nest was considered successful if it fledged at least one young.

Analysis

A BMDP program for stepwise multiple regression (Dixon 1981) was used to determine which variables contributed to the variance in the number of young fledged per nest. Twenty-three independent variables were originally entered. However, because of intercorrelations and missing values, the final analysis included 11 independent variables. Sixty-four of 102 breeding nests had complete measurements for all variables and were thus included in the analysis. I used a discriminant function analysis to separate successful and unsuccessful nests.

I also used a BMDP stepwise multiple regression (Dixon 1981) to determine the contribution of the independent variables to the variance in male pairing success (0, 1, 2, or 3 females). Originally 40 independent variables were entered into the multiple regression analysis. However, because of intercorrelations (e.g. variables measured before and after pairing were often highly correlated) and missing values, this sample was reduced to 17 independent variables. Fifty of 64 males had measurements for all variables. Discriminant function analysis was also used to separate males of diff~~ering~~ pairing success.

Sample sizes for all variables were equal because I used a listwise deletion of missing data (i.e., a male was deleted from the analysis if any variable was missing a value). I used a forward selection of variables, with a F value set at 4.0 for entry of variables into the analyses.

All proportions were normalized using the arc-sine transformation (Zar 1984). The logarithmic transformation was used to normalize variables besides proportions (Zar 1984). All means are ± 1 SD and statistical significance was set at $P = 0.05$. Unless stated otherwise, data from both sites were pooled.

RESULTS

Male Quality

Parental Care

Nine of 54 (16.6%) males observed during nest watches assisted females with feeding young. In all cases males fed older nestlings (8 days) only. Feeding males included 5 monogamists, 2 bigamists and 2 trigamists. Polygynous males fed the young of primary (3), secondary (1) and tertiary (1) females. Females with and without male feeding help laid a similar number of eggs (U=31.5, P=0.16; Table 11). Males and females with help had similar feeding rates (U=285, P=0.68). Feeding rates for females without help were not signficantly different from females with help (U=288, P=0.29; Table 11). ~~Pre-fle~~dging weights of both groups were similar (t=0.83, df=138, P=0.40). However, females with male help fledged significantly more young from successful nests (U=346.5, P=0.004; Table 11) than females without help.

Twenty-five males defended the nest area. There was no difference in clutch size (U=475.5 P=0.40) or the number of young fledged from nests with and without male defense (U=429, P=0.48; Table 11). In addition, there was no correlation between the time a male spent in defensive behaviours and the number of young fledged (Spearman rank correlation, $r_s=-0.16$, N=25, P=0.42).

Males may provision young because their territories are small and therefore contain less food. Thus male feeding may be associated with a low quality breeding situation rather than a high quality situation. However, there was no difference in the territory size of helping and non-helping males (t=-0.43, df=9, P=0.68; I will discuss food below).

Physical and Behavioural Correlates of Male Quality

Variance in female reproductive success (number of young fledged/nest) could not be explained by measured features of male quality. There were also no physical or behavioural features of male quality that contributed to the variance in male pairing success and therefore no significant correlations between these measures and male pairing success (Table 12). These results were also evident when each site was analyzed individually.

If male quality was important, then individual males should attract the same number of females in consecutive years. There could also be an increase in the number of females between years if males became more attractive with age/experience. Although my sample is small, I found that the harem size of only one of six returning males increased between years. In this instance the male returned in all three years and had harems of two, one, and two females each year. Two of six returning males had the same harem size between years and three of six had smaller harems in the following year.

Courtship intensity experiment

Male marsh wrens responded to female playbacks in 20 of 28 presentations. In 19 cases the male flew directly to the speaker and perched above it. Twelve of the 19 males that flew to the speaker also performed some form of courtship display (Welter 1935). There was no difference between males that responded and males that did not, with respect to female reproductive success (Mann-Whitney U, P=0.51) and male pairing success (Mann-Whitney U, $P>0.05$). There was also, no correlation between the four measures of response and female success (Figure 3), the order that females selected males (Figure 4) or male pairing success (Figure 5). There were also no differences between males that fed young and males that did not feed young, with respect to the four measures of response (Table 13).

Territory defense experiment

Twenty of 25 males responded to the playback of a male intruder. In 15 cases males approached the speaker from low in the vegetation and 13 of the 15 males came within 1 m of the speaker. There was no difference between males that responded and males that did not with regard to female success (Mann-Whitney U, $P>0.05$) and male pairing success (Mann-Whitney U, $P>0.05$). Again, there was no correlation between the levels of response and female reproductive success (Figure 6), female settlement (Figure 7) or male pairing success (Figure 8).

Territory Quality

Sixteen percent of the variance in the number of young fledged by females was explained by the density of vegetation at courtship nests (F=6.51, df=1,49, P<0.01). A discriminant function analysis using features of territories and nest sites successfully discriminated between successful (nests fledging at least one young) and unsuccessful nests. Again, the density of vegetation at courtship nests was the only variable entered into the discriminant analysis (F=7.96, df=1,62, P<0.01; 73.4% of cases correctly classified, eigenvalue of the discriminant function = 0.128). This variable also contributed 14.7% to the variance in male pairing success (F=8.31, df=1,48, P<0.01) and there was a significant negative correlation with male pairing success (e.g. bachelor males had courtship nests in sparser vegetation than monogamous males; Table 14). However, discriminant analysis of territory and nest site features could not successfully separate males of different pairing success.

When the two sites were separated, successful and unsuccessful nests could not be discriminated nor could the variance in female reproductive success and male pairing success be explained by any of the independent variables. There were also no significant correlations between any of the measured features and male pairing success within sites. In particular, there was no significant correlation between density of vegetation at courtship nests and male pairing success at Site 1 (r=-0.28, N=25, P>0.05) or at Site 2 (r=-0.07, N=25, P>0.05). This suggests that the above results may be an artifact of pooling data from the two study sites. That is, vegetation on territories and at nest sites is denser at Site 2 (Table 15) and more nests are successful and more males polygynous at this site (Chapter 1). Thus, a relationship between vegetation density at courtship nests, female reproductive success and male pairing success could result from the pooled data.

I was unable to alter male pairing success by manipulating the density of vegetation at courtship nests. If females chose males based on this feature, then experimental males (males with sparser vegetation at courtship nests) should be chosen after control males. There were no significant differences between control and experimental groups in the number of young fledged from all nests (t=0.30, df=28, P=0.77) or from successful nests (t=-0.30, df=6, P=0.77). However, the order in which males were chosen did not differ from random (Runs test, r=8, P>0.05). Control males were no more successful in recruiting females than experimental males (t=1.48, df=19, P=0.16). This further suggests that the above results were a function of pooled data. I should note however, that if the density of vegetation at courtship nests was not important, but rather was correlated with some other critical feature, my manipulations would be ineffective. I cannot evaluate this possibility.

Food Availability

Over 55% of the invertebrates collected from sticky plates were dipterans. Fourteen percent of the sample were coleopterans, 14% hymenopterans, 7% homopterans and 5% arachnids. Insects were collected from the plates at 50 and 100 cm only because so few were trapped on the 150 cm plates.

Within vegetation types there were insignificant differences in the mean number of insects, the mean number of species, and the mean length of insects (Table 16). There were no differences in the number of species ($F=1.11$, $df=2,94$, $P>0.05$) caught between vegetation types. However, there were significantly fewer insects trapped in phragmites patches (11.6 ± 6.57) than in cattail (23.8 ± 21.3) or mixed bulrush and cattail patches (20.2 ± 15.0; $F=4.68$, $df=2,96$, $P<0.05$). The insects trapped in cattail were longer (4.4 ± 1.9 mm) than those trapped in phragmites (3.0 ± 0.7 mm) or bulrush and cattail (3.2 ± 0.8 mm; $F=20.9$, $df=2,210$, $P>0.05$). Insect abundance and type appears to be determined to some extent by vegetation type. Males with large areas of phragmites on their territories may have poorer foraging areas than males with cattail or bulrush and cattail. However, there was no relationship between the proportion of different vegetation types on a males's territory and female reproductive success or male pairing success (see above).

Arbitrary Territories

If females choose males based on the quality of the territory, and the habitat does not change between years, then every year the same high quality areas should get more females than low quality areas. Also, the high quality areas should be chosen first each year. With one exception at Site 2, there was no correlation in the number of females settling in arbitrary territories between years nor in the order that these females settled between years (Table 17). Also, there was no correlation between years in the number of nests depredated in arbitrary territories, with the exception of Site 1, between 1983 and 1984 (Table 17). This suggests that predation within sites could not be predicted from habitat features.

Nest Sites

If nest sites are limiting, then males with many nest sites may recruit many females. Courtship and breeding nests at both sites were built in vegetation of similar height and density and in areas of similar water depth (Table 18). Because characteristics of breeding and courtship nest sites do not differ, and because male marsh wrens build approximately 15 nests every season, nest sites should not be limited.

DISCUSSION

Male Quality

With the exception of male feeding assistance, female reproductive success appeared not to be influenced by any features of male quality. Results of discriminate function analysis suggest that there was little variation among males of different pairing status with respect to the features I measured. Finally, there was no relationship between male quality and male pairing success at either study site.

Male parental care could have direct effects on female reproductive success. Male vigilance appears to decrease predation in Brewer's blackbirds (_Euphagus cyanocephalus_; Patterson et al. 1980) and male help with feeding young appears to increase the number of young fledged in other passserines (Dyrcz 1977; Wittenberger 1978; Patterson et al. 1980; Alatalo et al. 1981; Catchpole et al. 1985; Muldal et al. 1986). Few males in this population fed young (9/54), but when they did, female feeding rates were decreased and the number of young fledged/nest increased. However, because my sampling periods were short the number of feeding males in this population may be underestimated.

Male help may be correlated with courtship intensity, age or other predictors of feeding effort (Yasukawa et al. 1980; Searcy and Yasukawa 1983). However, in my population there was no difference in levels of courtship intensity between feeding and non-feeding males. Although the data are sparse, none of the males that returned between years fed young. Finally, male pairing success was not correlated with any of the features of male quality that I measured. Although male help may increase female fitness, females may be unable to predict which males will help.

Although choice based on genetic quality may occur, it is probably not important, especially in species where males provide care or resources (Searcy 1982; Searcy and Yasukawa 1983). Theoretical and empirical evidence shows that heritablity of fitness is low (Williams 1975; Maynard-Smith 1978; Van Noorduijk et al. 1980; Borgia 1981; Partridge 1983), and females may have difficulty assessing genetic quality (Searcy 1982). If males provide resources that affect a female's success in the present breeding season, then it is unlikely that they would forfeit immediate success for future benefits (Kirkpatrick 1985). In my population, behavioural and morphological characteristics of males were not correlated with female reproductive success or male pairing success. This suggests that male genetic quality has little influence on female fitness and choice.

Territory Quality

A male's territory could provide females with food, protection from predators, and nest sites, so it may be more important than male quality. Correlations, albeit weak in many cases, have been found between territory features and male pairing success for a number of passerines (Willson 1966; Zimmerman 1966; Holm 1973; Martin 1974; Carey and Nolan 1975; Pleszczynska 1978; Wittenberger 1978; Lenington 1980; Catchpole et al. 1985). However, spurious correlations can result when many relationships are measured (Garson et al. 1981), so they should be tested experimentally. Only one study has tried to do this (Pleszczynska and Hansell 1981).

In my study, female reproductive success within sites was not affected by features of the nest site or the territory, and nest sites at both study areas were not limited. Variance in male pairing success could also not be explained using territory or nest site features. I also could not discriminate between males of different pairing status within sites. In general, harem size, female settlement patterns, and predation rates on arbitrary territories between years were not correlated. These results suggest two possiblities 1) the features I measured were not important to females and so were not used as a basis for selection or 2) females could not discriminate between males based on the measured features.

It is also possible that I have failed to measure the appropriate variables. However, with the exception of song repertoire size, I measured features of the male and the territory that have been found to be important in other studies. I also looked at features, like male defense and nest site selection, that would be important in reducing predation, the most important cause of mortality in my study area. Because these features directly affect female success, they if any, should be important.

Results of a study on marsh wrens in the northwest United States suggested a relationship between the amount of emergent vegetation on a male's territory and male pairing success (Verner 1964). However, in a later study Verner and Engelsen (1970) failed to find a significant correlation between male mating success and any features of territory quality. They did, however, find a weak but significant correlation between the number of courtship nests built by a male and the number of females recruited. These authors suggested that nest number may be a predictor of the amount of food on a male's territory because males with more food spend less time foraging and more time building. Although territory features were correlated with male pairing success in these studies, the relevant variables were not consistent nor were they tested directly. In addition, I could find no relationship between nest number and male pairing success, even after manipulating the number of nests per territory

(Leonard and Picman 1986).

Despite the low variability within sites there were obvious differences between sites (Chapter 1). Thus, female selection may not be at the level of the male and territory, but rather of the habitat. There does appear to be some preference for Site 2 (i.e., more females settle there than expected by chance). However, if Site 2 were more attractive, then this site should be settled before Site 1. Males and early females settled at both sites simultaneously (Chapter 1). As suggested in Chapter 1, early arriving individuals may be not be able to accurately assess the important differences between the habitats.

In summary, I could find no correlation between male and territory quality and female reproductive success and male pairing success. Thus females may simply settle at random because features of the male and his territory do not affect their fitness, are invariant, or cannot be asssessed. However, a resident female could also affect the settlement of subsequent females by aggressively excluding them from the male's territory. These possiblities will be discussed in the next two chapters.

CHAPTER 3

FEMALE SETTLEMENT: IS IT AFFECTED BY OTHER FEMALES?

INTRODUCTION

A female's reproductive success and her choice of a mate may be affected by the quality of the male, the quality of the territory or the presence of other females (Garson et al. 1981). The influence of the first two features has been well studied (Verner 1964; Verner and Willson 1966; Zimmerman 1966; Orians 1969; Verner and Engelson 1970; Holm 1973; Carey and Nolan 1979; Pleszczynska 1978; Weatherhead and Robertson 1977, 1979; Searcy 1979; Garson 1980; Picman 1980b; Yasukawa 1981; Catchpole et al. 1985). However, the third possibility, that early settling females influence how later females settle, has received limited attention (Yasukawa and Searcy 1981a; Yasukawa and Searcy 1982; Hannon 1984; Hurly and Robertson 1985).

Competitive models of polygyny assume that females mating with an already-mated male will incur costs associated with group living (Orians 1969). Females of polygynous males may compete for important, nonshareable resources, such as food, nest sites, and male help in feeding young. If access to these resources greatly affects female reproductive success, then aggression among settling females may occur (LaPrade and Graves 1982; Yasukawa and Searcy 1982, Hurly and Robertson 1984).

If early females do not influence the settlement of later arriving females, then female settlement should be random with respect to the presence of other females. However, primary females could prevent (Wittenberger and Tilson 1980; Hannon 1984) or delay (Yasukawa and Searcy 1981b) the settlement of additional females. If primary females prevent settlement, then females that were ultimately monogamous may be more aggressive toward intruders than females that were joined by another female. If females delayed settlement, then female settlement within territories should be overdispersed in time. A delay in settlement could occur if primary females aggressively excluded subsequent females or if prospecting females avoided the territories of mated males.

Marsh wrens (Cistothorous palustris) are polygynous marsh-nesting passerines. Bigamy is the most common form of polygyny in this species (Welter 1935; Verner 1965), although trigamy (Verner 1965; this study) and tetragamy also occur (Picman pers. comm.). Both males and females of this species destroy the eggs and nestlings of other passerines, including conspecifics (Picman 1977; Picman and Belles-Isle 1986). Thus harem mates may be both predators and competitors.

Female marsh wrens are aggressive toward conspecifics of both sexes near their nests (Picman 1977; Picman and Belles-Isles 1986). Aggression in this context has been considered a means of nest defense (Picman 1977; Picman and Belles-Isles 1986). There have also been anecdotal reports of aggression among females during settlement, before the nesting stage (Welter 1935; Verner 1963). In this situation females may be aggressive toward each other in an attempt to guard nonshareable resources, in particular male help with feeding nestlings.

I have shown in Chapter 2 that female settlement is not affected by male and territory quality. The purpose of this chapter is to i) examine the responses of breeding females to playbacks of female intruders during different nesting stages, ii) determine the settlement patterns of females in time and space, and iii) test three models of female settlement based on random settlement and settlement influenced by aggression and avoidance.

METHODS

Female settlement was monitored from 1 May to 20 July 1983, 1984, and 1985 at two study sites in Delta, Manitoba (see Chapter 1 for a description of the study sites). Male pairing success was determined by the number of simultaneously active nests within a territory. Female pairing date was considered to be the date of the first egg. The time between the settlement of successive females on a territory is the number of days between first egg dates. All nests were checked twice a week and their contents noted.

Nest locations were plotted on a map of the study area and inter-female distances were determined from these maps. I compared the distribution of females in space against a Poisson distribution using coefficents of dispersion (C.D.; Sokal and Rohlf 1973). This value is 1 in distributions that are random, > 1 when samples are clumped and < 1 when samples are repulsed. I have combined the data from both sites because I am assuming that the effect of settled females should not vary between the sites.

