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FEMALE MATE CHOICE IN THE HOUSE WREN

by

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A thesis submitted to the Department of Biology in partial
fulfillment of the requirements for the degree of Master of
Science

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Chapter 3: Female mate choice strategies in the house wren.

Abstract

This study examined factors determining choice of a breeding situation by female House Wrens, <u>Troglodytes aedon</u>. The study consisted of three parts: (1) descriptive data on the breeding ecology of the species were collected to identify environmental variables affecting female fitness and female choice of a breeding situation, (2) experimental tests were designed to directly test the effect of these variables on female choice, and (3) a simulation approach was used to determine strategies employed by females to select a breeding situation.

Descriptive data suggest that predation was the most important factor reducing house wren reproductive success at Presqu'ile Provincial Park, Ontario, Canada. Although mammalian predation was relatively frequent, losses due to conspecific nest attacks appeared more important. Vegetation density around boxes influenced chances of success. Nests built in sparse vegetation suffered less predation than those in dense vegetation. It is suggested that the greater success of house wrens in sparse vegetation results from their more effective nest defence against intruding conspecifics. Two additional factors that

apparently influenced female fitness were male wing-length and density of vegetation on male territories. Male wing-length was positively correlated with nestling weight. Nestlings were also heavier when raised on densely vegetated territories. Nestling weight was used as a measure of post-fledging survival.

Data on female choice of nesting sites indicated that female house wrens preferred boxes in sparse vegetation, presumably because their success is higher at these sites. This preference was also exhibited by males. Because vegetation density had the strongest effect on female fitness, its role in female choice was tested experimentally. House wrens were given an opportunity to select a box from a group of 3 boxes that differed only in the density of the surrounding vegetation. This study demonstrated that individuals of both sexes exhibited a strong preference for the sparse nest sites. These findings were consistent with results of the descriptive study and demonstrated that female mate choice in house wrens is largely based on the quality of boxes defended by males. As indicated by descriptive and experimental data, female choice of a breeding situation was not affected by the other 2 factors identified in the descriptive study as significant determinants of female fitness (i.e. male wing-length and

vegetation density on territories).

The simulation study was designed to determine strategies female house wrens use to select a nesting site. Six hypothetical tactics were examined: (1) random choice, (2) the best-of-all situations strategy, (3) a minimum criterion tactic, (4) a sequential comparison tactic, (5) an area unlimited pool comparison tactic, and (6) an area limited pool comparison tactic. Results of this study suggest that female house wrens judged boxes on a relative basis rather than against a fixed threshold. Females, however, appeared to restrict their choice to a small number of boxes. These findings contradict the generally accepted assumption that, in birds, females sample all prospective situations before selecting one.

Résumé

Dans cette thèse, je me suis intéressé aux facteurs déterminant le choix d'une situation de reproduction par la femelle troglodyte familier (<u>Troglodytes aedon</u>).
L'étude comprend 3 parties:
(1) Approche descriptive: présentation de données sur l'écologie de reproduction de l'espèce, rassemblées afin d'identifier les variables environnementales affectant le succès des femelles et leur choix d'une situation de reproduction.
(2) Approche expérimentale: évaluation de ces variables sur le choix des femelles à l'aide de tests concus à cet effet.
(3) Approche par simulations informatisées: visant a déterminer la stratégie employée par les femelles pour sélectionner une situation de reproduction.

Les données descriptives suggèrent que la prédation représente le facteur majeur limitant le succès reproducteur du troglodyte au parc provincial de Presqu'ile (Ontario, Canada). Les pertes dues aux attaques des conspecifiques étaient plus importantes que celles dues à la prédation par les mammifères, elles-mêmes relativement importantes. Cependant, les nids construits en vegetation clairsemée étaient moins sujets à la prédation que ceux situés en

végétation dense. La plus grande efficacité dans la défense contre les attaques conspécifiques en végétation clairsemée pourrait expliquer le meilleur succès des troglodytes à ces sites. Plusieurs auteurs ont corrélé positivement le poids des jeunes avec leurs chances de survie après le départ du nid. Ce postulat nous permet d'inclure deux facteurs supplémentaires relatifs au succès des femelles dans la mesure où ils ont été tous deux corrélés positivement avec le poids des jeunes: (1) la longueur d'aile du mâle et (2) la densité de végétation sur le territoire du mâle.

D'après les données, les femelles troglodyte préféraient les nichoirs situés en végétation clairsemée, probablement à cause de leur plus grand succès dans ces zones. Les mâles montraient la même tendance. La densité de végétation étant le facteur principal influençant le succès reproducteur des femelles, son rôle dans le choix des femelles a donc été testé expérimentalement: chaque troglodyte pouvait choisir un nichoir parmi un groupe de trois, ces trois nichoirs différant seulement par la densité de végétation alentour. Les mâles comme les femelles montrèrent une préférence nette pour les sites de nidification à faible densité de végétation. Ce résultat concorde avec ceux de l'étude descriptive et montre que le choix du mâle chez la femelle troglodyte dépend fortement de la qualité du nichoir défendu par le mâle. D'après les

informations descriptives et expérimentales les deux autres facteurs identifiés comme déterminant du succès de la femelle (longueur d'aile du mâle et densité de végétation sur le territoire) n'affectent pas le choix de la femelle.

L'étude par simulations vise à déterminer la stratégie utilisée par les femelles troglodyte lors de la sélection du site de nidification. J'ai examiné 6 tactiques hypothétiques: (1) choix au hasard, (2) choix de la meilleure situation parmi toutes, (3) choix au hasard au-delà d'un seuil, (4) choix optimal par comparaison séquentielle, (5) choix optimal parmi n mâles et (6) choix optimal à l'intérieur d'un périmetre limité. Les résultats de cette étude suggèrent que les femelles troglodyte ont évalué les nichoirs sur une base comparative plutôt qu'à partir d'un seuil prédéterminé. Cependant, les femelles semblent avoir limité leur choix à un petit nombre de nichoirs. Ces conclusions infirment le postulat généralement admis selon lequel, chez les oiseaux, la femelle examine toutes les situations offertes pour en choisir une.

GENERAL INTRODUCTION

Darwin (1871) viewed sexual selection as distinct from natural selection. He argued that the driving force of the former was social rather than environmental. In the past 30 years, there has been a considerable amount of work concerned with testing this theory. Results of many studies suggest that sexual selection has played an important role in bringing about sexual differences in morphology and behavior (Searcy and Yasukawa 1983).

According to Darwin (1871) there are two mechanisms by which sexual selection could operate: (1) the non-random choice of mates (intersexual selection or epigamic selection) and (2) competition among members of the same sex for access to mates (intrasexual selection). More recently, Darwin's sexual selection theory has been reinterpreted in terms of parental investment (Bateman 1948, Maynard Smith 1956, Fisher 1958, Trivers 1972). When asymmetries exist in the amount of parental investment provided by each parent, members of the less investing sex (usually the male) are expected to compete for access to the other sex. In contrast, members of the more investing sex (usually the female) are expected to make choice from among potential mates. These predictions have now received some support (e.g. Burk 1983, Thornhill and Alcock 1983, Johnson and Hubbell 1984, Borgia 1985a-b, Borgia and Gore 1986, Lawrence 1986, Robertson 1986).

Current sexual selection theory holds that females may choose mates on the basis of male attributes that are important for their reproductive success. These attributes could be divided into three groups: (1) quality of territory males control, (2) parental quality, and (3) genetic quality (Borgia 1979, Searcy 1982). Material benefits such as resources or parental care can directly affect the number and condition of young a female could produce. In contrast, male genetic quality can benefit a female's success only indirectly through the fitness of the young. Since heritability of fitness is expected to be low (Falconer 1960, Searcy 1982), a choice based on male genetic quality should yield low benefit to a female. Male genetic quality, therefore, should have an important effect on mate choice only in species where males do not provide resources or parental care (Searcy and Yasukawa 1983).

In resource-defence mating systems, males defend resources important for female reproduction (Emlen and Oring 1977). When resource quality varies, females may preferentially mate with males possessing resources of high quality. Several studies have reported correlations between male mating success and resource holding by males (e.g. Verner 1964, Verner and Willson 1966, Zimmermen 1966, Verner and Engelsen 1970, Martin 1974, Pleszcynska 1978, Wittenberger 1980, Nagata 1986, and references in Thornhill and Alcock 1983). However, since in many species, male and resource quality are likely to be correlated, it has been difficult to separate their effect in female choice (Orians 1969, Christy 1983, Hedrick 1986). Hence, little information exists on specific criteria females use to discriminate among potential mates (Halliday 1983).

While most studies on mating systems have been interested in identifiying criteria used for making mate choice, few data exist concerning the tactics involved in gathering information about prospective mates (but see Brown 1981). Since Orians' (1969) model on polygyny, it has become axiomatic to most studies on mating systems that females choose from among all potential mates in the population. Theoreticians, however, have challenged this view by proposing alternative strategies females may use to select mates (Janetos 1980, Janetos et Cole 1981, Wittenberger 1983). Brown's (1981) study on mottled sculpins (Cottus bairdi) provides evidence that females may use a simpler strategy to select mates than the one of sampling all males.

In this study, I examined female mate choice in a resource defence species, the house wren (Troglodytes aedon). The two main questions that are addressed are: (1) What are the cues that females use to select their mates? and (2) What strategies do females employ to sample potential mates?

The house wrens is a suitable candidate for this study for several reasons. First, it tolerates human activities (Kendeigh 1941, 1952). Second, it readily breeds in boxes. Thus, nests are easy to find and site quality can be manipulated. Finally, females exhibit a low degree of site fidelity (Drilling 1984, Fink et al. 1986). Female mate choice, therefore, is not confounded by a territory tenacity factor (Eliason 1986). A further description of the breeding ecology of the species is given in the first chapter.

The thesis is subdivided into 3 chapters dealing with different aspects of female choice. In chapter one, I examined house wren reproductive success by addressing the following questions: (1) What are the main causes of nesting losses in house wrens? and (2) Do characteristics of male, female and territory quality correlate with reproductive success? In the second chapter, both descriptive and experimental approaches were used to test whether females choose mates on basis of attributes important for their reproductive success. Finally, in chapter three, I investigated tactics of mate choice by simulating possible choice strategies and comparing results of these simulations to the pattern of choice observed in the breeding population.

Chapter one

MORTALITY FACTORS AND CORRELATES OF REPRODUCTIVE SUCCESS IN THE HOUSE WREN

INTRODUCTION

Recent studies have attempted to identify characteristics that birds use when selecting a breeding situation (e.g. Verner 1964, Weatherhead and Robertson 1977, Best 1977, Pleszczynska 1978, Wittenberger 1980, Bedard and Lapointe 1984a, Askenmo 1984, Nagata 1986). These characteristics include features of the mate or of the territory (Searcy 1979). Whether or not a given characteristic is used to select a mate depends in part on its effect on reproductive success (Searcy 1979). Hence, knowledge of the sources of mortality and of the ecological correlates of reproductive success are critical to understanding the observed life-history tactic of a species.

The house wren (<u>Troglodytes</u> <u>aedon</u>) is an insectivorous, double brooded, passerine which breeds in forested areas of the North-American temperate zone. This cavity-nesting wren readily uses nest boxes and is very tolerant of human activities (Kendeigh 1952). There is no evident sexual dimorphism in plumage but males tend to be slightly larger than females. The first males usually arrive to the breeding ground a week before the first females. Settlement of both sexes, however, is largely staggered in time (Kendeigh 1941). Site fidelity of females is generally low (Drilling 1984, Fink et al. 1987). In contrast, males often return to the same breeding area for 2-3 subsequent years (Kendeigh 1941). Males defend all-purpose territories centered around one or a few cavities (Kendeigh 1941). Although, males do not incubate, they are closely attentive to the nest and commonly assist females with feeding nestlings (Kendeigh 1952). House wrens often destroy conspecific eggs or nestlings (Sherman 1925, Kendeigh 1941, Belles-Isles and Picman 1986a). Nonetheless, the impact of house wrens on conspecific reproductive success has been ignored by most recent studies (e.g. Drilling and Thompson 1984, Fink et al. 1987, but see Freed 1986).

In this chapter, I examined house wren reproductive success by addressing the following questions: (1) What are the main causes of nesting losses? and (2) Can variation in measures of reproductive success be related to habitat and parental characteristics?

METHODS

STUDY SITE

Data were collected during spring and summer of 1985 at Presqu'ile Provincial Park, Northumberland County, Ontario, Canada. In late April, 92 identical boxes (11 x 14 x 20 cm, entrance diameter = 3 cm) were distributed along two transects separated by 25 m. Both transects ran through a deciduous forest (65 boxes) and adjacent sand dunes (27 boxes), the total area encompassing about 17 ha. Nest boxes faced southeast, were approximately 1.5 m above ground, and were separated from each other by about 35 m. Boxes were attached to trees, or in the absence of trees, to 5 cm x 5 cm wooden poles.

The forest was primarily hardwood with sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), hop hornbeam (*Ostrya virgniana*), red oak (*Quercus rubra*), black ash (*Fraxinus nigra*) and red maple (*Acer rubrum*). The undergrowth was dense and supported a large diversity of herbaceous communities. The dunes were mainly forested with white cedar (*Thuja occidentalis*), cottonwood (*Populus deltoides*), and eastern red cedar (Juniperus virginiana). The undergrowth was relatively simple with common junipers (Juniperus communis), wild grape (Vitis riparia), and poison ivy (Rhus radicans) as dominant plants.

MEASURES OF REPRODUCTIVE SUCCESS

Every second day, from 27 April to 23 August, I recorded nest contents at all boxes. I concluded that nestlings had fledged if they were present at 15 or more days of age and then disappeared (Kendeigh 1941, Fink et al. 1987). Fledging success was considered to be the number of young fledged. A nest was successful if it fledged at least one young. When nest contents disappeared before the expected fledging date (see Kendeigh 1941), I assumed that the nest was depredated. Depredation by wrens was implied when eggs with holes were discovered and when clutches disappeared but the nesting material was intact (Belles-Isles and Picman 1986a). A nest was considered depredated by a mammal when broken shells or partially eaten young were discovered and when nesting material was pulled out or nest boxes were pulled down. Clutches were considered abandoned if cold eggs were present in at least two subsequent visits. If abnormally light nestlings were found dead in their nest, I assumed they starved.

Survival from fledging to the first breeding season is another important component of breeding performance (Searcy 1982). Survival rates are difficult to determine. To circumvent this problem, I used nestling weight as a correlated measure. Variation in nestling fat reserves has been proposed to yield differences in ability to confront stressful conditions (e.g. Perrins 1965, Lack 1966, von Haartman 1971, O'Connor 1976, Nur 1981, 1984). To avoid premature nest departure, young were weighed 8 days after the estimated hatching date (brood-day 8, see Kendeigh 1941).

CORRELATES OF REPRODUCTIVE SUCCESS

Male and female physical characteristics

Males were mist netted or trapped (Picman 1980a) usually within a few days of arrival. Females were captured as soon after egg-laying as possible using a box trap. All females were captured in mid-afternoon. Captured wrens were marked with a distinctive combination of colored plastic leg-bands. Birds were sexed by the presence of a cloacal protuberance (Wolfson 1952) or brood patch (Bailey 1952), and by subsequent behavior (Canadian Wildlife Service and

U.S. Fish and Wildlife Service 1977). At the time of banding, I recorded measurements of 4 variables. Weight was estimated to the nearest 0.25 g. Flattened wing-length, tarsus-length, and culmen-length were assessed to the nearest 0.5 mm (see Canadian Wildlife Service and U.S. Fish and Wildlife Service 1977 for methods).

A time-budget study was conducted at individual nests every day between 0600 and 1000 (i.e. during house wrens most active period), weather permitting. A maximum of 5 birds per day were observed for 30 minutes. Because of the great variation within individuals, an effort was made to monitor the same male at least twice before and after pairing. Observations were made from concealed locations. These natural blinds were located at least 15 m from the nests. Once at the blind, the observer waited 10 minutes before recording data so that birds could resume normal activities. Every 5 seconds, the behavior a male was engaged in was noted. From these records, I determined the proportion of time males spent singing, perching and foraging.

Territory characteristics

Information on individual territories was collected during nest checks. Territory boundaries were mapped by plotting location of song perches, flight paths, and foraging areas. Territory boundaries were delimited by the minimum convex polygon method. An Apple Graphics Tablet was used to calculate territory size.

To estimate vegetation density on territories, I randomly selected 5 points within a 35 m (i.e. distance between boxes) radius of each box. At each of these points, I positioned a 2 m stick with three 50 cm sticks attached perpendicularly and, counted the number of red dots visible on the horizontal bars from a distance of 2 and 5 m. The horizontal bars were attached at heights of 0.5, 1.0, and 1.5 m, and each had 20 evenly spaced red dots (1 cm in diameter) painted on it. The number of circles seen at 2 and 5 m was used as an index of vegetation density (i.e. high dot count = low vegetation density).

Canopy coverage was estimated and grouped into 5 arbitrary categories (0 %, 1 - 25 %, 26 - 50 %, 51 - 75 %, 76 - 100 %). I measured vegetation density around nests, using the dot count method described above. This time, the stick was positioned in front of the box (i.e. where the entrance was). Vegetation density was estimated in early July. I assume that the relative differences in vegetation density between boxes and territories did not vary throughout the season. All females settled after leaf emergence, therefore, these estimates should be a reliable index of vegetation density at settlement.