Experimental Study

The playback experiment was conducted from 24 May to 7 July 1985. The details of this experiment are identical to the courtship intensity playback described in Chapter

2, with the following exceptions. A resident female was considered to have responded to the playback if she perched high in the vegetation, called, or moved toward the speaker. Response to playback was tested during three stages of the breeding cycle; pre-laying, laying and incubation. I could not test females during the nestling and fledgling stages because the vegetation density prevented observations of females.

Sixty of 95 trials were conducted between 07:00 and 11:30. The remaining 35 were done between 18:00 and 20:00 and included females at all three nesting stages. The maximum number of trials per female was three (i.e., one per stage) while the minimum was one. This allowed testing for habituation. To allow comparisons between the pre-playback and playback period, females not responding in the pre-playback period were given the lowest value for each measure of response. Level of response refers to a measure of the strength of response, while a response in general refers to whether a female responded at all. All means are reported ± 1 SD.

Female Settlement Models

The purpose of the female settlement models was to test whether and how the presence of a resident female affects the settlement of later arriving females. I have assumed that females are affected by the breeding status of the male only and that males and territories do not differ significantly with respect to features that are important to females (see Chapter 2).

There were few trigamous males in this population (9/120), so most polygynous females settled on a territory with only one other female. Therefore, males were divided into two categories; bachelors and mated males. The probability that a female chose a bachelor male by chance was n_b/N, where n_b = the number of bachelors and N = the total number of males available. The probability of choosing a mated male was therefore $1-n_b/N$. As females settled, the proportion of bachelor versus mated males changed, so a new probability value was determined as each male paired. The expected number of bachelor and mated males chosen was the sum of their respective probabilities. Primary females are the first females to settle, while secondary females refer to the second settling females.

RESULTS

Experimental Study

When females responded to playbacks they usually perched high in the vegetation and then approached and circled the speaker, often within 1 m. Most females (23/34) that responded gave "kek kek" calls.

All four measures of response level showed a significant difference between the pre-playback and playback periods (Figure 9). These results show that female wrens were responding to the playback. Tests for habituation to playbacks showed that female response was independent of previous exposure to one or two playbacks ($X^2=1.33$, df=1, $P>0.70$).

Whether females responded or not depended on nesting stage, with proportionally more females responding in the pre-laying stage than in the laying and incubating stages (Figure 10, $X^2=36.1$, df=2, $P<0.001$). Also, levels of response during the incubation stage were significantly weaker than in the pre-laying and laying stages in three of the four measures of response (Table 19).

If female aggression prevented the settlement of second females, then monogamous females may respond more often or more strongly than primary females. Monogamous females did not respond more often ($X^2=0.83$, df=2, $P>0.70$) or more strongly (Figure 11) than primary or secondary females. If aggression by first females delayed settlement, then levels of aggression may be correlated with the number of days between the settlement of first and second females. However, there was no correlation between response level and the timing of female settlement (Table 20). Aggression between females could also serve to disperse them in space. There was a significant negative correlation between distance to closest approach and the distance between females (Table 20), although the other measures of response were not correlated with inter-female distance.

Settlement in Time and Space

I compared the distribution of female wrens in space against a Poisson distribution using coefficients of dispersion. Site 1 was a homogeneous marsh, as the test requires. But to meet this requirement at Site 2, I excluded a 60 m strip that encompassed the central ponds and the area occupied by yellow-headed blackbirds (Xanthocephalus xanthocephalus).

With the exception of Site 2 in 1984, nests were overdispersed in space at both sites in all three years (Site 1; 1983: C.D.=0.893, 1984: C.D.=0.579, 1985: C.D.=0.604; Site 2; 1983: C.D.=0.688, 1984: C.D.=1.04, 1985: C.D.=0.984). Distances between females decreased over the three years (1983: 48.0 ± 43.8 m, 1984: 32.4 ± 13.1 m, 1985: 28.6 ± 8.4 m; F=3.86, df=2,64, $P<0.05$).

Nesting attempts were also overdispersed in time. That is, for equal inter-nest distances, there was significantly more time between the dates of the first eggs of females (primary and secondary) within territories (9.2 ± 4.3 days, N=23) than between territories (2.8 ± 2.8 days, N=23; Mann-Whitney U test, U=327.5, P<0.001). There was also 9.4 ± 5.3 (N=9) days between the settlement of secondary and tertiary females.

Female Settlement Models

Random Model

If females select a mate without regard to the presence of other females, then bachelor males and mated males should be chosen in proportion to their numbers. To test whether females chose males as expected by chance, once a male was paired he was removed from the bachelor pool and placed in a pool of mated males. Females chose bachelor males more often than expected by chance (Table 21). This was significant in all three years of the study (Figure 12).

Female Aggression Model

Females may settle with bachelors more often than expected by chance because primary females prevent successive females from settling. Results of the experimental study showed that resident females responded more frequently and more intensively to female intruders during the pre-laying stage of the nesting cycle than during incubation. To test whether the distribution of female choices was a result of female aggression, I calculated a series of expected frequencies based on the assumption that once a male was paired he was unavailable to mate with another female until his primary female was incubating. At this time the male was re-entered into the pool of available males. Females settled with bachelor males significantly more often than predicted by this model (Table 21). Each of the three years shows similar trends, but the difference between the observed and the expected frequencies was not significant (Figure 13).

Female Avoidance Model

More bachelors may be selected than expected by chance if females actively avoid territories that are already settled. This model and the female aggression model are not mutually exclusive, although the assumptions differ. To test the female avoidance model, I calculated a series of expected frequencies such that once a male was paired he was removed from the pool of choices until all males had at least one female. At that point all males, then with one female each, became available. Female marsh wrens chose mated and bachelor males as expected by this model (Table 21). This was evident in each year of the study (Figure 14). Thus, the female avoidance model appears to be the best fit of the data, although I cannot totally exclude the possibility that aggression may contribute to avoidance.

DISCUSSION

Females nesting early may prevent (Wittenberger and Tilson 1980; Hannon 1984) or delay (Yasukawa and Searcy 1981a) the settlement of additional females. Because 47% of the males in this population recruited more than one mate, it appears that many females did not prevent the settlement of a second female. In addition, there was no difference in the response of monogamous and primary females, further suggesting that resident females could not prevent the settlement of subsequent females. There were, however, eight days between the settlement of primary and secondary females and nine days between the settlement of secondary and tertiary females. Asynchrony in settlement was evident only among harem mates, suggesting that the presence of the resident female may delay the settlement of subsequent females. A delay in settlement of females within territories has also been recorded for a western population of marsh wrens (Verner 1964). In this study staggered settlement was apparently related to whether males assisted females with feeding young.

Nesting attempts could be staggered if first settling females aggressively excluded intruders or if later-arriving females avoided mated males (Yasukawa and Searcy 1981a). Female marsh wrens responded aggressively to playbacks of female intruders. This response was greatest during the pre-laying stage and declined during the laying and incubation stages. Aggression by females could enforce the observed delay in nesting (Holm 1973; LaPrade and Graves 1982; Yasukawa and Searcy 1982; Hurly and Robertson 1984). However, the number of days between the settlement of successive females on a territory was not correlated with strength of response. In addition, my attempt to fit these data to the female aggression model was not successful. This suggests either that female marsh wrens were unable to delay the settlement of subsequent females or that aggression in this context has another function.

A delay in settlement could also occur if females avoided territories that already had females. The female avoidance model suggests that females settle with mated males only after bachelor males are paired. Females may avoid mated males because males and territories in this area tend to be of similar quality (Chapter 2), so polygynous females are not compensated for the costs of polygyny and should therefore try to mate monogamously. However, because the sex ratio is skewed in favour of females (Chapter 1), females that arrive late must settle with mated males if they are to breed. If females choose mated males only after most of the bachelors are paired, there is a greater probability that the settlement of harem mates will be staggered. This delay will reduce the overlap in nestling periods and thus reduce competition

1980; Yasukawa and Searcy 1981a).

The settlement pattern suggested by the female avoidance model could also occur if females were avoiding other females (costs of predation) rather than avoiding mated males (costs of polygyny). That is, females may avoid settling with another female because they are attempting to space themselves out and decrease conspecific predation, not because they are avoiding synchronous settlement in the same territory. Settlement within territories was more staggered than settlement between territories when the distance between females was held constant. This suggests that females were attempting to avoid newly mated males.

Nesting attempts at both sites were overdispersed in space as well as time. There was also a negative correlation between the closest approach made by a female to the speaker and inter-nest distance. Although I have no direct observations, these results suggest that females may defend subterritories within male boundaries. In red-winged blackbirds (Agelaius phoenecius), the area defended by females is largest during the pre-laying and laying stage and includes only the nest-site as the season progresses (Nero and Emlen 1951; Nero 1956; Hurly and Robertson 1984). Thus, a decrease in response with nesting stage is consistent with the defense of a subterritory (Orians 1980, Yasukawa and Searcy 1981a). Females may defend subterritories to sequester food (Nero 1956) or in the case of marsh wrens, to ensure that subsequent females do not settle near their nesting area. I had very few cases of nestling starvation, which suggests that food may not be limiting, but there were several cases of intraspecific nest destruction. Also, a decrease in distances between females over the three years was accompanied by a decrease in the number of young fledged from successful nests (Chapter 1). This suggests, albeit weakly, that partial losses increase as the distance between females decreases. Thus aggression among females may be important in spacing females out (Picman 1977; Yasukawa and Searcy 1981a).

In conclusion, female settlement patterns appear to be influenced by defense of subterritories and the avoidance of mated males by prospecting females. These behaviours result in an overdispersion of nesting attempts in both space and time. Presumably, these strategies would reduce interference among females and also reduce the costs of polygyny.

CHAPTER 4

POLYGYNY IN MARSH WRENS: A TEST OF THE POLYGYNY THRESHOLD MODEL

INTRODUCTION

Polygyny is expected to be advantageous to males because male reproductive success usually increases with harem size (Verner 1964; Orians 1969; Holm 1973; Weatherhead and Robertson 1977). Thus, the evolution of polygyny may depend on its advantages and disadvantages to females (Orians 1969). Females could benefit from settling polygynously if harem mates cooperated in nest defense, care of young, or locating food (Altmann et al. 1977; Picman 1980b). In this instance, polygyny may be adaptive because of the advantages associated with group living. However, it is more difficult to explain how polygyny could evolve if females suffer negative effects. The costs to females that choose to settle polygynously may include competition for food and nest sites, competition for male help in feeding young, and increased attraction to predators. Thus, for polygyny to evolve, females must be compensated for the costs they may incur if they settle with an already-mated male.

The Polygyny Threshold Model (PTM) was proposed to explain how females could be compensated for these costs and thus how polygyny could evolve (Verner and Willson 1966; Orians 1969; Altmann et al. 1977; Garson et al. 1981). The model suggests that females may overcome costs by settling on a high quality territory or with a high quality male. That is, females mating polygynously in a high quality breeding situation (Wittenberger 1976) must be as successful as females mating monogamously in a lower quality situation. The necessary difference in quality was termed "the polygyny threshold". Quality, in this context, refers to features of the breeding situation that affect female fitness (see Chapter 2).

The Verner-Willson-Orians version of the PTM assumes a strong correlation between male and territory quality. That is, a female choosing a high quality territory necessarily acquires a high quality male. An alternative version, the Sexy Son Hypothesis, suggests that male quality need not be correlated with territory quality. Instead, females may be compensated by features of the male that do not affect their immediate reproductive success (Weatherhead and Robertson 1979). Females selecting "sexy" males should have "sexy sons" that recruit many females. Thus a female may forfeit her immediate success for long-term benefits. This version of the PTM has received much criticism (Heisler 1981; Wittenberger 1981b; Searcy and Yasukawa 1981). Kirkpatrick (1985) has shown that the model is untenable because female preferences for characters not conferring immediate benefits would not be evolutionarily stable.

Thus, in this paper I will only discuss the Verner-Willson-Orians version of the PTM.

Several assumptions are implicit in the PTM (Orians 1969; Altmann et al. 1977; Garson et al. 1981). Females must make optimal choices, to maximize their immediate reproductive success. Hence females should always select the breeding situation that will confer the highest fitness. Another assumption of the model is that the addition of females to the harem may reduce the fitness of all harem mates. This assumption is important because the first female to settle on a territory may not be able to predict her ultimate reproductive success. Finally, females must be able to discriminate among males and/or territories. That is, males must differ with respect to features important to females and females must be able to assess these features.

Altmann et al. (1977) and Garson et al. (1981) described several predictions that could be used to test the PTM. If the PTM is the best description for the evolution of polygyny then the following predictions should be supported:

i) Male and/or territory quality should be positively correlated with male pairing success (Altmann et al. 1977; Garson et al. 1981). This is because females should settle in the highest quality breeding situation available.

ii) The order in which first females choose breeding situations should be positively correlated with the order in which subsequent females choose (Altmann et al.1977). That is, the first females should choose the best situation and these choices should also be the best for later females if they are to be compensated for mating polygynously.

iii) Male pairing success (harem size) should be negatively correlated with the order in which females settle (Altmann et al. 1977; Garson et al. 1981). That is, the males that acquire the most females should also get the first females.

iv) Female reproductive success should be negatively correlated with the order in which females settle because the first females to arrive should settle in the best breeding situations (Garson et al. 1981). However, the reproductive success of the last females to settle may be a better test of this prediction because they are the females that make the decision to settle polygynously. They should be better able to predict their expected success than the first females which settle monogamously. Fretwell and Lucas (1969) suggested that increasing density may balance the effects of quality and thus, all individuals should have equal fitness. This prediction assumes that despite increasing density on high quality territories, the "best" territories will always remain better than the poorest quality territories. This seems realistic if polygynous females are to be compensated for the costs of polygyny.

v) Within a given harem size, there should be a negative correlation between female settling order and reproductive success (Altmann et al. 1977). Again, females should make choices that maximize their reproductive success in that season. This prediction controls for the effects of females on each other by comparing reproductive success within a given harem size. The latter two predictions assume that there are no seasonal effects that may influence female fitness. Females in this population settle over a 3 week period so this assumption is probably valid.

The PTM has been widely accepted as being the best description for the evolution of resource defense polygyny (Emlen and Oring 1977) in many avian species (Verner 1964; Verner and Willson 1966; Zimmerman 1966, 1971; Orians 1969; Verner and Engelson 1970; Martin 1974; Carey and Nolan 1975; Wittenberger 1976). There have been few studies that directly test the model using the female settlement predictions. These predictions may be more reliable than correlations with male and territory quality because they do not depend on our ability to measure features that are important to females.

The PTM was first described using data from a population of marsh wrens (Cistothorus palustris; Verner 1964; Verner and Willson 1966) and it is generally assumed that this model best describes the evolution of polygyny in this species. In this chapter I test five predictions of the PTM for my population of marsh wrens, using data on male and territory features presented in Chapter 2 and data on the settlement and reproductive success of female marsh wrens. I also present an alternative model that may be a better explanation for the evolution and maintenance of polygyny in this population.

METHODS

This study was conducted from 1 May to 20 July 1983 and 1984 in Delta, Manitoba. See Chapter 1 for a description of the study sites. Details on measures of male and territory quality were reported in Chapter 2. All courting and breeding nests were checked twice a week. Male pairing success is based on the maximum number of simultaneously active nests on a male's territory. The order that females settled was ranked according to the date of the first egg.

I measured two aspects of female reproductive success: the number of young fledged from all nests and the number of young fledged from successful nests. I considered a nest successful if at least one young was fledged. I pooled the information from each site for the two years of the study.

RESULTS

As assumed, the mean number of young fledged/male increased as harem size increased (Table 22). However, there was no difference in the mean number of young fledged/female in different sized harems (Table 22).

Prediction 1: Male and Territory Quality

I could find no relationship between my measures of male and territory quality and male pairing success (Chapter 2). I was also unable to separate males of different pairing status using discriminant function analysis. This suggests that there was little variation in male or territory features and that the variation that existed was not important in female choice.

Predictions 2 & 3: Female Settlement

At Site 2, the order in which first females settled was significantly correlated with the order in which second females settled (Figure 15). At Site 1, however, the correlation was not significant presumably because of the smaller sample size. Contrary to the prediction of the PTM, there was no correlation between male pairing success and the order in which primary females settled at Site 1 and Site 2 (Figure 16).

Predictions 4 & 5: Female Success

The number of young fledged from all nests (this includes successful and unsuccessful nests) for all females and for the last females in harems was not correlated with the order in which these females settled (Figures 17 and 18). The number of young fledged from successful nests for both groups was also not correlated with settlement order at Site 1 (r_s=0.25, N=37, P=0.22, for all females; and r_s=-0.39, N=7, P=0.34; for final females) or Site 2 (r_s=0.23, N=48, P=0.12, for all females; and r_s=0.29, N=16, P=0.25, for final females). The number of young fledged from all nests (successful and unsuccessful) for bigamous females was also not correlated with the order in which these females settled (Figure 19). In addition, the number of young fledged from successful nests was not correlated with female settlement at Site 1 (r_s=0.48, N=15, P=0.07) or at Site 2 (r_s=0.29, N=32, P=0.10).

DISCUSSION

Four of the five predictions of the PTM tested in this study were not supported. In fact, results of discriminant function analysis (Chapter 2) suggest that variation among breeding situations, with regard to female choice was low, contrary to one of the major assumptions of the model. Although the PTM is one of the more widely accepted explanations for the evolution of avian polygyny, there has been only one study (Pleszczynska 1978) that provides strong support for the model. Many studies show that the second females to settle are less successful (Alatalo et al. 1981; Catchpole et al. 1985) or that females do not settle according to the predictions of the model (Lenington 1980; Garson 1980).