ANALYSIS

Because nesting success is a binary variable (e.g. success vs failure), I used a stepwise logistic regression to determine which variable(s) affect(s) nesting success (Cox 1970, Dixon et al. 1983). A listwise deletion of missing data was used (Dixon et al. 1983). To estimate the relative contribution of the independent variables to the variance in fledging success and nesting weight, I used a stepwise multiple linear regression analysis. As above, a listwise deletion of missing data was used. Following Dixon et al. (1983), the F value for entry of variables into the analysis was set at 4.0. An all possible subset linear regression analysis was also used to force entry of variables with an F to enter inferior to 4 but superior to 3.9 (Dixon et al. 1983). In this latter analysis the T-test on the regression line was set at a value of 2.0 (i.e 5 % significance; Dixon et al. 1983). Proportions were normalized using the angular transformation. The logarithmic transformation was used to convert skewed distribution into normal ones. Differences were considered statistically significant when $P < 0.05$.

RESULTS

NESTING LOSSES AND MORTALITY FACTORS

Seventy-seven clutches were initiated. The temporal pattern of clutch initiation is shown in figure 1.1. About 48 % ($n = 37$) of the active nests failed to fledge any young. Nesting success between sites ranged from 88.5 % (23/26) in the dunes to 33.3 % (17/51) in the forest. Predation was the most important source of nesting failure, accounting for 84 % ($n = 31$) of failed nests. One nest (1.3 %) failed because of starvation, presumably following desertion by parents. Three females (3.9 % of nesting failure) abandoned their nest in the incubation stage. In the remaining two cases (2.6 %) eggs failed to hatch. Partial losses were due to predation (12 nests; 13 eggs, 7 nestlings) and to egg infertility (4 nests; 5 eggs). Table 1.1 gives the total number of eggs and nestlings lost to the above mortality factors. Nest success of boxes placed on poles did not differ significantly from that of boxes attached to trees ($X^2 = 0.05$, df = 1; $P > 0.75$). Nest support type, therefore, did not significantly affect nesting success.

House wrens were apparently the most important predator responsible for 45 % (14/31) of complete nest failure and for all partial nest losses due to predation (n = 12). Mammalian predators accounted for 32 % (10/31) of complete nest losses. Remaining cases of predation were uncertain. The total number of eggs and nestlings presumably lost to wrens and mammals are given in Table 1.2. I have no direct evidence on the species of mammals depredating nests. However, raccoons (Procyon lotor), red squirrel (Tamiasciurus hudsonicus), short-tailed weasel (Mustela erminea), deer mice (Peromyscus maniculatus), and white-footed mice (Peromyscus leucopus) were observed at the study site. Snakes were generally rare in the area (D. McRae, pers. communication).

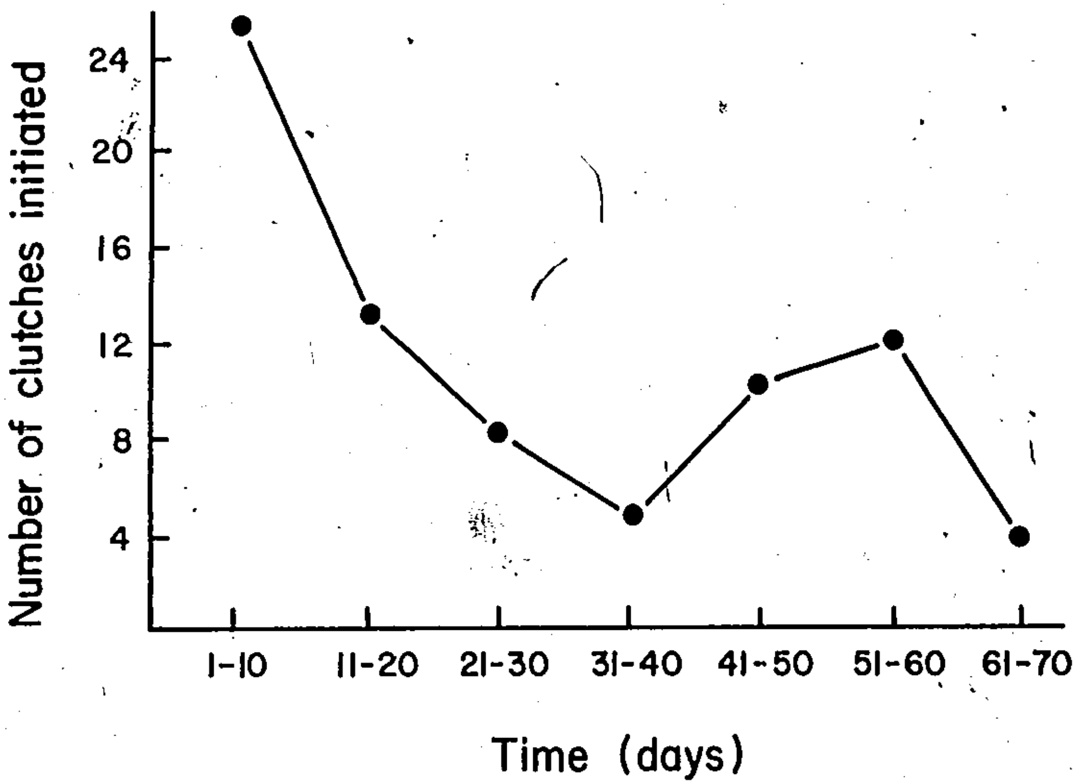

Number of clutches initiated
24
20
16
12
8
4
1-10
11-20
21-30
31-40
41-50
51-60
61-70
Time (days)

Figure 1.1. Number of clutches initiated in relation to time in the breeding season. The first egg was laid on day one (14 May).

Table 1.1: Number of house wren eggs and nestlings lost to different mortality factors at Presqu'ile Provincial Park in 1985.

Habitat	No. of eggs	No. of eggs lost to predators	No. of eggs that failed to hatch*	No. of nestlings lost to predators	No. of starved nestlings	No. of fledglings
Dunes	153	13	11	14	0	115
Forest	278	123	25	25	7	98

* This category includes abandoned and infertile eggs

TABLE 1.2: Number of eggs and nestlings presumably lost to wrens and mammals for each habitat at Presqu'ile Provincial Park in 1985.

Habitat	No. of eggs lost to wrens	No of eggs lost to mammals	No. of nestlings lost to wrens	No. of nestlings lost to mammals	Undetermined losses
Dunes	13	0	10	4	0
Forest	58	23	4	17	46

CORRELATES OF REPRODUCTIVE SUCCESS

Variables with a high number of missing values (i.e. 20 % of cases or more with missing values), which were not significantly correlated with the measures of reproductive success were removed from further analyses. For this reason, the proportion of time mated and unmated males spent singing, perching, and foraging were removed. Because of multicolinearity (Zar 1984), male and female culmen-length were also removed from later analyses. The final analyses were conducted with 9 independent variables (habitat was entered as a dummy variable).

Because habitat was an important predictor of all dependent variables, I performed the analyses for the dunes and the forest separately. In the forest, vegetation density around boxes ($F = 3.8$, $df = 1,41$, $P = 0.05$) and female weight ($F = 4.2$, $df = 1,40$, $P = 0.05$) were the only two variables entered into the logistic regression analysis. The logistic model was appropriate for the data (Hosmer's $X^2 = 5.45$, $df = 8$, $P = 0.71$). Female weight ($T = -2.5$, $df = 1$, $P < 0.02$) and vegetation density around boxes ($T = 2.0$, $df = 1$, $P < 0.05$) were also the only variables entered into the all possible subsets regression analysis. Female weight and vegetation density accounted for 3.9 % and 6.7 % of the variance in fledging success, respectively. In both analyses the index of vegetation density at nest boxes (i.e. high dot count = sparse vegetation) was positively correlated with success. Thus, sparser sites were more successful. Female weight was negatively correlated with reproductive success.

Vegetation density on territories ($F = 11.74$, $df = 1,115$, $P < 0.01$) and male wing-length ($F = 8.50$, $df = 2,114$, $P < 0.01$) explained 9.3 % and 6.3 % of the variance in nestling weight, respectively. Regression coefficients revealed that male wing-length was positively correlated with nestling weight. The index of vegetation density on territories was negatively correlated with the dependant variable. Heavier nestlings were found on territories with denser vegetation.

In the dunes, female weight was the only variable entered into the logistic regression analysis ($F = 6.65$, $df = 1,24$, $P < 0.02$). The result of a Hosmer's X^2 goodness of fit test, suggests an excellent fit of the logistic model to the data ($X^2 = 0.94$, $df = 4$, $P = 0.92$). However, on the basis of the selected variables, I was unable to find a significant predictor of fledging success.

In the dunes, two variables significantly explained part of the variance in nestling weight. As determined by a stepwise multiple linear regression analysis, vegetation density on territory (F = 11.69, df = 1,115, P < 0.01) and male wing-length (F = 9.74, df = 2,114, P < 0.01) explained 9.2 % and 5.4 % of the variance, respectively. As for the forest, partial regression coefficients indicate that male wing-length was positively correlated with nestling weight, whereas the index of vegetation density on territories was negatively correlated.