For marsh wrens in particular, the results are equivocal. Verner (1964) found that male pairing success was correlated with the amount of emergent vegetation and the size of a male's territory. However, in a later study (Verner and Engelsen 1970) there was no correlation between male pairing success and any features of the territory. Instead, there was a correlation between the number of courtship nests built over the season and pairing success. Also, there was no relationship between the order in which females settled and male pairing success (Verner 1965). The results of my study are also not consistent with the predictions of the PTM. Although the PTM is often assumed to be the best description for polygyny in this species, the data are not convincing.

Alternative Model of Polygyny

The PTM suggests that females could be compensated for the costs of polygyny by settling in a high quality breeding situation. However, it is difficult to explain how polygyny could evolve if there is no variation in male or territory quality and thus females are not compensated. Presumably, if variation in the quality of the breeding situation was low and the costs of polygyny high, the best strategy for a female would be to mate monogamously. Alternatively, a female could adopt a strategy that would reduce her potential costs. This model suggests that costs may be reduced if female settlement within territories is staggered. That is, if females settle asynchronously the overlap in the nestling stage is reduced and therefore competition for resources and male help would also be reduced (Verner 1964; Orians 1969). Thus, the alternative model suggests that polygyny could evolve because costs to females are reduced through asynchronous settlement.

In my study area there appeared to be little predictable variation among males and territories. However, females did benefit from male help with feeding young. This resource is non-shareable and in this population, potentially available to all females, regardless of status. Although males feed infrequently, all females could benefit from settling asynchronously and increasing their chances of assistance. Competition for food on a male's territory would also be reduced if female settlement was staggered.

The operational sex ratio (Emlen and Oring 1977), in my study was skewed in favour of females (Chapter 1) and thus, some females were forced to settle polygynously. However, settlement of females within territories was overdispersed in time which reduced the overlap in nestling periods. My results indicate that females were equally successful, which suggests that polygynous females were apparently not suffering increased costs.

Predictions of the Alternative Model

The assumptions of the alternative model are less stringent and probably more realistic than the assumptions of the PTM. The alternative model does not assume that females must discriminate between several breeding situations and make complex decisions based on multiple criteria. Rather, it assumes that females can detect the presence of another female on a male's territory and determine its nesting stage. This assumption is valid for marsh wrens. Because primary females are aggressive to intruders early in the nesting stage (Chapter 3), prospecting females are informed of a male's status.

Both the PTM and the alternative model predict that the order in which first and second females settle should be correlated. If female settlement is staggered, then the territories of the earliest females to settle should become available sooner than the territories of the females that settle later. Thus, second-settling females would necessarily settle on the territories of the early females first. This prediction is consistent with both models. However, the strength of the correlation may differ. The PTM model predicts a strong positive relationship. That is, if the first females choose males 1, 2, 3, and 4 and the next females chose 1, 4, and 3 then the prediction would not be supported (Altmann et al. 1977). The alternative model may permit a weaker relationship because if some early females settle simultaneously their territories would be equally attractive to later females. My data show a weak, positive relationship.

Both the PTM and the alternative model predict that the order in which females settle should be negatively correlated with male pairing success. Again, this is because the first territories to be settled will be opened to subsequent females sooner than other territories. My results did not support this prediction.

Finally, the alternative model predicts that there will be no relationship between female reproductive success and the order in which territories are settled. This is because all breeding situations are similar with respect to features affecting female success. My data supported the prediction.

Factors Affecting Male Success

If the alternative model is the best description for the evolution or maintenance of polygyny in this population of marsh wrens, then the best strategy for a male wren is to arrive early on the breeding ground and establish a territory prior to the arrival of the first females. That is, the earlier a male recruits his first female, the more likely he is to gain a second. Older males in many species are usually the first to arrive in the spring migration. In addition, returning males tend to settle on the same territories between years (Nero 1956; Yasukawa 1979; Wittenberger 1980; Picman 1987). Males may establish territories more quickly and easily because of site fidelity (Yasukawa 1979). Thus, the alternative model would predict that older, returning males should recruit more females. Unfortunately, very few males in this population returned between years, so it is difficult to assess this prediction.

Conditions for the Evolution of Polygyny

Avian polygyny could evolve, or be maintained, under several different selective regimes. Thus, one hypothesis may not explain polygyny in all species or even within one species under different selection pressures. The PTM may work best for populations where breeding situations vary in quality and where females can assess this variation (e.g. Yasukawa and Searcy 1986). However, it is not a satisfactory explanation for situations in which females cannot assess male status (Alatalo et al. 1981; Catchpole et al. 1985) or when there is little variation among breeding situations (Bedard and LaPointe 1984; Lightbody 1986; this study).

Alternatively, the model proposed in this thesis may explain polygyny in populations where there is little variation in quality and costs to settling polygynously are high. The alternative model may be tenable for situations in which a female biased sex ratio forces some individuals to settle polygynously. It could also function, regardless of the sex ratio, if female arrival was staggered. That is, if the time lag between females was sufficient (i.e., prevented an overlap in nestling stages) the first territories settled should be as attractive as bachelor territories and later arriving females should choose from among the remaining territories at random.

Contrary to earlier studies, the PTM appears not to be the best description for the evolution and maintenance of polygyny for this population of marsh wrens. An alternative model, based on reducing the costs of polygyny through staggered settlement may be more appropriate. Whether this model is generally applicable remains to be seen. However, several studies have failed to support the main predictions of the PTM (Bedard and LaPointe 1984; Catchpole et al. 1985; Davies and Houston 1986; Lightbody 1986; this study) and thus, alternative models are becoming increasingly necessary.

CONCLUSIONS

1. The two study sites differed with respect to physical features, such as vegetation density, vegetation height, and water depth. Female marsh wrens at the site with denser vegetation and deeper water (Site 2) had a greater probability of having a successful nest. However, females at the sparser, shallower site (Site 1) fledged more young per successful nest.

2. Male marsh wrens settled at both sites in numbers expected by chance. However, significantly more females settled at Site 2 than would be predicted by chance. Males and females settled at both sites simultaneously.

3. Physical and behavioural measures of male quality were not correlated with male pairing success. The features that I measured varied little among males with respect to female choice. With one exception, features of male quality were not correlated with female reproductive success. Male help with feeding young increased the number of young fledged per nest. However, male wrens helped infrequently and apparently without regard to female status.

4. There was no correlation between measures of territory and nest site quality and male pairing success within sites.

In addition, there appeared to be little variation among territories and nest sites, with respect to the measured features. Territory and nest site features did not influence female reproductive success within sites.

5. Primary females responded aggressively to taped playbacks of female marsh wrens. The responses were stronger and more frequent during the pre-laying and laying stages than during incubation. All females, regardless of status, responded in the same manner.

6. Female settlement was overdispersed in space and time. Dispersion in space was probably enforced through aggression and related to conspecific predation. Dispersion in time was related to a preference by females for bachelor males.

7. The major predictions of the Polygyny Threshold Model were not supported for this population of marsh wrens. A~~n~~ alternative model, for polygynous populations in which males and territories are homogen~~eous~~ and polygyny is costly, is proposed. This models suggests that polygyny could evolve because females reduce the costs of polygyny by settling asynchronously.

Figure 1. Mean (± SD) vegetation height (cm), vegetation density (number of clearly visible dots of 20), and water depth (cm), for Site 1 (1) and Site 2 (2) in 1983, as measured before (early) and after (late) the growth of new vegetation. The numbers above the bars represent the number of measurements taken. The difference between sites was compared using a Student t-test.

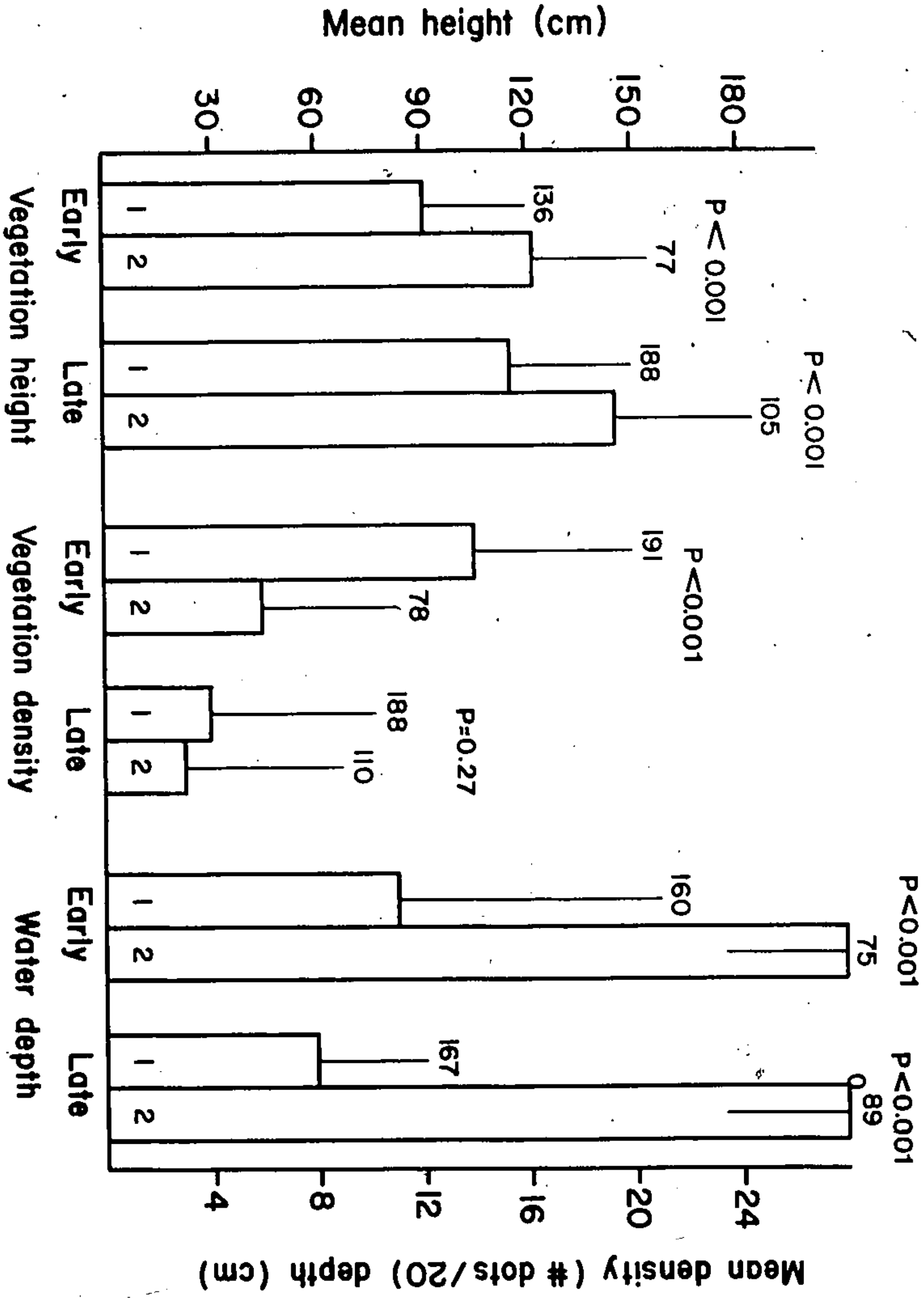

Mean height (cm)
30
60
90
120
150
180
Vegetation height
Early
Late
1
2
136
77
P< 0.001
188
105
P< 0.001
Vegetation density
191
78
P<0.001
188
110
P=0.27
Water depth
160
75
P<0.001
167
89
P<0.001
4
8
12
16
20
24
Mean density (# dots/20) depth (cm)

Figure 2. Mean (± SD) vegetation height (cm), vegetation density (number of clearly visible dots of 20), and water depth (cm), for Site 1 (1) and Site 2 (2), in 1984, as measured before (early) and after (late) the growth of new vegetation. The numbers above the bars represent the number of measurements taken. The difference between sites was compared using a Student t-test.

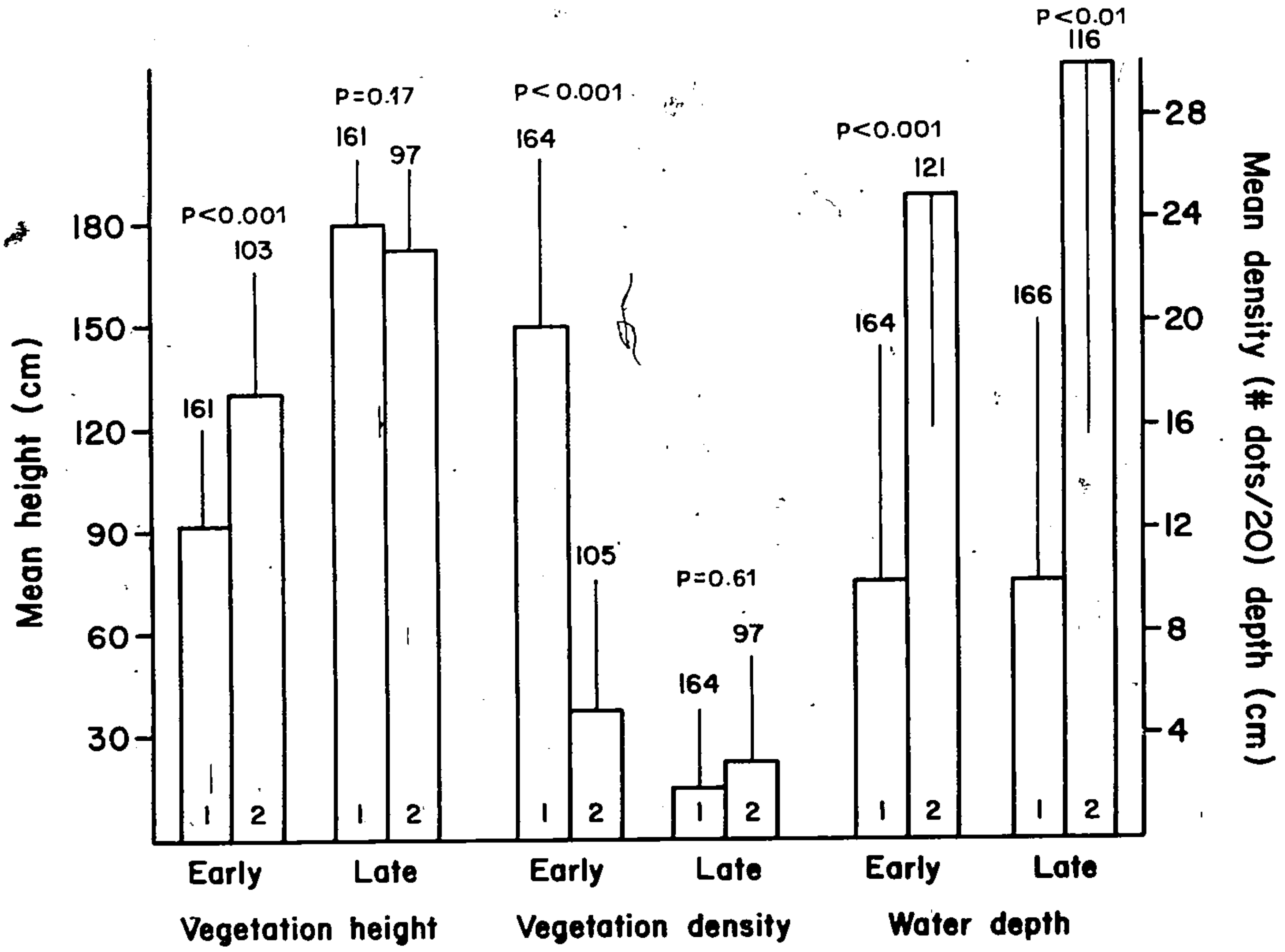

Mean height (cm)
180
150
120
90
60
30
Mean density (# dots/20) depth (cm)
28
24
20
16
12
8
4
P<0.001
161
103
P=0.17
161
97
P< 0.001
164
105
P=0.61
164
97
P<0.001
164
121
P<0.01
166
116
1
2
Early
Late
Vegetation height
Vegetation density
Water depth

Figure 3. The number of young fledged/female in relation to the response of male marsh wrens to playbacks of female calls.