Results are consistent for the two habitats with the exception of vegetation density at nest sites. In the dunes, however, there was only a small amount of variation in vegetation density at boxes as opposed to the forest where variation was more pronounced (figure 1.2).

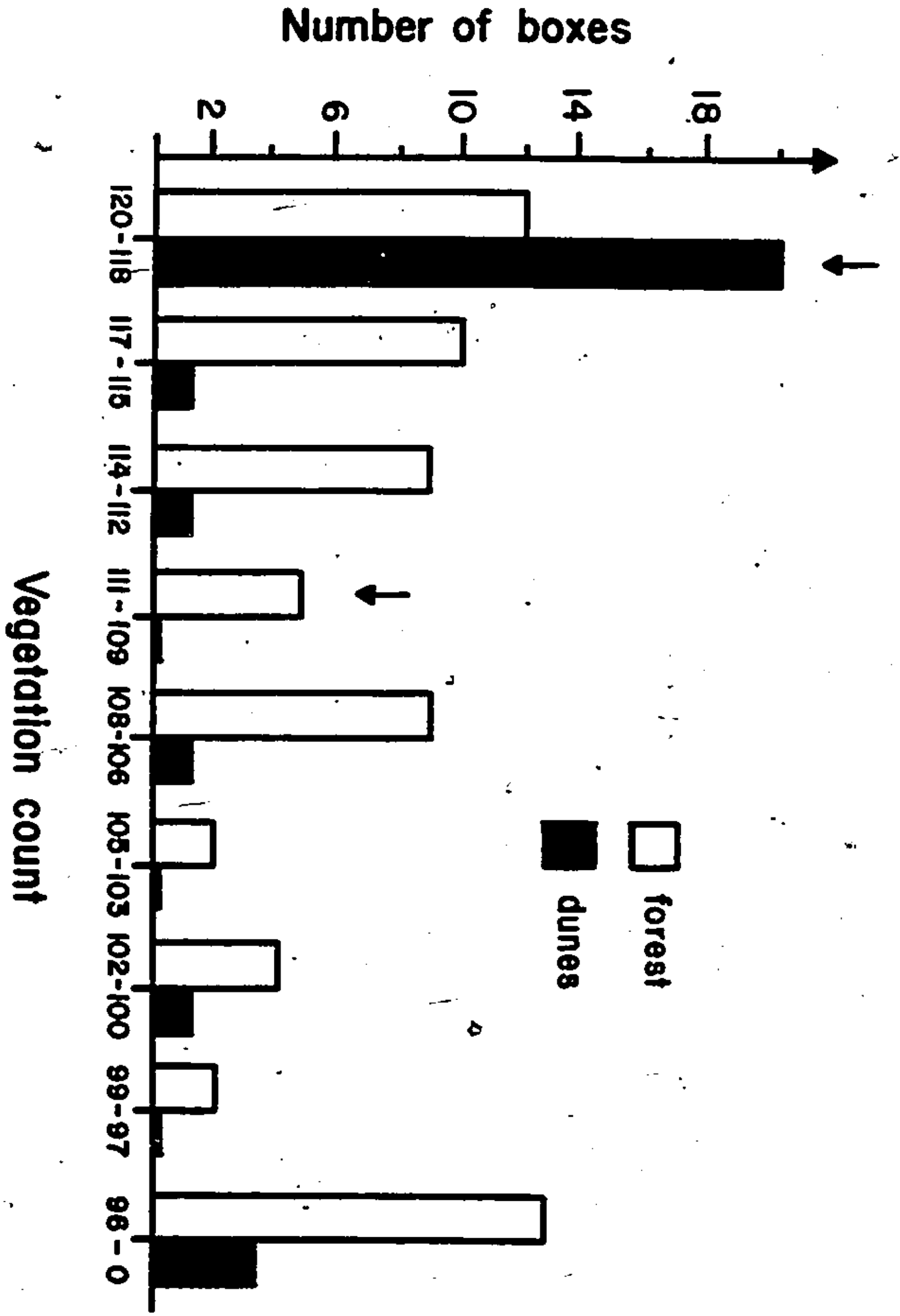

Number of boxes
2
6
10
14
18
120-118
117-115
114-112
111-109
108-106
105-103
102-100
99-97
96-0
Vegetation count
forest
dunes

Figure 1.2. Frequency distribution of the number of boxes placed in vegetation of different density for the forest and the dunes. Medians are indicated by arrows.

DISCUSSION

Destruction of eggs by small passerines is a relatively rare phenomenon which has been observed mainly in members of two families: Troglodytidae and Mimidae (Belles-Isles and Picman 1986a). In contrast to predators that characteristically consume eggs and nestlings, most of these species only peck and remove eggs and nestlings from the attacked nests (e.g. Picman 1977, Picman and Picman 1980, Belles-Isles and Picman 1986a, b). Nest-destruction by small passerines is believed to act as a mechanism of interference competition (e.g. Verner 1975, Picman 1977, Belles-Isles and Picman 1986a, Freed 1986). That is, by destroying nests of conspecifics and forcing them to breed farther away, wrens may reduce intraspecific competition. This hypothesis of interference competition is supported in some species by the finding that the occurrence of intraspecific attacks on nests in a population is positively correlated with the density of breeding birds (Picman 1984, Belles-Isles and Picman 1986a). Contrary to previous beliefs that the house wren nest-destroying behavior was restricted to a few males (Baldwin 1925, Sherman 1925, McAtee 1926, Kendeigh 1941), Belles-Isles and Picman (1986a) showed that the behavior was exhibited by all non-breeding adult individuals. Hence, house wrens are likely to have a more important impact on conspecific reproductive success than previously thought (Freed 1986).

Drilling and Thompson (1984) reduced mammalian predation on wren nests by mounting boxes on greased electrical line conduits. Despite this, the mean number of house wrens that survived to fledging ranged from 21 to 90 % of the initial clutch size depending on year and habitat. Nestling starvation alone could not explain these losses since low fledging success areas were presumably associated with higher food supply (Drilling and Thompson 1984). This suggests that wren predation was also important at their study sites. This idea is further supported by the observation that lower fledgling success in logged areas was associated with higher male density.

Fink et al (1986) reported that after elimination of mammalian predation, 18.5 % (40/216) of unmanipulated nests failed to fledge any young. Food was probably not limiting in this case since nestlings from experimentally enlarged broods weighed as much as those from unmanipulated and experimentally decreased broods. Wrens, therefore, were likely responsible for these losses. The figure reported by these researchers is similar to the 18.2 % (14/77) of nests that failed to fledged young due to conspecific nest attacks, in my population.

Although less important than wrens, in my study, mammalian predators were apparently responsible for a large proportion of nesting losses. Mammals generally rely on olfaction to locate nests (Best 1978). My research activity, therefore, may have increased the incidence of mammalian predation (e.g. Snelling 1968, Osborne and Osborne 1980, Westmoreland and Best 1985). In contrast, because avian predators rely mostly on sight for finding prey (Best 1978), human activity should have a negligible effect on wren predation. Hence, my study may overestimate the relative importance of mammalian predation.

As the largest source of mortality, wren predation should represent an important selective pressure. By breeding in sparse vegetation wrens may reduce losses to conspecifics. The importance of nest concealment varies with the type of predators operating at a given time and place (Colias and Colias 1984). Dense vegetation is believed to be safer from the point of view of mammalian predation (e.g. Goddard and Board 1967, Holm 1973, Richter 1984). However, when nest surveillance is important, sparse vegetation may provide a better view of intruding predators (Holm 1973, Picman 1980b). By breeding in cavities, house wrens presumably reduce predation by larger animals (Nice 1957, Lack 1968). Although wrens can successfully defend their nests against conspecifics (Kendeigh 1941, Grove 1981), it should be easier for intruding wrens to approach nest cavities in dense vegetation. Thus, nests in sparse vegetation are probably less vulnerable to attacks from conspecifics. Only 3 of 23 nests in the dunes failed to fledge any young presumably because boxes were consistently in sparse vegetation.

Vigilance may protect the nest from conspecific attacks. Nest departure by female wrens is generally associated with the presence of the male in the vicinity of the nest and vice versa. Hence, wren nests are almost constantly attended by parents (Kendeigh 1952, unpublished data). Female weight was negatively correlated with nest survival rate and fledgling production. The reason for this difference is not fully understood, but it may be that heavier females are less efficient at nest defence than the lighter ones. Heavier females may have to spend more time foraging away from the nest to meet their basic energy requirements, with less time for nest defence. Testing this idea requires further study.

Older individuals often have longer wings than younger individuals (e.g. Stewart 1963, Thorne 1975, Laaksonen and Lehikoinen 1976, Alatalo, Gustafsson and Lundberg 1984, Bedard and LaPointe 1984b). This relationship appears to be true for the house wren (unpublished data). The finding that male wing-length is positively correlated with nestling weight is not supported by other studies on house wrens but is consistent with Yasukawa's (1981) study on red-winged blackbirds

(Agelaius phoeniceus) and Ross' (1980) study on savannah sparrows (Passerculus sandwichensis). Both authors showed that older males were more efficient at rearing nestlings.