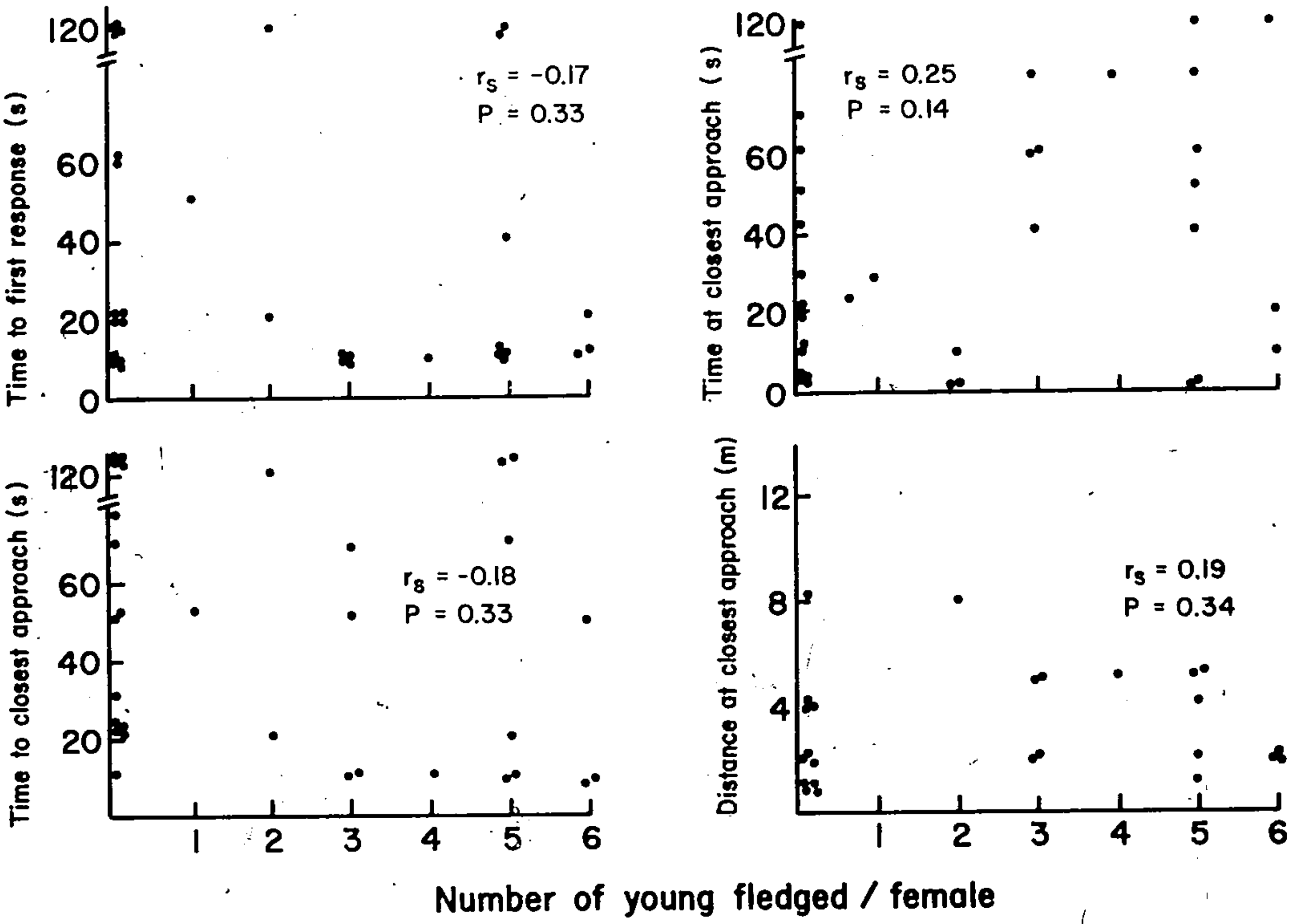

Time to first response (s)
120
60
40
20
0
r_s = −0.17
P = 0.33
Time at closest approach (s)
120
60
40
20
0
r_s = 0.25
P = 0.14
Time to closest approach (s)
120
60
40
20
r_s = −0.18
P = 0.33
Distance at closest approach (m)
12
8
4
r_s = 0.19
P = 0.34
1
2
3
4
5
6
Number of young fledged / female

Figure 4. The order in which females settled with males in relation to the response of those males to playbacks of female calls.

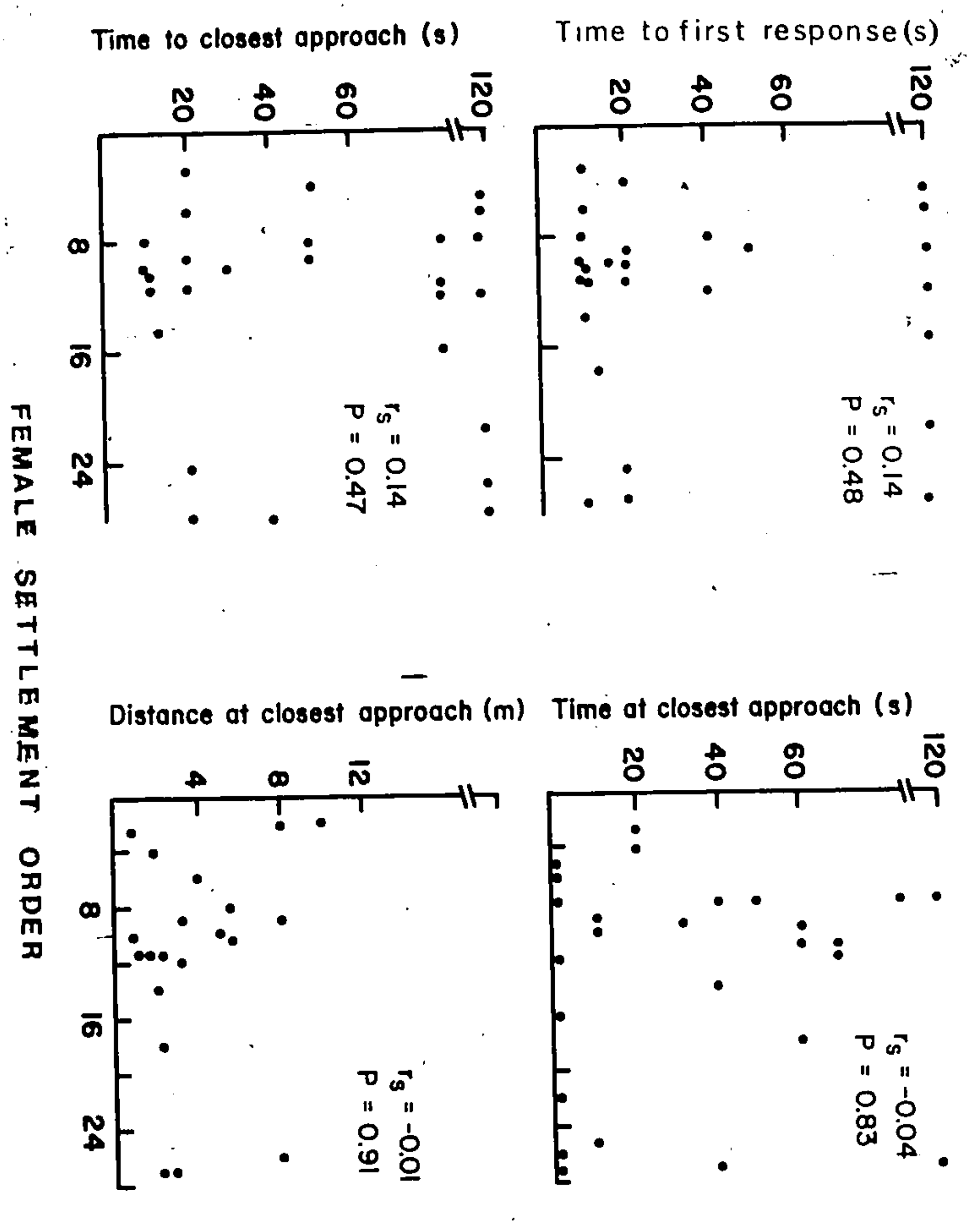

Time to first response(s)
120
60
40
20
$r_s = 0.14$
P = 0.48
Time to closest approach (s)
120
60
40
20
8
16
24
$r_s = 0.14$
P = 0.47
Time at closest approach (s)
120
60
40
20
$r_s = -0.04$
P = 0.83
Distance at closest approach (m)
12
8
4
8
16
24
$r_s = -0.01$
P = 0.91
FEMALE SETTLEMENT ORDER

Figure 5. Male pairing success (harem size) in relation to the response of male marsh wrens to playbacks of female calls.

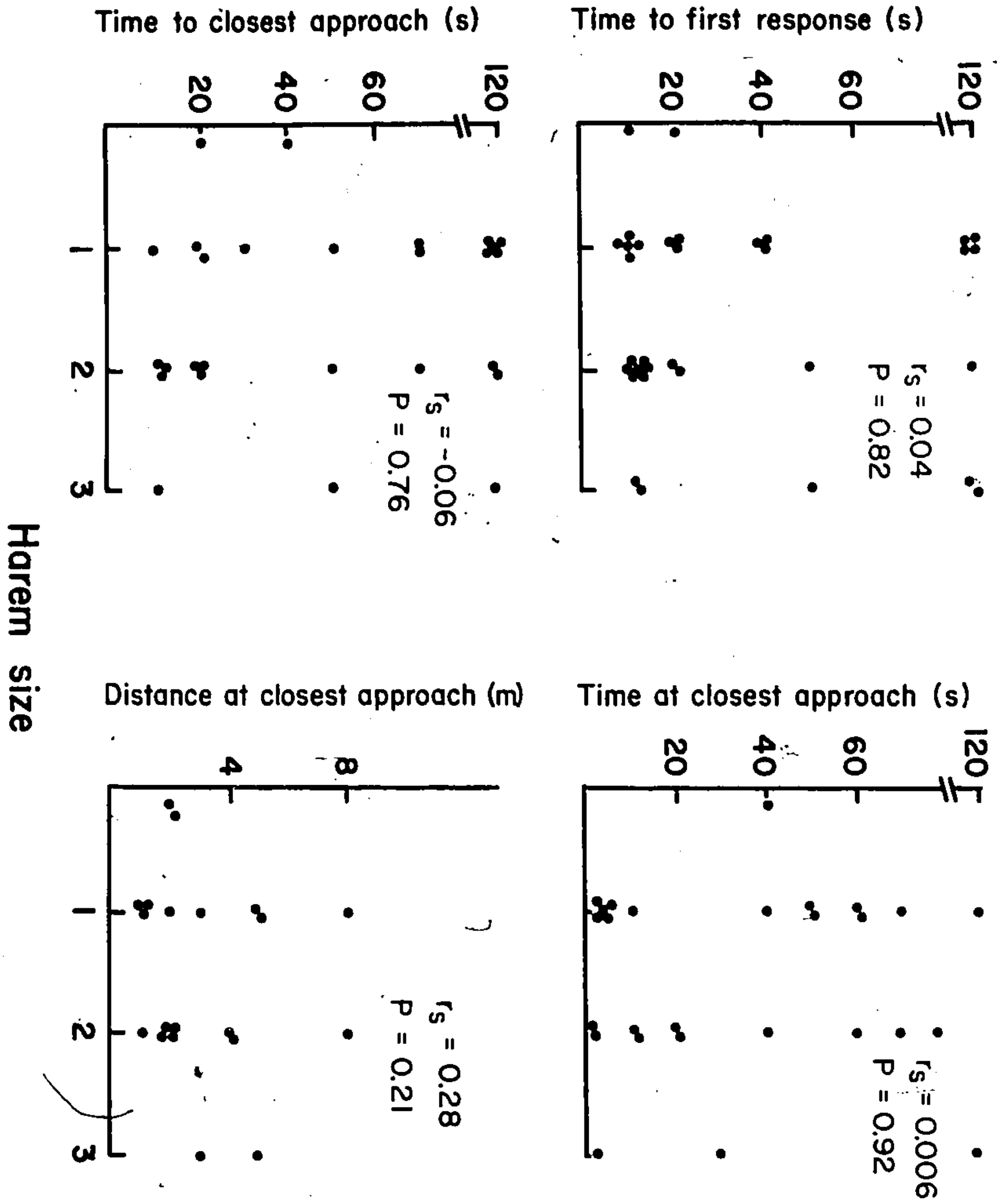

Time to first response (s)
120
60
40
20
1
2
3
rs = 0.04
P = 0.82
Time to closest approach (s)
120
60
40
20
1
2
3
rs = -0.06
P = 0.76
Time at closest approach (s)
120
60
40
20
rs = 0.006
P = 0.92
Distance at closest approach (m)
8
4
1
2
3
rs = 0.28
P = 0.21
Harem size

Figure 6. The number of young fledged/female in relation to the response of male marsh wrens to playbacks of male song.

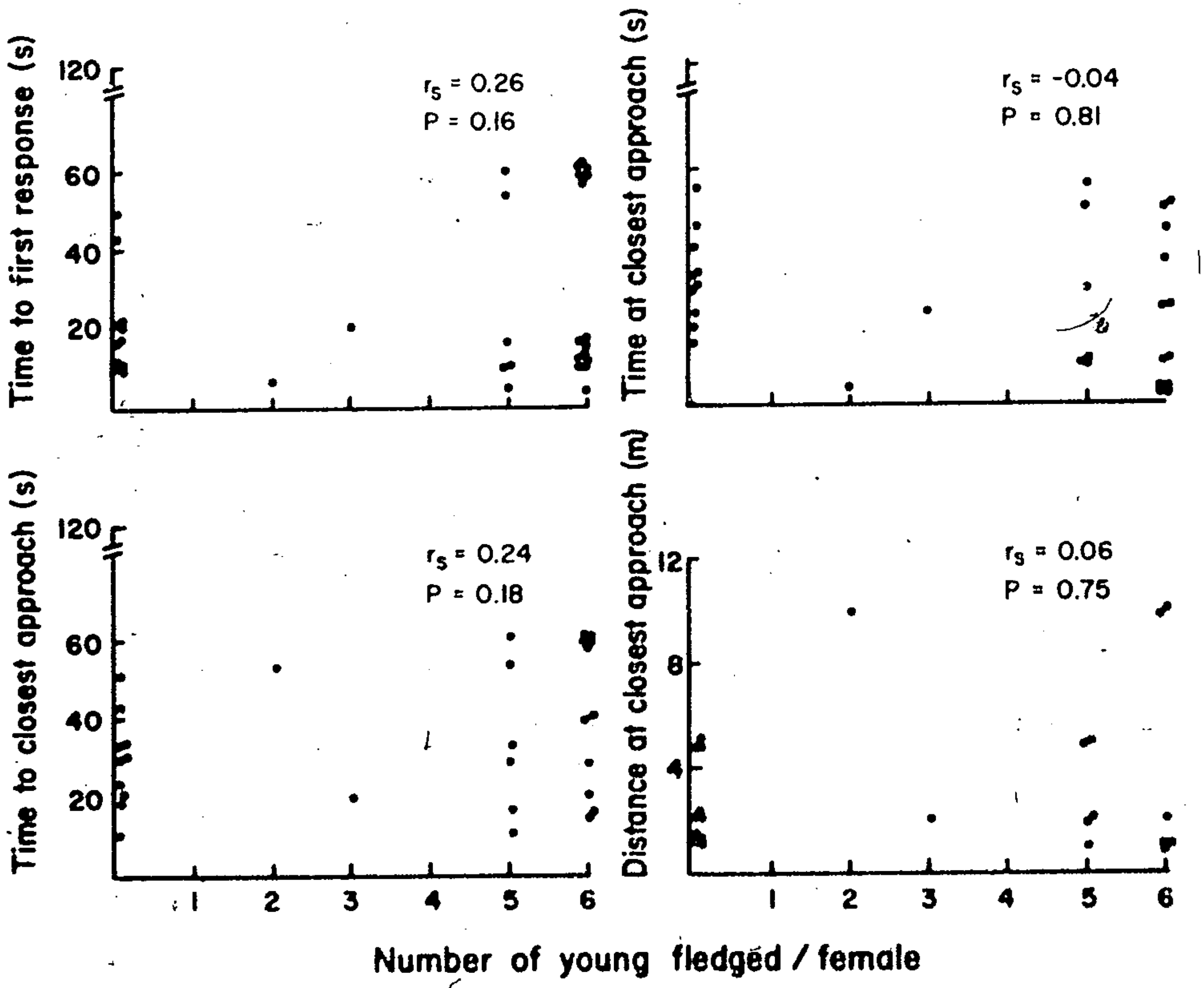

Time to first response (s)
120
60
40
20
r_s = 0.26
P = 0.16
Time at closest approach (s)
r_s = -0.04
P = 0.81
Time to closest approach (s)
120
60
40
20
r_s = 0.24
P = 0.18
Distance at closest approach (m)
12
8
4
r_s = 0.06
P = 0.75
1
2
3
4
5
6
1
2
3
4
5
6
Number of young fledged / female

Figure 7. The order in which females settled with males in relation to the response of those males to playbacks of male song.