House wren diets have been studied primarily in old field and suburban habitats (Kendeigh 1952, Freed 1981). Evidence from these studies indicates that ground foraging is probably important (see also Balda 1969). Similarly, Franzreb (1977) reported increased foraging in logged areas. Logged areas are considered to have fewer canopy layers, saplings, and trees but denser herbaceous vegetation (Hager 1960, Franzreb 1977, Blake 1982, Drilling and Thompson 1984). My results are consistent with these finding since density of low vegetation (up to 1.5 m high) was positively correlated with nestling weight. Heavier nestlings were associated with territories in denser vegetation. This study also corroborates Ross' (1980) findings that show that nestling savannah sparrows raised in dense habitat were heavier than nestlings raised in less vegetated habitat.

On the basis of selected variables, I failed to explain most of the variation in reproductive success. These results suggest that either I have missed some important variables or that most of the variation is the product of random events. Testing these hypotheses requires more research.

Chapter 2

FEMALE MATE PREFERENCES IN THE HOUSE WREN

INTRODUCTION

From Darwin (1871) to the present, students of mating systems have argued that in most species females decide which male to mate with while males are less discriminating. The greater investment of females into reproduction has been used to explain this apparent rule (e.g. Bateman 1948, Maynard Smith 1956, Trivers 1972).

Current selection theory holds that characteristics used in mate choice should directly affect female reproductive success or be correlated with characteristics that influence female fitness. Characteristics used in female choice could be divided into 2 categories: i) features of the male and ii) features of his territory (Searcy 1979). Even if male or territory characteristics affected female fitness, they should influence female choice only if they are assessable by females prior to mating. Some characteristics may simply not be expressed in any form that a female can evaluate (Wittenberger 1980). Others such as male parental care may be expressed only after the female has made her choice (Searcy 1979).

Male wing-length, vegetation density at nest sites and on territories were significantly correlated with house wren reproductive success (see Chapter 1) and thus, could potentially affect female choice. In this chapter, I investigate whether female house wrens select mates on the basis of these characteristics.

METHODS

Data were collected during spring and summer of 1985 and 1986 at two locations in Ontario, Canada: Presqu'ile Provincial Park (PPP) and Mer Bleue Bog near Ottawa (MBB). Descriptive information was collected at PPP in 1985 and experiments on nest site preferences and female preferences of males were conducted at MBB in 1985 and 1986, respectively.

DESCRIPTIVE INFORMATION ON FEMALE MATE PREFERENCES

To examine whether females select mates on the basis of characteristics important for their reproductive success, I distributed 92 identical nest boxes along two transects. The two transects ran through a deciduous forest and adjacent sand dunes. Boxes were similar with respect to orientation and height above ground. A detailed description of the study area is given in the first chapter.

Males were captured usually within a few days from arrival. Captured wrens were individually marked with colored plastic leg-bands. For all marked individuals, I recorded measurements of their flattened wing-length. Every second day from April to August, I walked along the transects and attempted to identify all individuals present on the study area. I also identified birds during time budget studies described in Chapter 1. This allowed me to associate birds with individual territories. During the census walks, I recorded nest contents at all boxes. Possession of boxes by males was determined by the presence of twigs in boxes (Kendeigh 1941, 1952). Female selection was determined from nesting attempts. After desertion, boxes were emptied to allow determination of later selection. Vegetation density at boxes and on territories was estimated using the dot count technique described in the first chapter. Vegetation density was estimated in early July. For details of methodology see Chapter 1.

Because selection of boxes is a binary variable (i.e. a female selected a box or not), I used a stepwise logistic regression to determine which variable(s) affect( ) box selection (Cox 1970, Dixon et al 1983). Only advertised boxes were entered in the analysis. Nest boxes that were advertised more than once (either sequentially by the same male or by different males) were considered as distinct cases. Independant variables entered into the calculation include density of vegetation at boxes, vegetation density on territories, and male wing-length.

DESCRIPTIVE INFORMATION ON MALE NEST SITE PREFERENCES

If boxes vary in some quality important in female choice, males should exhibit a preference for these high quality breeding sites (Searcy 1979). I used a logistic regression to examine whether males, at PPP, exhibit a preference for certain nest sites. Possession of a box by males was entered as dependent variable. Because house wrens are double-brooded, I assumed that each box could have been defended by at least two males or by the same male for two breeding attempts. Hence, I entered each box twice in the analysis. Boxes that were not available during the first half of the season because of usage by tree swallows (*Tachycinema bicolor*), were entered only once. Density of vegetation at the box and on territories were the independant variables.

EXPERIMENTAL TEST OF NEST SITE PREFERENCES

To test for the effect of vegetation density on house wren nest site selection, 60 nest boxes identical to those used at PPP, were offered at MBB in early April, before wren arrival. Nest boxes also faced southeast and were erected

1.5 m above ground. Boxes were placed in groups of three in a triangular pattern (5-10 m apart, depending on the availability of trees). In each group, one box was placed in what I perceived as sparse, medium, and dense vegetation. To verify my estimates, in early July, vegetation density was measured using the dot count technique described in Chapter 1. Boxes in dense and medium vegetation were attached to trees and those in sparse vegetation were fastened to 5 cm x 5 cm wooden poles, similar to those used at PPP (see Chapter 1). Territorial males could, therefore, defend three boxes that differed in the density of surrounding vegetation. Groups of boxes were separated by at least 60 m. The dominant tree species of this study site were speckled alder (*Alnus rugosa*), basswood (*Tilia americana*), pussy willow (*Salix discolor*) and, choke cherry (*Prunus virginiana*). Ground flora was dense and dominated by Canada mannagrass (*Glyceria canadensis*), red-stalked aster (*Aster puniceus*), and joe-pye-weed (*Eupatorium maculatum*).

All boxes were checked once a week and their contents noted. Male preference for certain nest sites was measured by the quantity of twigs present in nest boxes. I assumed that the relative amount of nest material in boxes within a group reflects male preference (i.e. the more twigs the more they prefer the box, ~~see~~ Kendeigh 1941). Female selection was measured by nesting attempts (i.e. at least one egg in the nest regardless of subsequent fate). Following territory abandonment (e.g. after successful breeding), I emptied all three boxes in the group to allow determination of nest site choice in later breeding attempts. A 1-tail X^2 goodness of fit test was performed to examine whether male and female house wrens selected the sparser sites more often than predicted by chance.

EXPERIMENTAL TEST OF FEMALE PREFERENCE FOR MALES WITH LONGER WINGS

To test whether females preferentially select males with longer wings, in April 1986 at MBB, I offered house wrens 60 identical boxes in open areas. By offering boxes in open vegetation, I controlled for the effect of vegetation density at nest sites on female mate choice. As above, box orientation and height above ground were constant. Boxes were attached to 5 cm x 5 cm wooden poles and were separated from each other by about 50 m. In June, vegetation density was measured at each box and at 5 randomly selected points within 35 m of each box. Vegetation density was measured by the dot count method described in Chapter 1. Boxes were visited every second day from early May to mid-July. Box selection by either sex was determined as above. Males were mist netted and their wings measured. To minimize possible confounding factors arising from habitat heterogeneity, selected males were compared with males possessing the neighboring box at the time females settled. The compared males defended boxes that were separated from each other by appproximatively 50 m. I used a 1-tail X^2 test to evaluate if females choose the males with longer wings more often than predicted by chance.

RESULTS

DESCRIPTIVE INFORMATION ON FEMALE MATE PREFERENCES

Figure 2.1 shows that unmated males were available throughout the breeding season. Female house wrens, therefore, had the possibility to choose from among several candidates.

To control for differences between habitats, I examined data from the forest and the dunes separately. As suggested by a stepwise logistic regression analysis, forest males defending boxes in dense vegetation were less likely to attract a female than males defending boxes in sparser vegetation ($F = 4.55$, $df = 1,95$, $P = 0.036$). Vegetation density on territories and male wing-length did not enter the equation. The logistic model was appropriate for the data (Hosmer's $X^2 = 11.912$, $df = 8$, $P = 0.16$). In the dunes, however, none of the selected variables entered the logistic regression. Most of the boxes in the dunes were in sparse vegetation (median vegetation density equal 120/120 dots, see Chapter 1), and thus, most were presumably suitable for breeding.