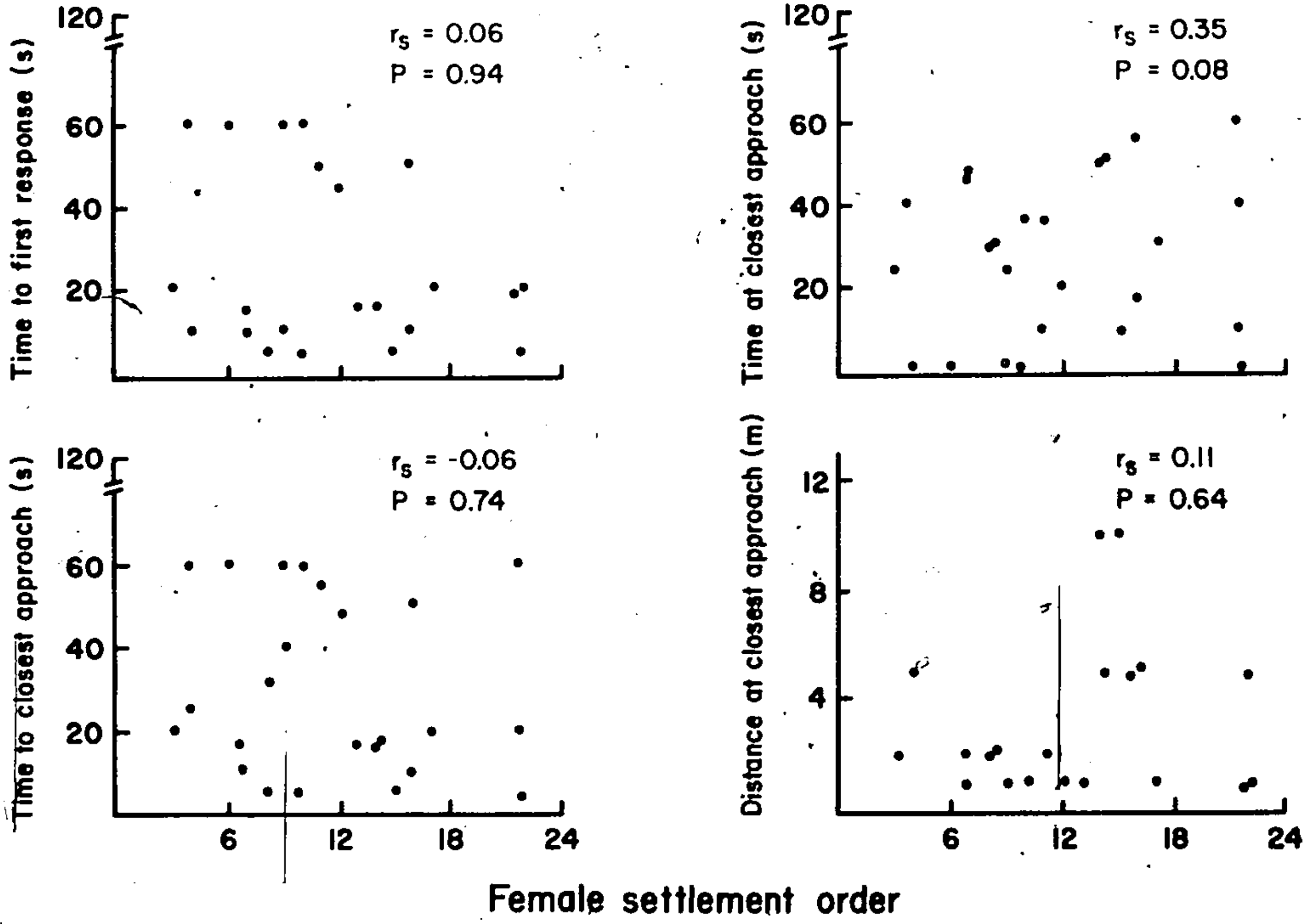

Time to first response (s)
120
60
40
20
r_s = 0.06
P = 0.94
Time at closest approach (s)
120
60
40
20
r_s = 0.35
P = 0.08
Time to closest approach (s)
120
60
40
20
r_s = -0.06
P = 0.74
6
12
18
24
Distance at closest approach (m)
12
8
4
r_s = 0.11
P = 0.64
6
12
18
24
Female settlement order

Figure 8. Male pairing success (harem size) in relation to the response of male marsh wrens to playbacks of female calls.

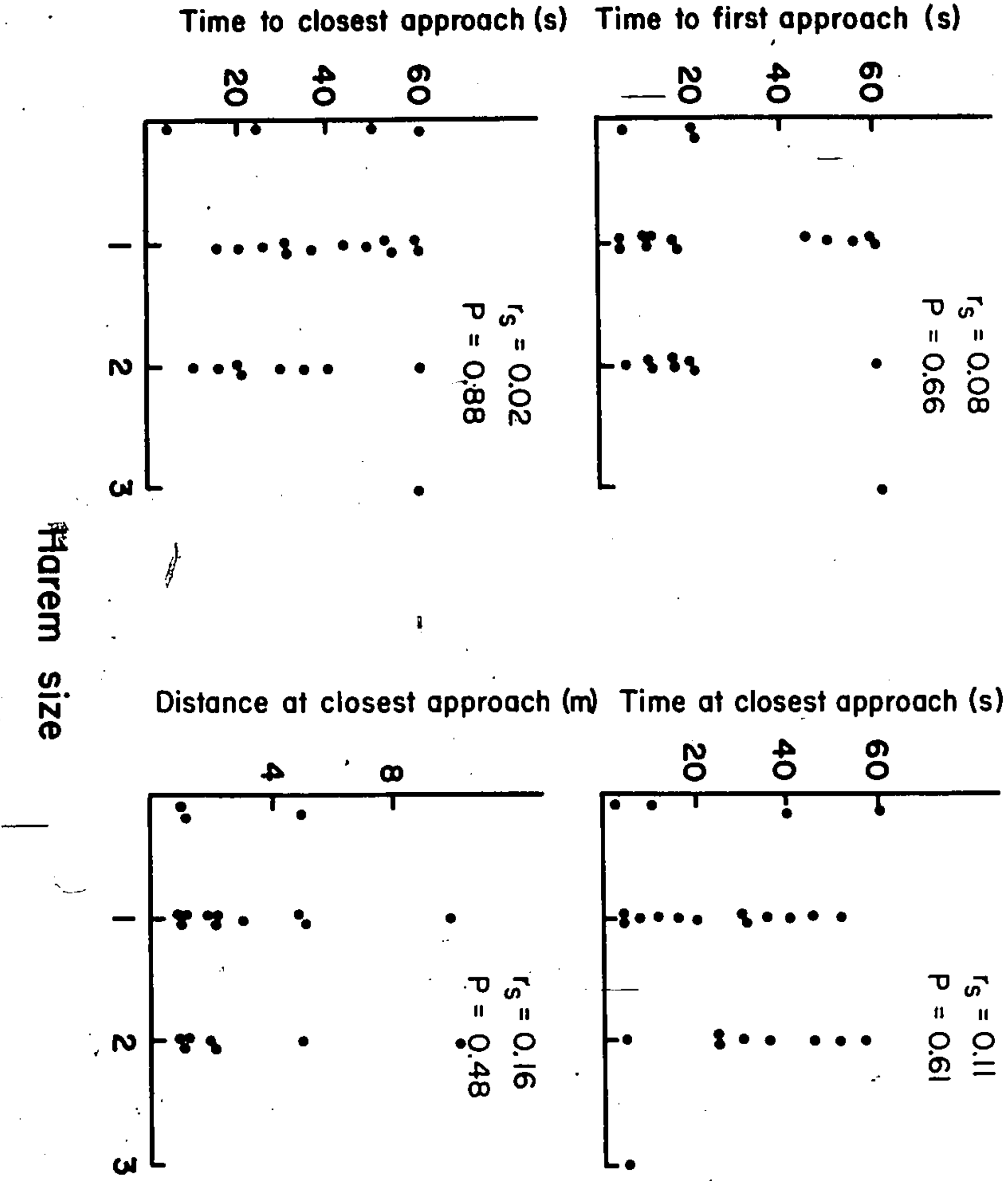

Time to closest approach (s)
20
40
60
1
2
3
r_s = 0.02
P = 0.88
Time to first approach (s)
20
40
60
r_s = 0.08
P = 0.66
Distance at closest approach (m)
4
8
1
2
3
r_s = 0.16
P = 0.48
Time at closest approach (s)
20
40
60
r_s = 0.11
P = 0.61
Harem size

Figure 9. Mean (± SD) levels of response to pre-playback and playback trials for pre-laying females. Results of a Mann-Whitney U-test were significantly different at the P=0.001 level. N=21 for all measures. Striped bars represent the pre-playback response and clear bars the playback response.

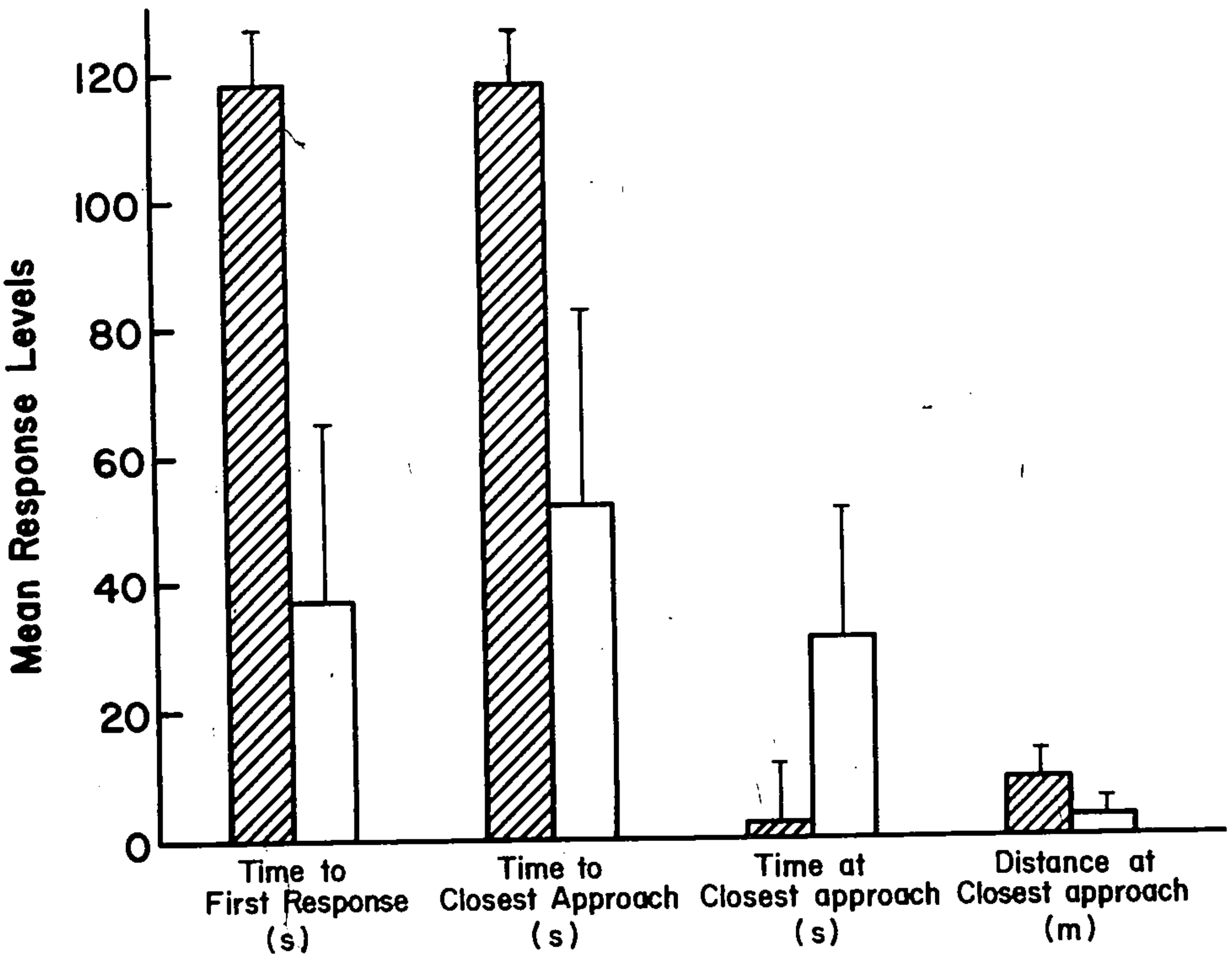

Mean Response Levels
0
20
40
60
80
100
120
Time to First Response (s)
Time to Closest Approach (s)
Time at Closest approach (s)
Distance at Closest approach (m)

Figure 10. Percent of females responding during each nesting stage. The numbers above the bars represent the number of females in each trial.

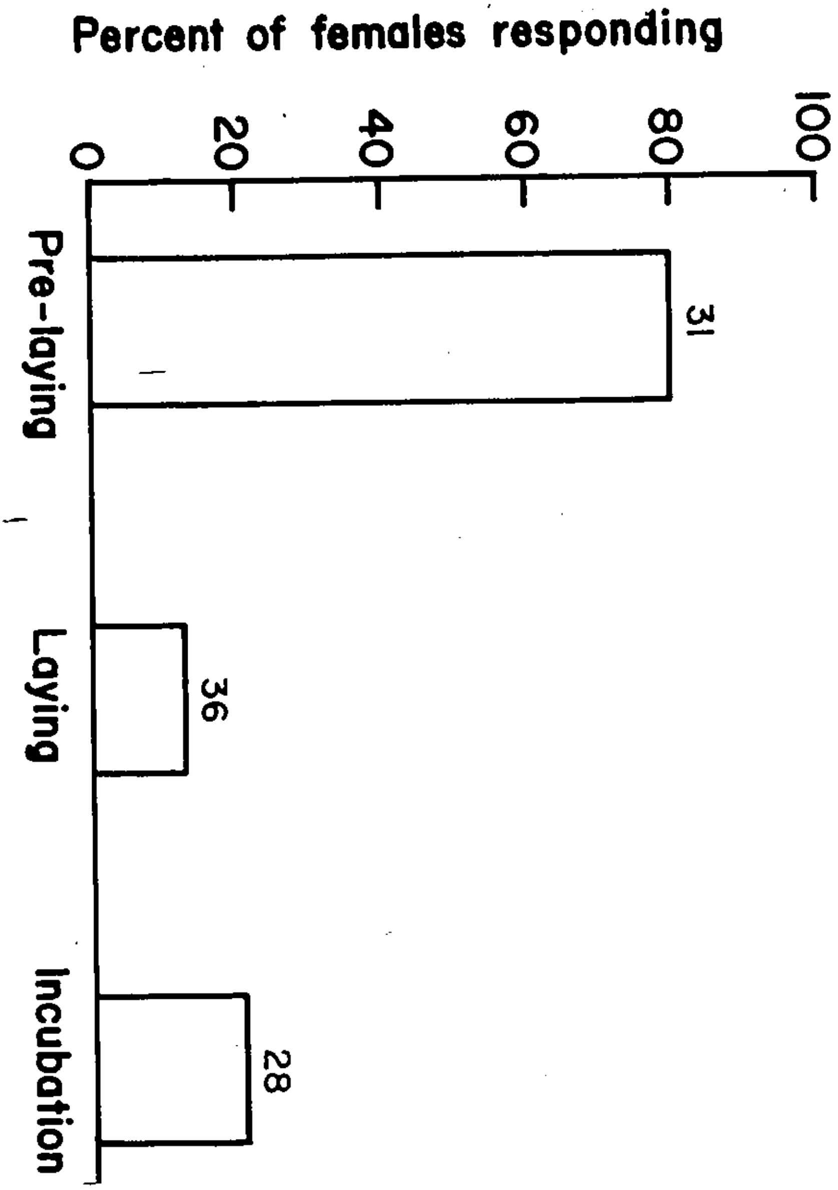

Percent of females responding
0
20
40
60
80
100
Pre-laying
31
Laying
36
Incubation
28

Figure 11. Mean (± SD) levels of response of females during the pre-laying stage with respect to status. Results of a Kruskal-Wallis test showed no significant difference for all measures except distance to closest approach (Time to first response: $H=3.1$, $P>0.50$; Time to closest approach: $H=2.2$, $P>0.50$; Time at closest approach: $H=1.3$, $P>0.75$; Distance at closest approach: $H=38.2$, $P<0.01$). Numbers above the bars represent the sample size. M = monogamous, 1° = primary female, and 2° = secondary female.