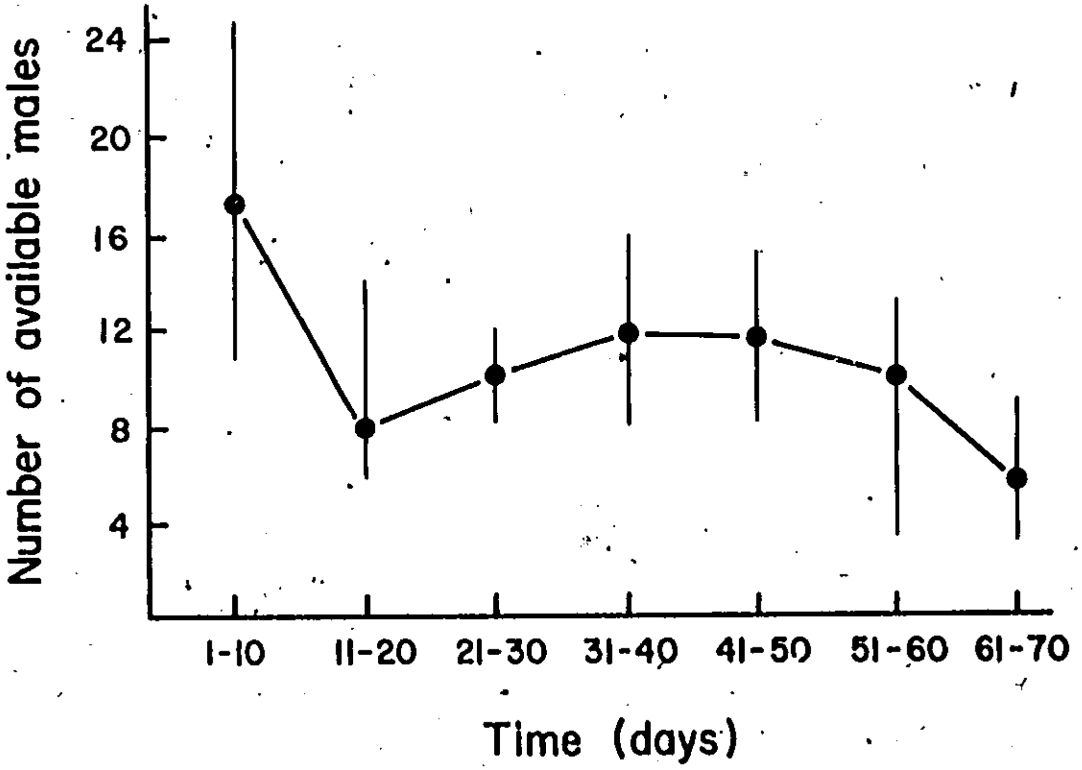
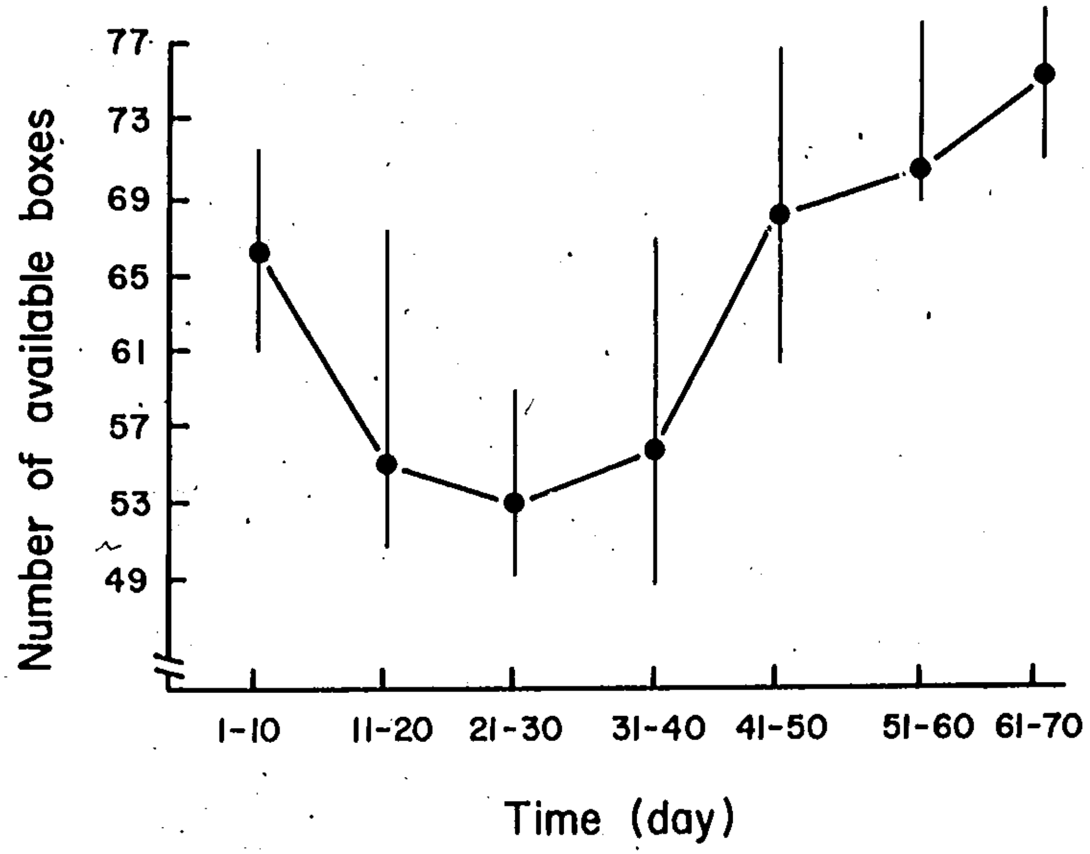

Number of available males
24
20
16
12
8
4
1-10
11-20
21-30
31-40
41-50
51-60
61-70
Time (days)

Figure 2.1. Number of available males (i.e. unmated) in relation to time in the breeding season. Shown at each interval of ten days is the mean and the range (vertical line). Day one = 14 May.

DESCRIPTIVE INFORMATION ON MALE NEST SITE PREFERENCES

Throughout the season, undefended boxes were available (fig. 2.2). Hence, males had a choice between several boxes.

Results of the logistic regression indicate that boxes in sparse vegetation were more likely to be defended by males than boxes in dense vegetation ($F = 9.69$, $df = 1,182$, $P < 0.01$). The dependent variable, however, was not significantly affected by the density of vegetation on territories. A Hosmer's X^2 goodness of fit test indicate that the logistic model was appropriate for the data ($X^2 = 5.64$, $df = 8$, $P = 0.69$). Hence, male house wrens at PPP preferentially defended boxes that were in sparse vegetation.



77
73
69
65
61
57
53
49
Number of available boxes
1-10
11-20
21-30
31-40
41-50
51-60
61-70
Time (day)

Figure 2.2. Number of available boxes (i.e. undefended) in relation to time in the season. Shown at each interval of ten days is the the mean and the range (vertical line). Day one = 14 May.

EXPERIMENTAL TEST OF NEST SITE PREFERENCES

I tested house wren nest site preferences at MBB by offering wrens 20 groups of 3 boxes placed in vegetation of different densities. Nest boxes differed in density of surrounding vegetation (Fig. 2.3; 1-way ANOVA: $F_{2,57} = 23.0$, $P < 0.01$). Presumably, within each group, boxes differed only in the density of surrounding vegetation. Nineteen of 20 groups of boxes attracted male wrens. No males included two groups of boxes within their territories. The only group that failed to attract a male had all three boxes in relatively dense vegetation. At each of these 3 boxes the vegetation index was below the mean vegetation count for dense vegetation (dense = 28 dots, medium = 37 dots, sparse = 44 dots). A total of 4 groups of boxes failed to attract a female. Most of these boxes, however, were advertised during the second half of July when no new clutches were laid. Nine groups of boxes were emptied after the first brood fledged and nests were reestablished in 4 of these

Both male and female wrens at MBB selected boxes in sparse vegetation more often than predicted by chance (Table 2.1). Two of the 4 boxes in medium vegetation selected by a male or a female had sparser vegetation than the average density for sparse sites. Neither sex selected boxes in dense vegetation. Within groups, twigs were often found in all 3 boxes, indicating that males knew about all cavities. Males, therefore, did not select sparsest sites because they were easiest to find. This, presumably, holds also for females. One female laid eggs in a different box than the one preferred by the male. This observation suggests that males and females pick cavities independantly. Hence, when given an opportunity, wrens preferentially selected boxes in sparse vegetation. These results are consistant with the descriptive information collected at PPP.

Only two nests at MBB suffered depredation. One was presumably lost to a mammalian predator since the box was pulled down. Three of 6 eggs were lost at the second nest. I concluded that a wren was responsible since a punctured egg was found in the nest. This nest, however, was built at one of the densest selected sites (87 dots). These results are consistent with the proposition made in Chapter 1 that wrens may reduce conspecific predation by breeding in sparse vegetation.