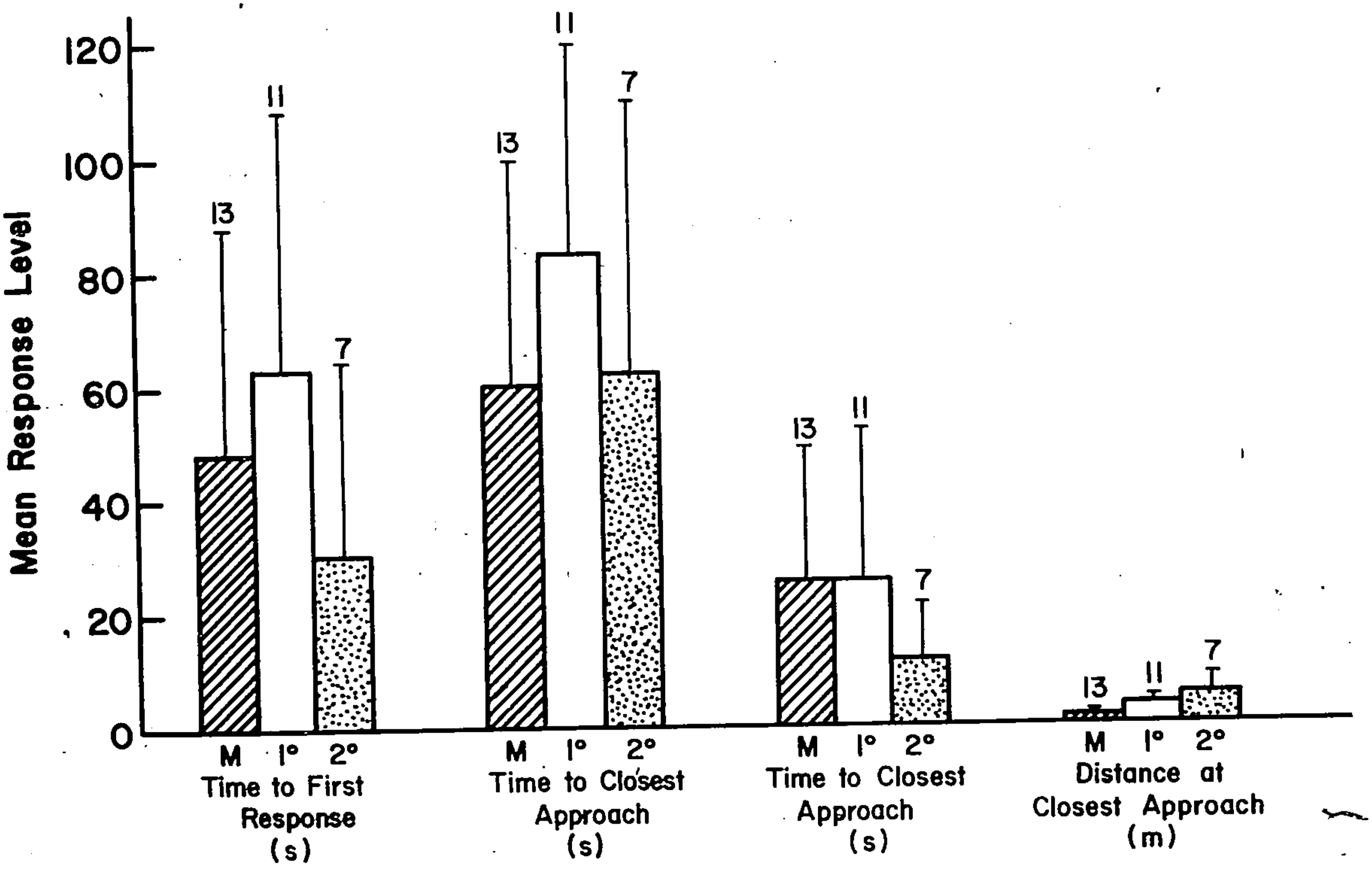
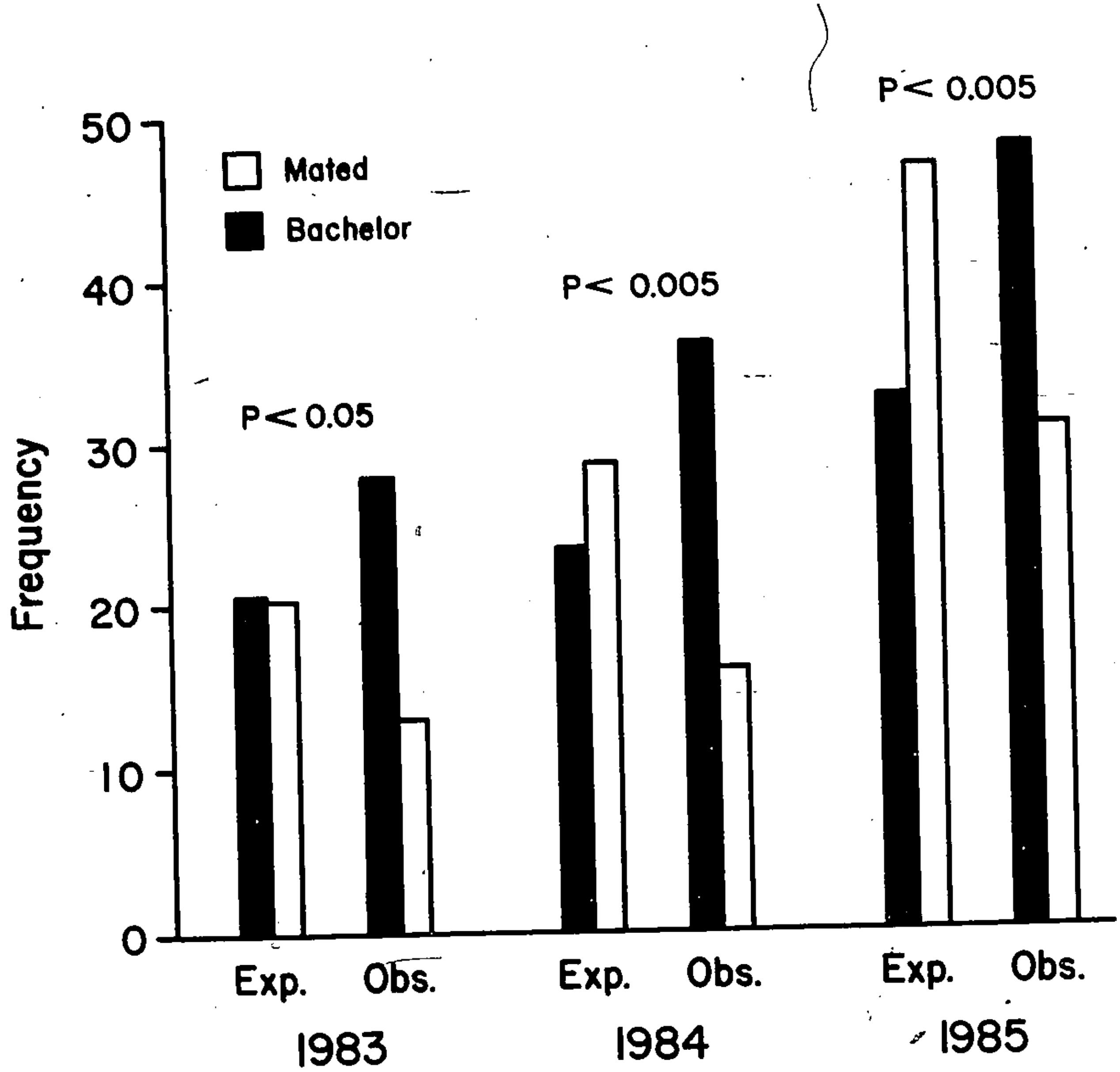
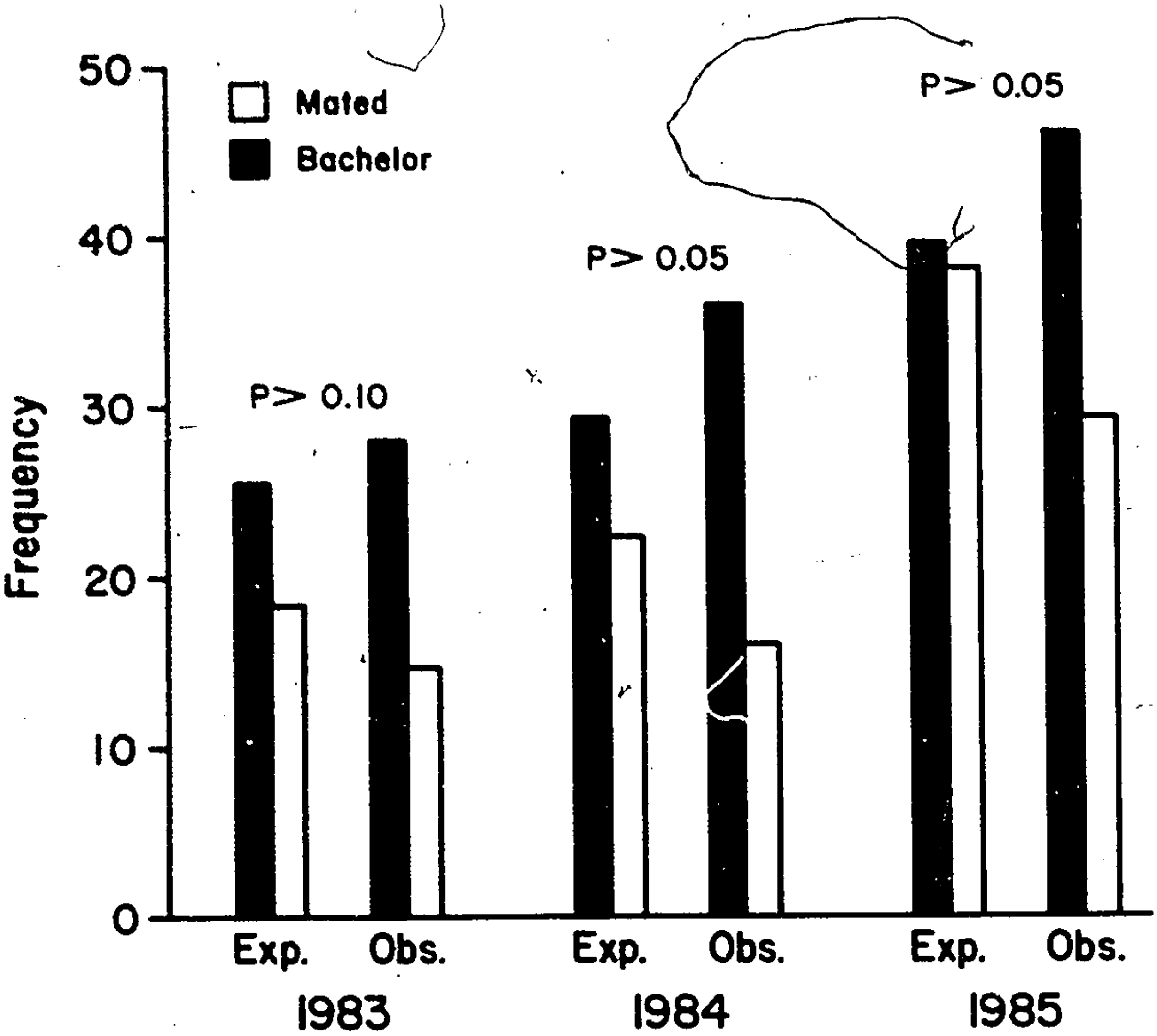

Mean Response Level
0
20
40
60
80
100
120
13
11
7
13
11
7
13
11
7
13
11
7
M 1° 2°
Time to First Response (s)
M 1° 2°
Time to Closest Approach (s)
M 1° 2°
Time to Closest Approach (s)
M 1° 2°
Distance at Closest Approach (m)

Figure 12. Expected and observed frequencies for female choice of mates for each year of the study. The expected frequency is assuming that females choose males randomly with respect to the presence of another female. A X^2 test was used to test for differences between expected and observed frequencies.



Mated
Bachelor
Frequency
50
40
30
20
10
0
P< 0.05
P< 0.005
P< 0.005
Exp.
Obs.
Exp.
Obs.
Exp.
Obs.
1983
1984
1985

Figure 13. Expected and observed frequencies for female choice of mates for each year of the study. The expected frequency is assuming that males are unavailable to second females until their first females are incubating. A X^2 test was used to test for differences between expected and observed frequencies.



50
40
30
20
10
0
Frequency
☐ Mated
■ Bachelor
P> 0.10
P> 0.05
P> 0.05
Exp.
Obs.
Exp.
Obs.
Exp.
Obs.
1983
1984
1985

Figure 14. Expected and observed frequencies for female choice of mates for each year of the study. The expected frequency is assuming that once a male is paired it is unavailable to second females until all other males are paired. A X^2 test was used to test for differences between observed and expected frequencies.

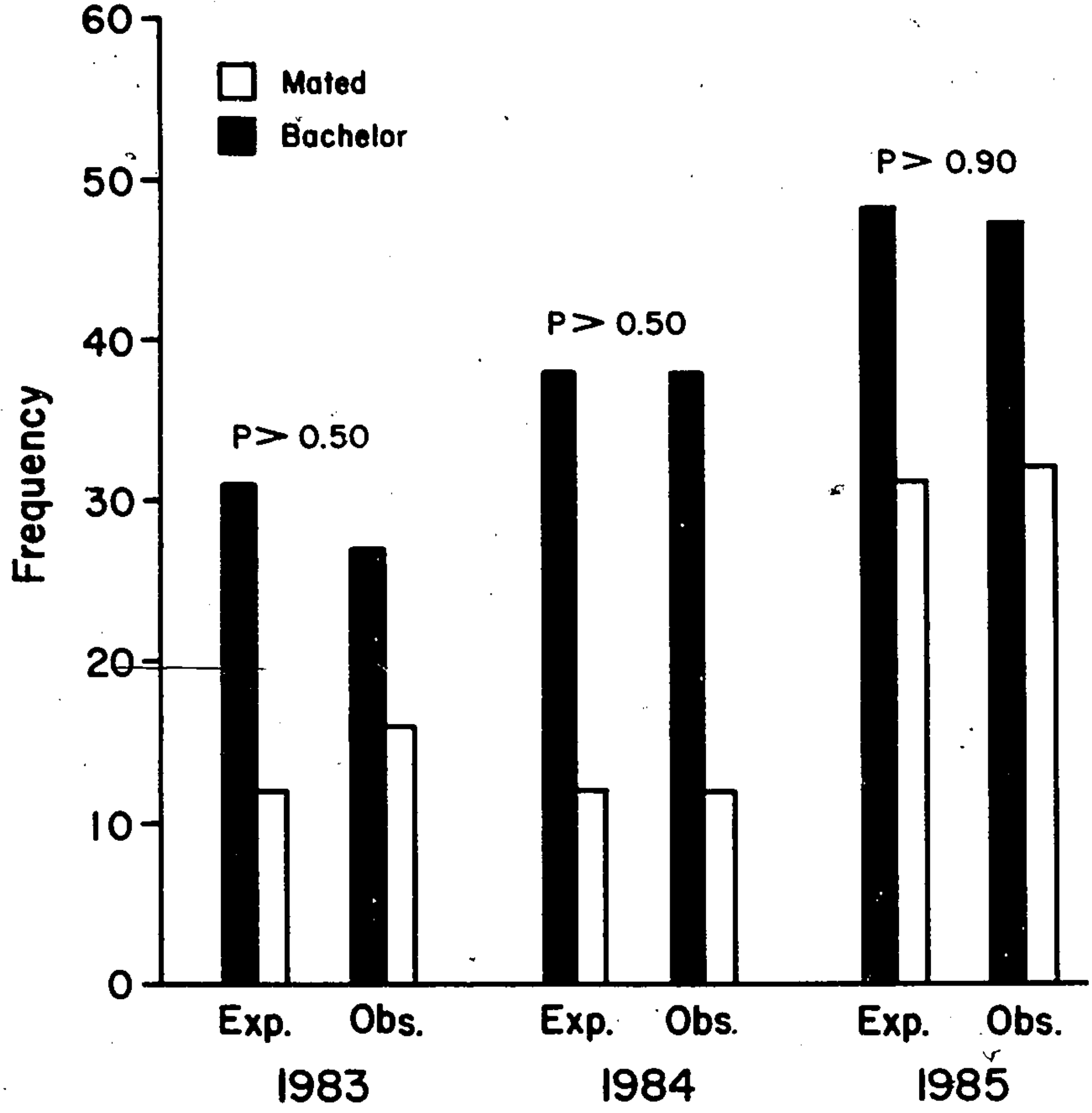

60
50
40
30
20
10
0
Frequency
☐ Mated
■ Bachelor
P> 0.50
P> 0.50
P> 0.90
Exp.
Obs.
Exp.
Obs.
Exp.
Obs.
1983
1984
1985

Figure 15. Order of settlement of first females in relation to the order of settlement of second females on the same territories, at Site 1 and Site 2, in 1983 and 1984.

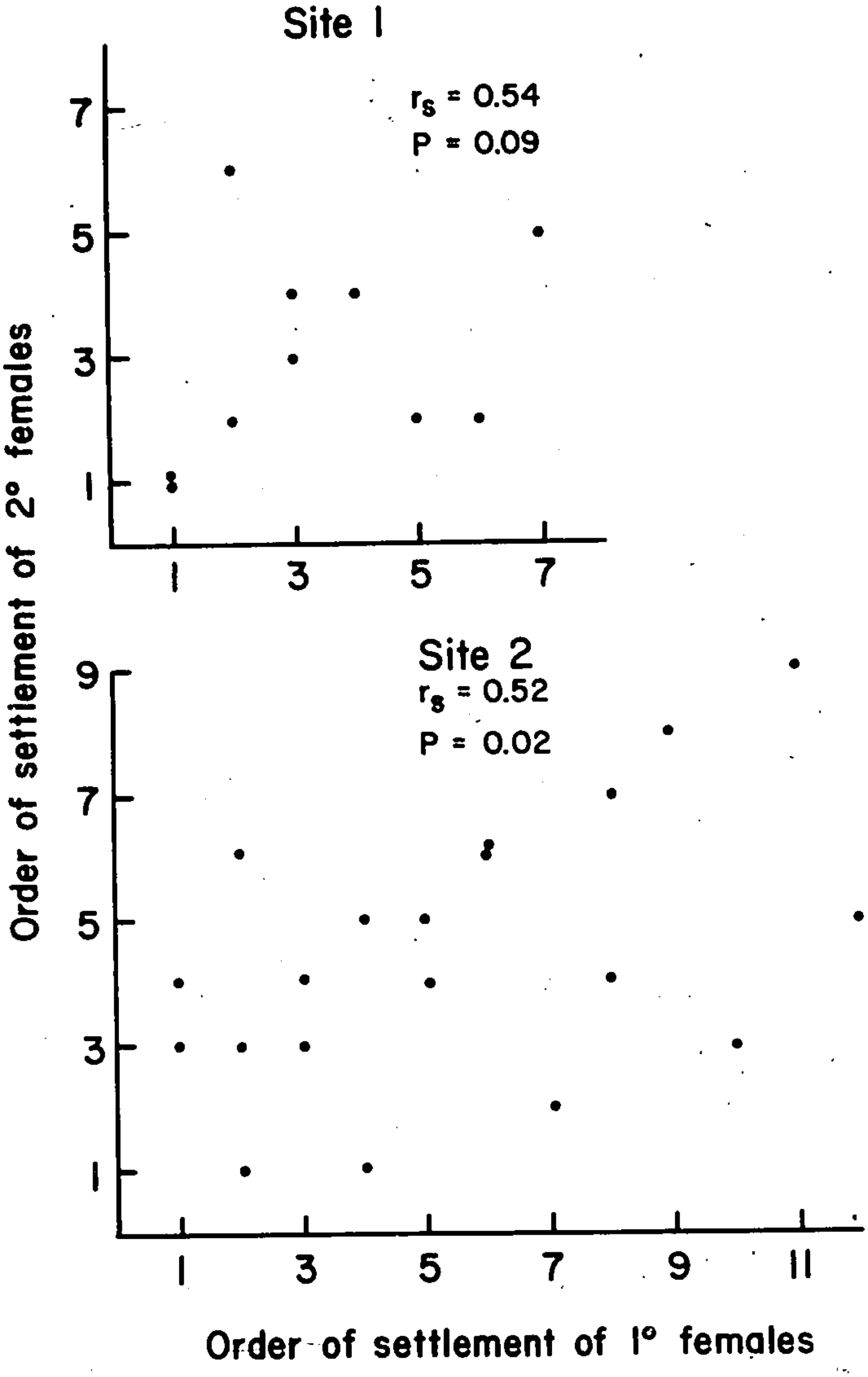

Site 1
r_s = 0.54
P = 0.09
7
5
3
1
1
3
5
7
Site 2
r_s = 0.52
P = 0.02
9
7
5
3
1
1
3
5
7
9
11
Order of settlement of 2° females
Order of settlement of 1° females

Figure 16. Order in which territories were settled in relation to male pairing success (harem size) at Site 1 and Site 2, in 1983 and 1984.