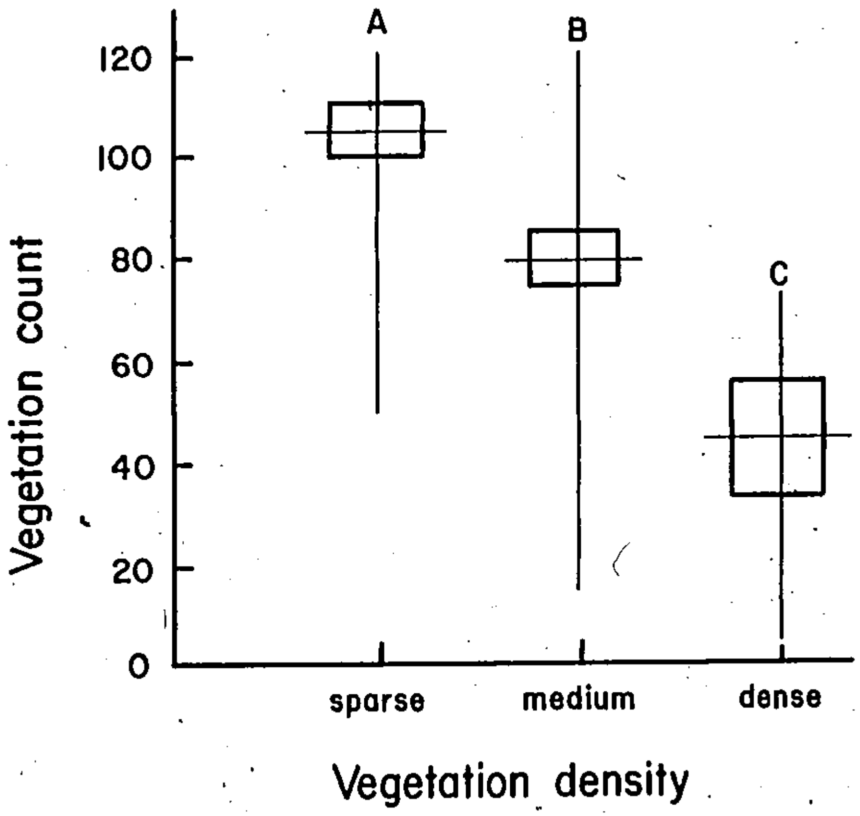

A
B
C
120
100
80
60
40
20
0
Vegetation count
sparse
medium
dense
Vegetation density

Figure 2.3. Vegetation count for boxes placed in sparse, medium, and dense vegetation. Shown is the mean ± standard error (vertical rectangle) and the range (vertical line). For each group n = 20. Significant differences between means as determined by a Tukey's multiple range test (P = 0.01) are represented by different letters.

TABLE 2.1: Nest site selection by house wrens at MBB in relation to vegetation density. The number (%) of nesting boxes used by male and female under each vegetation density condition is given.

	Vegetation Density						
Sex	Sparse	Medium	Dense	Total	X^2	df	Prob.*
Male	20 (87)	3 (13)	0 (0)	23	30.4	2	< 0.001
Female	17 (81)	4 (19)	0 (0)	21	22.6	2	< 0.001

*One-tail test.

EXPERIMENTAL TEST OF FEMALE PREFERENCE FOR MALES WITH LONGER WINGS

To test female preference for males with longer wings, I compared wrens possessing territories of apparently similar quality. Vegetation density at boxes and on territories between selected boxes and non-selected boxes did not significantly differ (for vegetation at boxes: Pratt's matched-pairs sign test $T = 41$, $Z = 7$, $n = 7$, $P > 0.10$; for vegetation on territories: Pratt's matched-pairs sign test $T = 45$, $Z = 3$, $n = 11$, $P > 0.10$; see Rahe (1974) for critical values). Boxes may have differed in some other qualities important in female choice. However, since I compared neighboring boxes (approximatly 50 m apart), I assume that these characteristics, if any, are negligible, and, therefore, that boxes vary only with regard to male quality. Female house wrens at MBB did not select the males with longer wings more often that predicted by chance (Table 2.2).

TABLE 2.2: Relationship between female mate selection and male wing length when neighboring pairs of males are compared.

Wing-length of selected males	Observed	Expected*	χ^2	df	P**
Longer	8	7	0.29	1	0.30
Shorter	6	7			

* Assuming random choice with respect to male wing-length.

** One-tail test.

DISCUSSION

CUES USED BY FEMALES FOR SELECTING A MATE

It has been suggested that female house wrens select mates on the basis of nest site qualities (Sherman 1925, Kendeigh 1941). If it is so, nest sites should vary in some quality(ies) important for succesful breeding, and both male and female should exhibit a preference for these high quality nest sites. Results of this study support this proposition. Both male and female house wrens prefer to nest in sparse vegetation where they average higher reproductive success (see Chapter 1). Therefore, a male's mating success might be closely tied to his ability to monopolize attractive nest sites.

In contrast to the finding that males and females preferentially select sparse nest sites for breeding, Bent (1948) stated that house wrens prefer cryptic nesting cavities. Occupation, however, does not necessarily indicate preference (Nilsson 1984). Suitable nesting cavities are probably scarce in natural settings (e.g. von Haartman 1957, Hilden 1965, Pinkowski 1977), and intense competition might force some birds to select lower quality nesting sites. Bent (1948) did not offer house wrens a choice between nest sites of different quality. His data, therefore, provide a poor indication of house wren nest site preference.

Although male wing-length was correlated with nestling weight, females, seemingly, did not select males on the basis of this characteristic. In order for females to select males on the basis of the quality of parental care males will provide to the young, there should be reliable correlates of parental care (Searcy 1982). Apart from Yasukawa's (1981) study on red-winged blackbirds which showed that males providing superior parental care could be recognized by their courtship behavior there is little evidence that female choice is affected by parental care in passerines (Searcy 1979, Bradbury and Gibson 1983, but see Nisbet 1973, Niebuhr 1981, Wiggins and Morris 1986 for evidence in Larids). Data that would allow us to examine whether females use correlates of male parental care in mate choice are not available for the house wren.

Vegetation density on territories is also significantly correlated with nestling weight. Despite this, females did not select mates on the basis of vegetation density on territories. In house wrens, however, evidence that post-fledging survival is related to size remains to be demonstrated.

Most studies on mate choice have focused on a single criterion of choice (e.g.Lill and Wood-Gush 1965, O'Donald and Davis 1977, Weatherhead and Robertson 1977, Plesczynska 1978). However, as pointed out by Garson (1980) and Burley (1981), since there are many determinants of fitness, mate choice could be based on multiple criteria. My study failed to support the multiple criteria hypothesis but further testing is required before this hypothesis could be definitively rejected for the house wren.

Chapter 3

FEMALE CHOICE STRATEGIES IN THE HOUSE WREN

INTRODUCTION

Implicit to most work on mating systems is the assumption that females inspect all available males and then mate with the best one. As there might be several constraints on a female's behavior, the strategies that actually appear may at best approximate the optimal decision (Janetos 1980, Janetos and Cole 1981, Wittenberger 1983). To date little attention has been paid to the tactics females may use to sample mates. The clarification of such mate-choice patterns, however, should eventually lead to an understanding of the origin of mating systems (Wittenberger 1983).

Before making a choice, females must acquire information about prospective mates. To that end, several strategies could be used. Apart from random mating, the simpliest tactic a female may adopt is the **minimum criterion tactic**. This tactic states that a female mate with the first encountered male who meets some minimum criteria (Janetos 1980, Wittenberger 1983). The minimum criterion tactic should be one of those strategies that yield the worsT return to females, and should not be adopted unless the cost/benefit ratio of comparing several candidates is relatively high (Janetos 1980, Wittenberger 1983).

When choice is based on qualitative characteristics (i.e. presence or absence of a trait) the minimum criterion tactic would be most suitable. However, if the quality of mates fluctuates, it would be advantageous for females to judge and rank males on a relative basis, rather than against an absolute criterion (Janetos 1980, Wittenberger 1983). To compare alternatives, females may adopt several tactics. First, a female may use a sequential comparison tactic. When this tactic is used, a female should continue visiting prospective mates until the last male encountered is worse than the previous one (Wittenberger 1983). This tactic, however, greatly limits the number of candidates that will be considered and consequently may entail risks of making suboptimal choices. An alternative to the sequential comparison tactic is the pool comparison tactic. This tactic states that a female should assess the relative quality of a restricted number of candidates and then mate with the best one (Janetos 1980, Wittenberger 1983). There are two strategies included in this category: (1) area limited pool comparison tactic, and (2) area unlimited pool comparison tactic. The first, the area unlimited strategy states that a female will visit a predetermined number of candidates, regardless of the distance she will have to travel. This strategy may be favored when females are restrained by their memory capacities. A female adopting the second strategy, the area limited pool comparison tactic, is expected to sample all situations within a restriced area. This tactic may be selected when time and/or mobility constrain female behaviour. The pool comparison tactics are expected to best approximate the optimal choice (Janetos 1980, Wittenberger 1983). The above female choice tactics are summarized in Table 3.1.