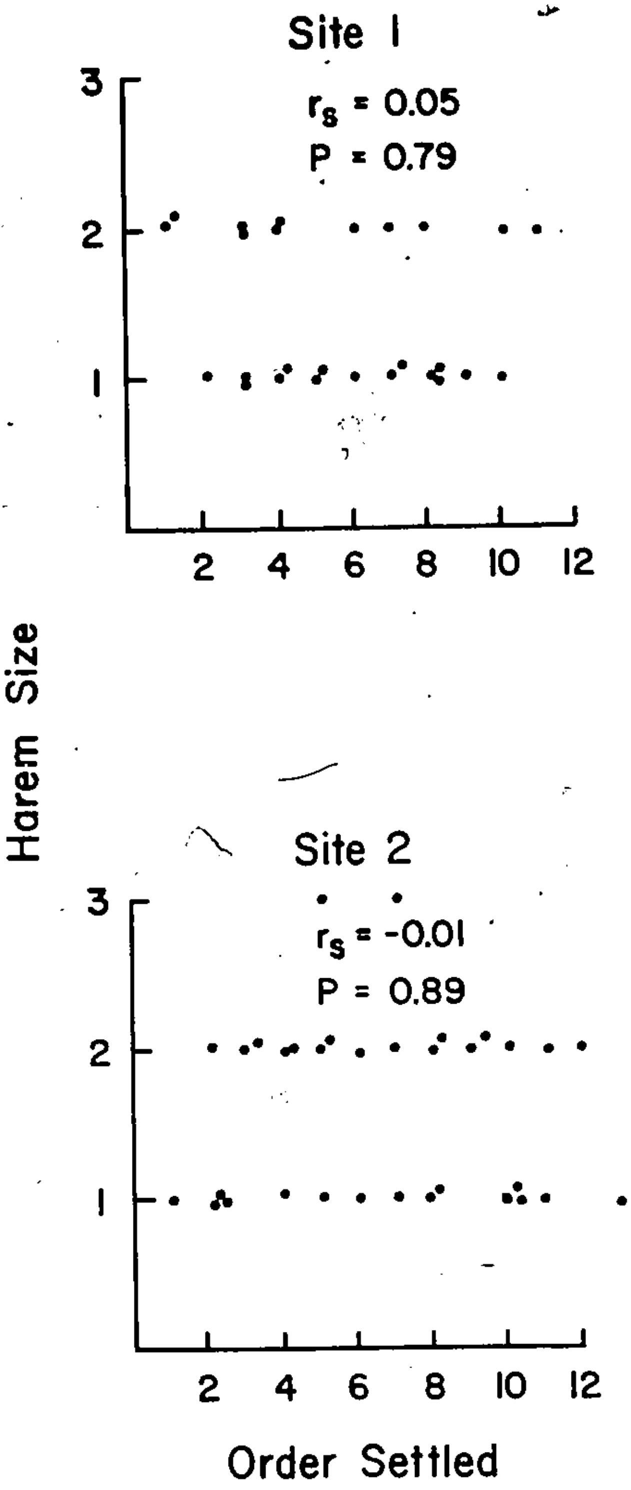

Site 1
$r_s = 0.05$
$P = 0.79$
3
2
1
2
4
6
8
10
12
Harem Size
Site 2
$r_s = -0.01$
$P = 0.89$
3
2
1
2
4
6
8
10
12
Order Settled

Figure 17. Number of young fledged/female in relation to the order of settlement of all females at Site 1 and Site 2, for 1983 and 1984, combined.

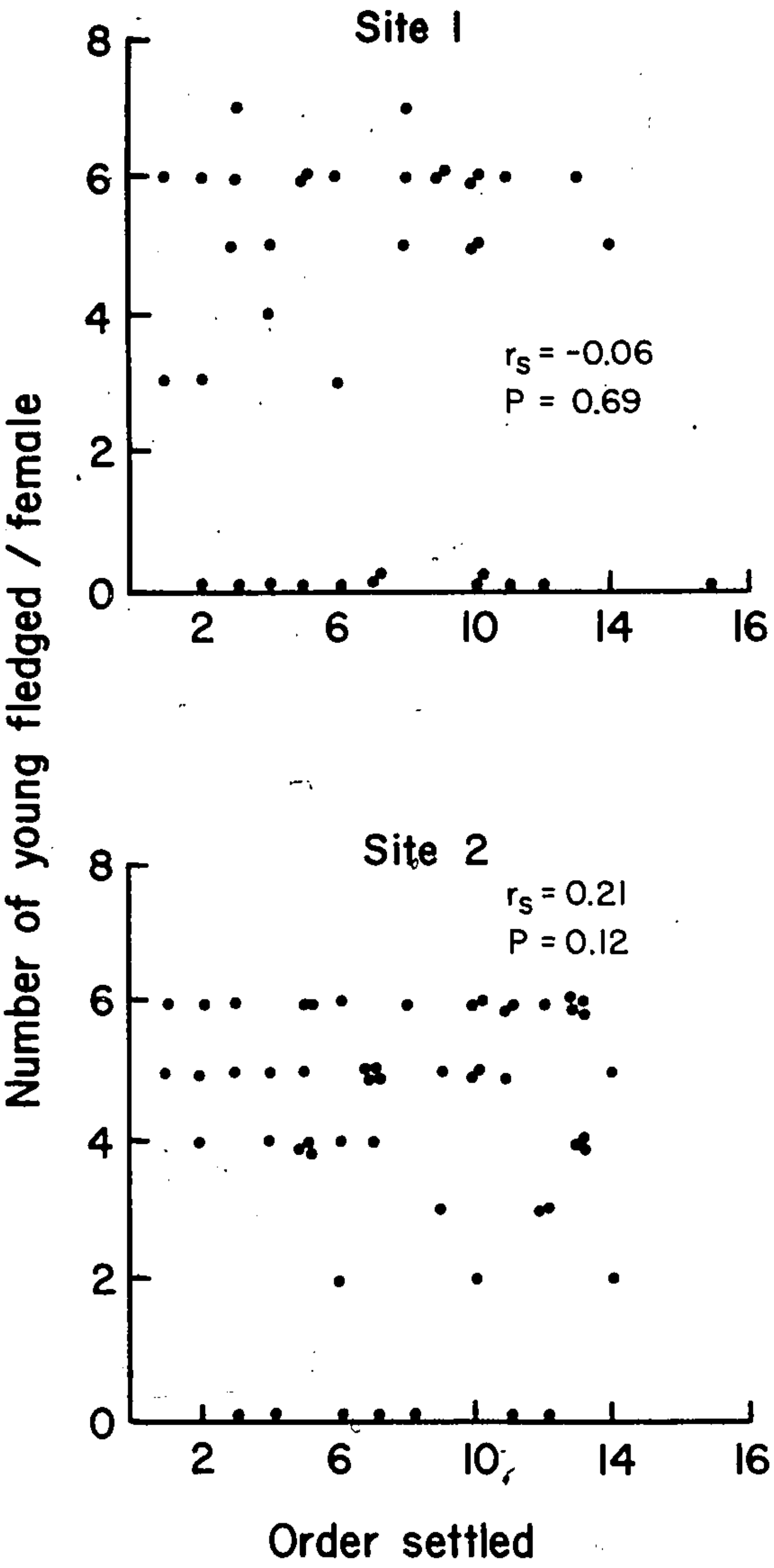

Site 1
r_S = -0.06
P = 0.69
Site 2
r_S = 0.21
P = 0.12
Number of young fledged / female
Order settled
0
2
4
6
8
2
6
10
14
16

Figure 18. Number of young fledged/female in relation to the order of settlement of the last females to settle in each territory, at Site 1 and Site 2, for 1983 and 1984, combined.

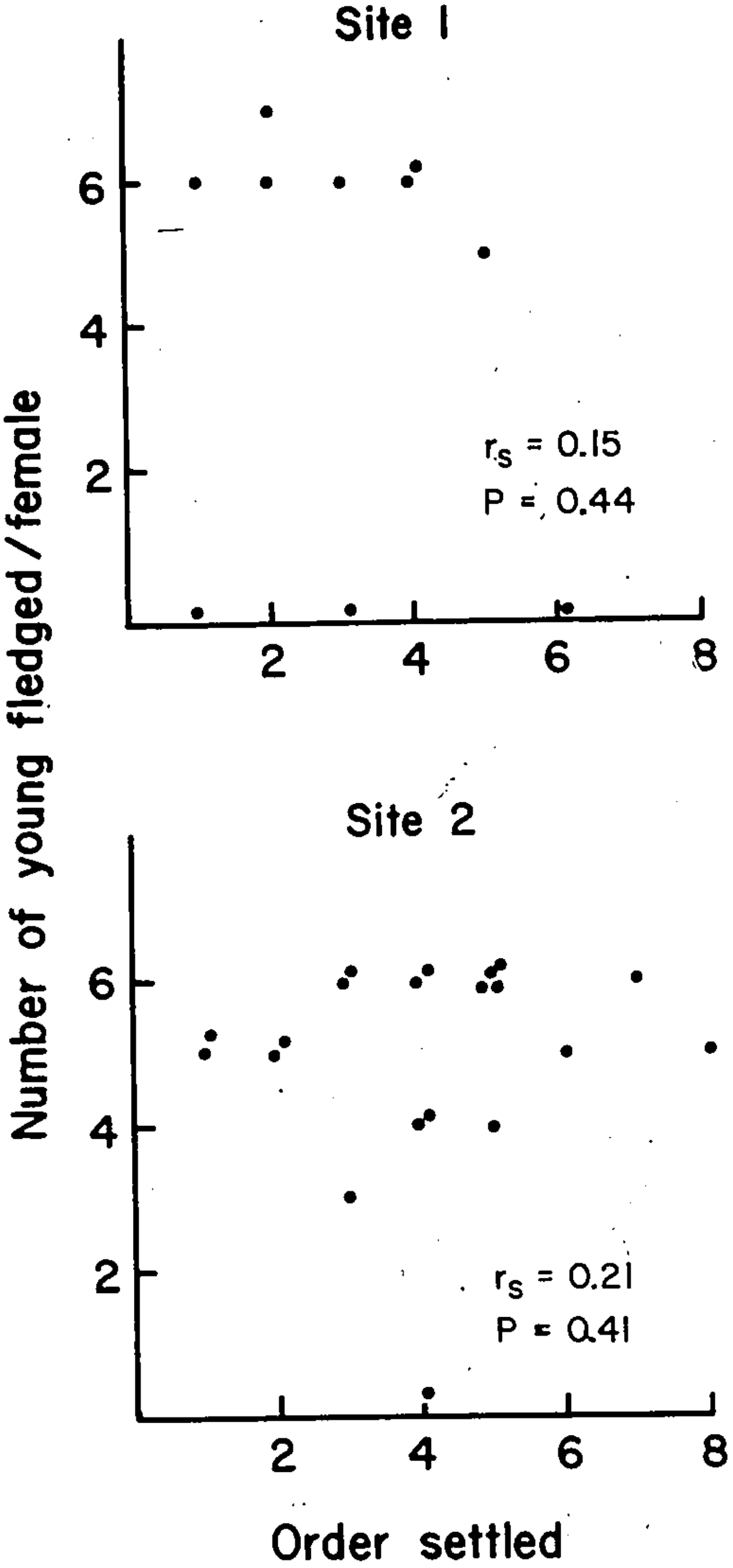

Site 1
6
4
2
2
4
6
8
r_s = 0.15
P = 0.44
Site 2
6
4
2
2
4
6
8
r_s = 0.21
P = 0.41
Number of young fledged / female
Order settled

Figure 19. Number of young fledged/female in relation to the order of settlement of bigamous females, at Site 1 and Site 2, for 1983 and 1984, combined.

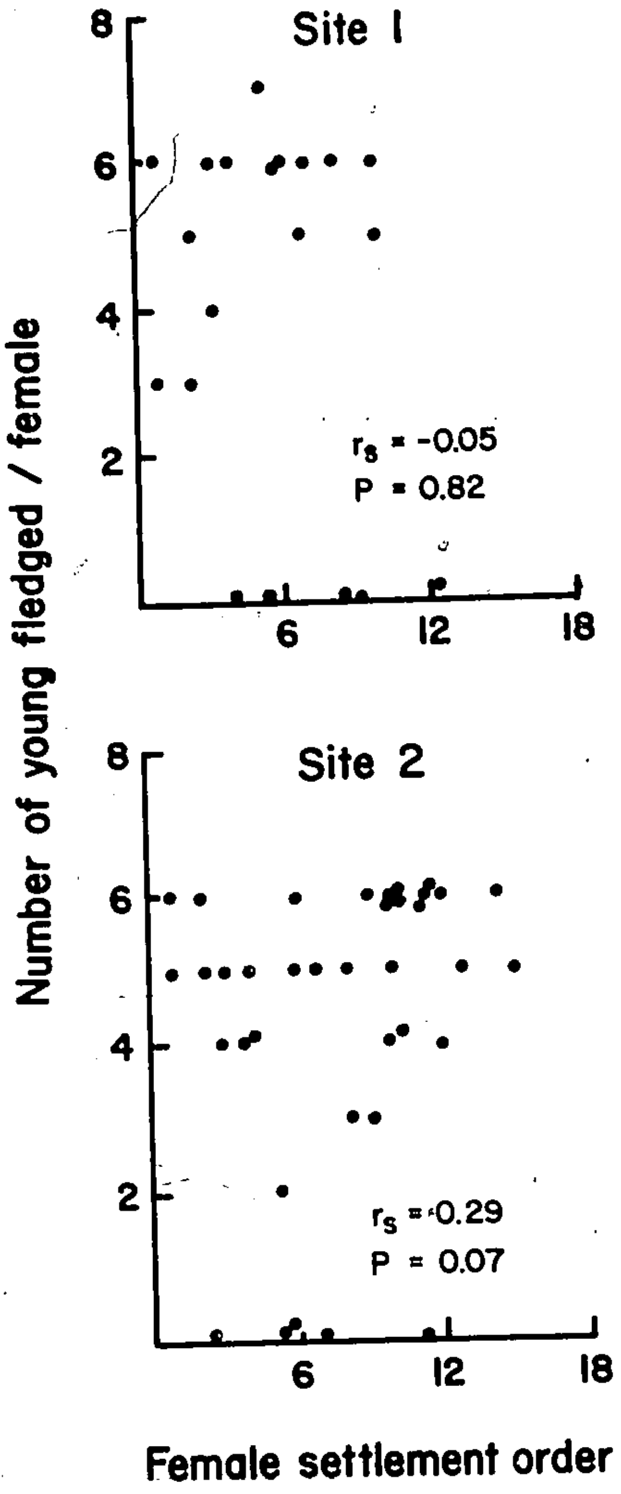

Site 1
Site 2
Number of young fledged / female
Female settlement order
8
6
4
2
6
12
18
r_s = -0.05
P = 0.82
r_s = 0.29
P = 0.07

Table 1. Percent of males of each mating class for Site 1 and Site 2 for 1983, 1984, and 1985 combined, (N). A Mann-Whitney U-test was used to test whether harem sizes differed between sites.

	Site 1	Site 2
Bachelor	11.3 (7)	4.9 (3)
Monogamous	47.5 (28)	41.0 (25)
Bigamous	37.3 (22)	42.6 (26)
Trigamous	3.4 (2)	11.5 (7)

$Z=2.3$ $P=0.01$

Table 2. Percent of males of each mating class for Sites 1 and 2 in 1983, 1984, and 1985, (N). A Mann-Whitney U-test was used to test whether harem sizes differed between sites.

	1983		1984		1985	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
Bachelor	14.3 (2)	11.8 (2)	21.0 (4)	0.0 (0)	3.8 (1)	4.4 (1)
Monogamous	57.1 (8)	23.5 (4)	36.8 (7)	59.2 (13)	50.0 (13)	33.5 (7)
Bigamous	28.6 (4)	58.8 (10)	42.2 (8)	36.3 (8)	38.6 (10)	38.3 (8)
Trigamous	0.0 (0)	5.9 (1)	0.0 (0)	4.5 (1)	7.6 (2)	23.8 (5)
	U=140, P>0.10		U=181.5, P>0.05		U=330, P>0.05	

Table 3. Operational sex ratios for Site 1 and 2 for all years combined. Expected frequencies assuming a 50:50 ratio. Males that were not present until after females settled were not included in the analyses.

	Site 1		Site 2		Both	
	Observed	Expected	Observed	Expected	Observed	Expected
Males	56	67	60	79	120	148
Females	78	67	98	79	176	148
	$\chi^2=3.6$		$\chi^2=9.1$		$\chi^2=10.6$	
	$P>0.05$		$P<0.005$		$P<0.005$	

Table 4. Operational sex ratios for Site 1 and Site 2 for 1983, 1984, 1985. Expected frequencies assuming a 50:50 ratio. Males that were not present until after females settled were not included in the analyses. (1) = Site 1 and (2) = Site 2.

	1983		1984		1985	
	Observed	Expected	Observed	Expected	Observed	Expected
Males (1)	14	14.5	18	20.5	25	32.5
Females (1)	16	14.5	23	20.5	40	32.5
	$\chi^2=0.3$ $P>0.90$		$\chi^2=0.6$ $P>0.50$		$\chi^2=3.4$ $P>0.05$	
Males (2)	16	21.5	22	27	21	29.5
Females (2)	27	21.5	32	27	38	29.5
	$\chi^2=2.8$ $P>0.10$		$\chi^2=1.8$ $P>0.50$		$\chi^2=4.9$ $P<0.05$	

Table 5. Mean (± SD) clutch size, number hatching from all nests, number fledging from all nests, and number fledging from successful nests for Sites 1 and 2, 1983, 1984, and 1985 combined, (N). A Student t-test was used to test for differences between sites.

	Site 1	Site 2	t	df	P
Clutch size	5.78 ± 0.75 (79)	5.56 ± 0.75 (96)	1.95	167	0.06
Hatched from all nests	2.97 ± 2.79 (83)	3.86 ± 2.21 (94)	-2.31	155	0.02
Fledged from all nests	2.30 ± 2.65 (81)	3.42 ± 2.22 (95)	-3.09	156	0.002
Fledged from successful nests	5.08 ± 1.21 (37)	4.53 ± 1.31 (71)	2.10	78	0.03

Table 6. Mean (± SD) clutch size, number hatched from all nests, number fledged from all nests, and number fledged from successful nests for Site 1 and 2 in 1983, 1984, and 1985, (N). * P<0.05 using a Mann-Whitney U-test.

	1983		1984		1985	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
N	19	27	20	37	44	30
Clutch size	5.47 ± 1.46	5.59 ± 0.69	5.60 ± 0.75	5.51 ± 0.69	5.83 ± 0.73	5.60 ± 0.91
Hatched all nests	4.00 ± 2.60	4.80 ± 1.61	3.42 ± 2.79	4.29 ± 2.05	2.43 ± 2.78	2.46 ± 2.25
Fledged all nests	3.68 ± 2.72	4.46 ± 1.63	2.84 ± 2.87	4.21 ± 2.00	1.42 ± 2.25	1.74 ± 1.96
Fledged successful nests	5.38 ± 1.12 (13)	5.10 ± 0.85 (20)	5.40 ± 1.32 (10)	4.87 ± 1.15 (32)	4.57 ± 1.28 (14)	3.57 ± 1.09 (14) *

Table 7. Sources of egg and nestling mortality for all three years of the study combined.

	Egg Losses				Nestling Losses			
Source	N	% of eggs laid	% of egg mortality	% of total mortality	N	% of nestlings	% of nestling mortality	% of total mortality
Predation	188	19.1	50.4	40.2	80	15.5	84.2	15.5
Unhatched	62	6.3	16.6	13.2	----	----	----	----
Weather	43	4.4	11.5	9.1	0	0.0	0.0	0.0
Abandoned	30	3.1	8.1	6.4	0	0.0	0.0	0.0
Fallen	0	0.0	0.0	0.0	2	0.4	2.2	2.3
Unknown	50	5.0	13.4	10.6	13	2.1	13.6	2.7
Total	373	37.9	100.0	79.5	95	18.0	100.0	20.5

Table 8. Number of nests (%) with partial losses and the apparent causes for Site 1 and Site 2 for all years combined.

	Site 1	Site 2	Both
Successful	37	73	110
All eggs fledge	20 (54.1)	29 (39.7)	49 (44.5)
Partial loss	17 (45.9)	44 (60.3)	61 (55.5)
Unhatched eggs	10 (58.8)	43 (97.7)	53 (86.8)
Eggs lost to marsh wrens	4 (23.5)	5 (11.4)	9 (14.8)
Nestlings lost to marsh wrens	1 (5.8)	5 (11.4)	6 (9.8)
Starvation	0 (0.0)	3 (6.8)	3 (4.9)
Fallen nestlings	1 (5.8)	1 (2.3)	2 (3.2)
Losses unknown	2 (11.8)	2 (4.5)	4 (6.6)

Table 9. Mean (±SD) number of days between consecutively settling males and females for Site 1 and Site 2, (N). Differences between sites were compared using a Mann-Whitney U-test.

	Female			Male		
Year	Site 1	Site 2	P	Site 1	Site 2	P
1983	2.57 ± 1.71	1.53 ± 0.96	>0.05	1.40 ± 0.96	1.36 ± 0.67	>0.05
	(7)	(13)		(10)	(11)	
1984	1.54 ± 0.82	1.08 ± 0.28	>0.05	1.28 ± 0.49	1.29 ± 0.49	>0.05
	(11)	(12)		(7)	(7)	
1985	1.15 ± 0.37	1.33 ± 0.61	>0.05	1.50 ± 0.84	1.80 ± 1.30	>0.05
	(13)	(15)		(6)	(5)	
All Years	1.61 ± 1.08	1.31 ± 0.69	0.42	1.39 ± 0.78	1.43 ± 0.79	0.83
	(31)	(40)		(23)	(23)	

Table 10. Number of males and females settling at the two sites versus numbers expected if individuals settled at the two sites in proportion to the available area, 1.= Site 1 and 2. = Site 2.

		Males			Females		
		Observed	Expected	X^2/P	Observed	Expected	X^2/P
1983	1.	14	19.8	4.7	16	27.5	13.3
	2.	17	11.2	$P<0.05$	27	15.5	$P<0.001$
1984	1.	19	22.9	1.5	23	30.8	4.3
	2.	22	18.1	$P>0.30$	32	24.2	$P<0.05$
1985	1.	28	27.4	0.3	39	56.7	12.3
	2.	21	21.6	$P>0.70$	64	46.3	$P<0.001$
All Years	1.	61	67.8	1.6	78	112.5	24.1
	2.	60	53.2	$P>0.30$	123	88.5	$P<0.001$

Table 11. Mean (± SD) of clutch sizes, feeding rates, nestling weights and number fledged from the successful nests of females with and without male assistance in feeding young and defending the nesting area. * difference is significant at $P=0.01$, (N).

Female Status	Clutch Size	Feeding Rate/30 min	Nestling Weight (g)	Number Fledged
Females with male feeding	6.2 ± 0.6 (10)	5.7 ± 3.6 (10)	9.1 ± 1.2 (54)	5.5 ± 0.7 (10)
Females without male feeding	5.8 ± 0.7 (34)	6.9 ± 2.6 (64)	8.9 ± 1.5 (86)	4.8 ± 1.3 * (57)
Females with male defense	6.1 ± 0.9 (14)	--------	---------	4.8 ± 1.3 (15)
Females without male defense	5.8 ± 0.7 (20)	--------	---------	4.5 ± 1.4 (44)

Females mated to males that fed were not included in analyses for defending males.

Table 12. Simple correlation coefficients for male pairing success and measures of male quality. N=50

Variables	Correlation Coefficient	P
Condition	0.14	> 0.50
Tarsus length	0.09	> 0.50
Max. number courtship nests	0.13	> 0.50
Courtship nests before females	0.03	> 0.50
Song rate over the season	-0.20	> 0.20
Time spent chasing yellowheads	0.08	> 0.50
Time spent singing over the season	-0.25	> 0.10
Time spent building nests	0.07	> 0.50
Time spent foraging over the season	0.21	> 0.20

Table 13. Response levels of male marsh wrens that assisted female wrens with feeding and males that did not feed young, to playbacks of female wrens, (N). Differences were compared using a Mann-Whitney U test.

Response	Feeding Male	Non-feeding Male	
Time to First Response (s)	17.5 ± 15.0 (4)	18.5 ± 14.6 (7)	U=16, P>0.10
Time to Closest Approach (s)	27.5 ± 28.7 (4)	40.0 ± 26.5 (7)	U=16.5, P>0.10
Time at Closest Approach (s)	80.0 ± 40.0 (4)	48.5 ± 29.1 (7)	U=20, P>0.10
Distance at Closest Approach (m)	3.3 ± 1.5 (4)	3.5 ± 2.4 (7)	U=14, P>0.10

Table 14. Simple correlation coefficients for territory quality variables and male pairing success. N=50.

Variable	Correlation coefficient	P
Max. territory size	0.00	> 0.50
Density of veg. at courtship nests	-0.38	< 0.005
Mean height veg. at courtship nests	0.19	> 0.20
Height of courtship nests	0.22	> 0.20
Prop. cattail on territory	-0.26	> 0.10
Prop. bulrush on territory	0.17	> 0.50
Prop. water on territory	0.00	> 0.50
Density of veg. on territory	-0.10	> 0.50

Table 15. Mean (± SD) density of vegetation at courtship nests and on the territory, (N). Differences in density were compared using a Mann-Whitney U-test.

Density	Site 1	Site 2	P
Territory density	14.4 ± 2.6 (24)	5.9 ± 3.8 (22)	<0.001
Nest site density	5.8 ± 2.2 (24)	2.5 ± 0.9 (24)	<0.001
P	<0.001	<0.001	

Table 16. Mean (± SD) number of insects, mean number of species and mean length (mm) of insects collected on sticky traps at three patches each of bulrush/cattail and pure phragmites pure cattails. Samples include insects collected at 50 and 100 cm high plates.

	Bulrush/Cattail			Phragmites			Cattail		
	1	2	3	1	2	3	1	2	3
Number of insects	25.0 ± 21.0	20.1 ± 19.9	14.7 ± 15.1	9.4 ± 3.7	11.8 ± 9.6	13.7 ± 10.9	25.6 ± 21.4	23.1 ± 21.6	23.5 ± 22.1
N	(24)	(28)	(28)	(8)	(20)	(18)	(29)	(29)	(30)
	F=1.94, df=2,79 P>0.05			F=0.59, df=2,45 P>0.05			F=0.12, df=2,87 P>0.05		
Number of species	4.1 ± 1.7	4.0 ± 1.8	3.6 ± 1.7	3.5 ± 0.8	4.4 ± 2.8	3.8 ± 2.2	4.2 ± 1.7	4.5 ± 1.8	4.3 ± 1.9
N	(23)	(28)	(28)	(8)	(20)	(18)	(29)	(29)	(30)
	F=0.52, df=2,78 P>0.05			F=0.46, df=2,45 P>0.05			F=0.25, df=2,87 P>0.05		
Length (mm)	3.4 ± 0.8	3.1 ± 0.7	3.2 ± 0.9	3.1 ± 0.9	3.0 ± 0.6	2.9 ± 0.7	4.5 ± 0.2	4.2 ± 1.9	4.6 ± 2.0
N	(25)	(29)	(29)	(29)	(30)	(28)	(10)	(17)	(16)
	F=0.76, df=2,80 P>0.05			F=0.10, df=2,40 P>0.05			F=0.34, df=2,85 P>0.05		

Table 17. Spearman rank correlation coefficients for the number of females and order in which females settled on arbitrary territories between years and the number of nests depredated between years on arbitrary territories. I increased the area sampled at Site 2 in 1984. For this reason I cannot compare the order of settlement from 1983 with 1984 or 1985.

	Site 1			Site 2		
	1983vs1984	1984vs1985	1983vs1985	1983vs1984	1984vs1985	1983vs1985
Harem size	0.28 (36)	-0.19 (36)	0.28 (36)	0.76 * (16)	0.22 (27)	0.14 (17)
Order of settlement	-0.11 (8)	0.20 (19)	0.37 (11)	----	0.08 (29)	----
Predation	1.00 * (5)	0.25 (15)	-0.04 (5)	0.56 (11)	0.09 (14)	0.33 (9)

* significant correlation at $P<0.05$

6

Table 18. Mean (±SD) water depth (cm), vegetation density, height of tallest supporting vegetation (cm), and height of the majority stems (cm) supporting breeding and courtship nests. Nests were compared using a Mann-Whitney U-test, (N).

	Site 1			Site 2		
	Breeding	Courtship	P	Breeding	Courtship	P
Water depth	20.5 ± 12.6 (26)	15.5 ± 8.0 (33)	0.07	20.6 ± 7.5 (33)	20.7 ± 4.6 (39)	0.53
Veg. density	4.8 ± 3.6 (26)	5.7 ± 1.9 (33)	0.06	2.6 ± 2.1 (34)	2.7 ± 1.2 (38)	0.37
Tallest stem	134.5 ± 28.5 (26)	125.5 ± 18.3 (33)	0.27	162.2 ± 17.9 (34)	161.7 ± 15.6 (39)	0.26
Majority stem	106.5 ± 14.2 (26)	105.4 ± 15.7 (33)	0.38	123.0 ± 18.1 (33)	124.9 ± 11.0 (39)	0.19

Table 19. Mean (±SD) level of response for all female marsh wrens during each nesting stage. Differences between groups were tested using a Kruskal-Wallis test. Sample sizes are included in parentheses. Significant differences between means as determined by a Dunn's Multiple Range test ($P<0.05$) are represented by different letters in parentheses.

	Pre-laying	Laying	Incubation	
Time to First Response (s)	34.5 ± 28.0 (22, a)	23.3 ± 21.6 (6, a)	72.8 ± 35.0 (7, b)	$H=7.3$ $P<0.05$
Time to Closest Approach (s)	54.7 ± 34.8 (19, a)	45.0 ± 31.0 (6, a)	103.3 ± 19.6 (7, b)	$H=12.9$ $P<0.005$
Time at Closest Approach (s)	34.5 ± 28.2 (22)	48.0 ± 39.6 (5)	11.7 ± 14.7 (6)	$H=5.3$ $P>0.05$
Distance at Closest Approach (m)	2.84 ± 2.90 (25, a)	2.00 ± 1.70 (5, a)	6.60 ± 3.10 (5, b)	$H=9.6$ $P<0.01$

Table 20. Spearman rank correlation coefficents for the number of days between primary and secondary females and (1) the strength of response to playbacks of female intruders and (2) the distance (m) to the closest active nest and strength of response. * significance at $P < 0.05$, (N).

	Days	P	Distance	P
Time to First Response (s)	0.14 (16)	0.53	-0.16 (21)	0.48
Time to Closest Approach (s)	0.43 (15)	0.11	0.04 (21)	0.84
Time at Closest Approach (s)	-0.17 (15)	0.54	-0.07 (21)	0.76
Distance at Closest Approach (m)	0.09 (12)	0.73	-0.54 (18)	0.05 *

Table 21. Observed and expected frequencies for female choice with respect to male status, assuming: a) females settle at random with respect to male status; b) females settle with mated males after their first females are incubating; and c) females settle with mated males after all males have one mate.

	Number of Females Settling			
	Observed	Expected[a]	Expected[b]	Expected[c]
Bachelor Males	112	76.7	93	117
Mated Males	60	95.3	79	55
		$X^2=29.3$ $P < 0.001$	$X^2=8.4$ $P < 0.025$	$X^2=0.66$ $P > 0.50$

Table 22. Mean (± SD) number of young fledged for males of different harem sizes and females of different status, (N)

	Number of Females/Male			
Male Success	1	2	3	H/P
Site 1	2.88 ± 2.81 (26)	6.75 ± 3.35 (16)	9.00 ± 7.07 (2)	6.94 P<0.01
Site 2	3.52 ± 1.77 (19)	7.88 ± 2.61 (25)	12.80 ± 5.67 (4)	38.7 P<0.001
Female Success				
Site 1	2.88 ± 2.81 (26)	2.57 ± 2.06 (21)	2.95 ± 2.33 (2)	2.1 P>.05
Site 2	3.52 ± 1.77 (19)	3.69 ± 1.65 (26)	4.20 ± 1.89 (4)	3.1 P>0.05

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