The purpose of this chapter is to investigate female mate choice strategies in the house wren. Tactics of mate choice have rarely been studied mostly because of the difficulty of following females throughout the mating process. To circumvent this difficulty, I approached the problem by simulating female choice and by comparing results of the simulations with the observed pattern (see Brown 1981). In the previous chapters, I showed that female house wrens preferentially select males possessing boxes in sparse vegetation, presumably, because there they average higher success. Male quality and other features of habitat quality, however, did not appear important in female mate choice. Therefore, in the simulations females selected breeding situation only on the basis of vegetation density around nesting boxes. Because female box selection is likely to be affected by their ability to assess variation in vegetation density, I simulated, whenever appropriate, choices made by accurate and inaccurate females. The following questions were addressed in this study: (1) Do female house wrens select nesting sites randomly with regard to density of vegetation at boxes? (2) Do females select the best box among available ones? (3) Do female wrens judge boxes on a relative or absolute basis? (4) Do females sample boxes according to the sequential or a pool comparison tactic?

Table 3.1. Summary of female mate choice tactics and their main predictions.

Tactic	definition
Random choice	Females select situations at random.
Best-of-all situations	Females select the best situation in the entire population.
Minimum criterion	Females select only situations above the threshold. Choice among suitable situations is random.
Sequential comparison	Females survey situations until the last visited situation is worse than the previous one. They select the best of the last two visited situations.
Area unlimited pool comparison	Females survey a predetermined number of situations and select the best one.
Area limited pool comparison	Females survey all situations within a restricted area and select the best one.

METHODS

Data were collected in 1985 at Presqu'ile Provincial Park, Ontario, Canada. Nest boxes were uniformly distributed along two transects separated by 25 m. The transects ran through a deciduous forest and adjacent sand dunes. Nesting boxes were identical in orientation, height above ground and were separated from each other by about 35 m. A general description of the study area is given in Chapter 1.

Males and females were captured and marked with a unique combination of color leg-bands (see Chapter 1 for details). Every second morning, from May to August, I walked along the transects and recorded presence of marked territorial males. Males were also identified during the time budget study described in the first chapter. During the morning census, I recorded box contents. Possession of boxes by males was determined by the presence of twigs in them (Kendeigh 1941, 1952). I concluded that a male had abandoned a site if he was not observed for at least 2 subsequents visits. A box was considered to be accepted by a female on the day I found fine nesting material in it (see Kendeigh 1941). For each female, I determined boxes that were available at the time of settlement. A box was defined as available to a female if advertised by an unmated male. The second breeding attempts by females were disregarded. Thus, simulations were conducted with 54 females (35 from the forest and 19 from the dunes territories).

Vegetation density at boxes was estimated, in early July, using the dot count technique described in the first chapter.

RANDOM CHOICE

To test whether females selected boxes randomly with regard to vegetation density, I compared the density of vegetation at chosen boxes with that at randomly selected boxes. Boxes were randomly selected from among those that were available at the time each female settled (i.e. there was a male defending the box). If females choose nest boxes randomly then the density of vegetation at chosen and randomly selected boxes should not differ.

OPTIMAL CHOICE

To test whether females selected the best box among the available ones, I compared the density of vegetation at the selected box with that at the sparsest non-selected one. Only boxes available at the time of female settlement were used in the analysis. If females selected the best available box then the density of vegetation at selected boxes should be sparser or equal to the density at the sparsest available non-selected ones.

MINIMUM CRITERION TACTIC

If females use a minimum criterion tactic then they should select only boxes that are above the threshold and their choice above this threshold should be random. To test whether females behaved according to the threshold tactic, I compared the density of vegetation at selected boxes with that at randomly selected ones. Boxes were randomly selected from among those that were available at the time females settled. Only defended boxes that were selected by females at least once in the season were considered available. Hence, females were simulated to choose boxes randomly from among boxes that were above the threshold (i.e. acceptable to female for breeding). This model differs from the random choice model tested above in that boxes were randomly selected from a smaller pool (i.e. boxes above the threshold). If females used the threshold tactic to select boxes then the vegetation density at chosen and randomly determined boxes should not significantly differ.

SEQUENTIAL COMPARISON TACTIC

To test the sequential tactic, females were simulated to sample boxes as long as the last box visited was in sparser or equal density vegetation than the previous one. Sampling started from a focal box which was randomly selected from among those available at the time each female settled. Sampling proceeded by inspecting, in succession, the closest boxes. In situations where two boxes were equidistant from the randomly selected box, females were allowed to select randomly which box to sample first. The outcome of this simulated choice was that females selected the sparsest of the last two visited sites.

In addition, in this simulation, I introduced a problem dealing with different abilities of females to assess the quality of nesting sites (i.e. vegetation density) by simulating two types of females. The first type of females was allowed to assess fine differences in vegetation density (i.e. 1 dot). The second group of females, however, was allowed to detect only gross differences (i.e. 6 dots). This arbitrarily selected value represents 10 % of the variation in vegetation density at available boxes. The sequential comparison tactic predicts that density of vegetation at boxes chosen by actual and simulated females should be similar.

POOL COMPARISON TACTIC

I tested two subsets of the pool comparison tactic. First, female strategy was simulated so that females sampled the closest 2, 3, and 4 available boxes from a randomly determined one. As above, when boxes were equidistant from the focal box, the first visited nest site was randomly selected. In this simulation females were free to move but were limited by the number of candidates they could sample (area unlimited pool comparison tactic). In the second case, I simulated a situation where females could sample all available boxes within 100, 200, 300 and, 400 m radius from a randomly determined box. In this case females were not limited by the number of boxes they could visit but instead were limited by the distance they could cover (area limited pool comparison tactic).

For the two pool comparison models, I also simulated two types of females. The first group of females were allowed to select the sparsest site from among those surveyed, regardless of how small differences between compared sites were. In the second situation, females were allowed to assess only gross variation in vegetation density. Thus, as for the sequential tactic, the minimum detectable difference for this second group of females was 6 dots. Hence, females were allowed to select the sparsest site given that differences between sampled boxes were large enough. When differences were too small to be assessable, the selected box was randomly determined. The pool comparison tactic predicts that density of vegetation at chosen boxes should be similar to that at simulated boxes.

ANALYSIS

I performed 100 computer simulations for any version of a model, with the exception of the optimal choice model. The simulations were written in basic and executed on an IBM AT personal computer. I used a Pratt's match pair sign test (critical values are given in Rahe 1974) to determine whether vegetation density at chosen and simulated boxes differed. A model was considered to adequately explain the box selection by female house wrens, if no more than 5 % of simulations indicated significant differences (i.e. fewer than 6 simulations). For the optimal choice model, a 1-tail Pratt matched paired sign test was used to compare vegetation density at chosen and available non-selected boxes.

RESULTS

DO FEMALES MATE RANDOMLY?

Sixty-nine simulations showed significant differences in vegetation density between chosen and randomly selected boxes. Females selected sparser sites than predicted by a random choice model (Table 3.2). The random model, therefore, cannot adequately explain box selection by female house wrens.

DO FEMALES SELECT THE BEST POSSIBLE BOX AMONG THOSE AVAILABLE?

The density of vegetation at chosen boxes was significantly higher than the density at the sparsest of the available non-selected boxes (T= 0, Z = 19, N = 35, P < 0.005). Hence, females did not select the sparsest available sites in the entire population.

DO FEMALES EVALUATE BOXES AGAINST A MINIMUM CRITERION?

Vegetation density at chosen boxes differed significantly from that at selected boxes for 25 simulations. Chosen boxes were in sparser vegetation than randomly selected boxes (Table 3.2). Females, therefore, did not select boxes randomly from among those that were above the threshold. Hence, female house wrens did not evaluate boxes against a minimum criterion but instead weighed their relative quality.

DO FEMALES SAMPLE BOXES ACCORDING TO THE SEQUENTIAL COMPARISON TACTIC?

Females that surveyed boxes according to the sequential tactic visited 2.6 ± 0.1 (SD) or 3.1 ± 0.1 boxes depending on their ability to discriminate fine or gross differences in vegetation density. The lower level of accuracy in assessment of vegetation density resulted in visits of more boxes ($T = 29.6$, $df = 198$, $P < 0.001$). The first group of females traveled 441 ± 81 m to sample boxes, whereas, the second group traveled 672 ± 90 m. The difference between the two groups of females was again statistically significant (T = 19.7, df = 198, $P < 0.001$).

When females were simulated to detect small differences in vegetation density (i.e. 1 dot), 13 % of the simulations indicated that vegetation density at boxes selected by actual females significantly differed from that at the sequentially [illegible]ed boxes. This figure increased to 35 % when females [illegible] simulated to detect only larger differences. For the two types of females, vegetation density around boxes was denser at actually chosen boxes than at simulated boxes (Table 3.2). Regardless of the type of females I simulated (i.e. accurate vs inaccurate), the sequential model cannot adequately explain female selection of nesting sites in house wrens.

DO FEMALES SAMPLE BOXES ACCORDING TO A POOL COMPARISON TACTIC?

A-Area unlimited

Females may pick the best of a predetermined number of encountered boxes. The average distance traveled by simulated females to sample different number of boxes is given in Table 3.3.

Regardless of the type of females simulated (i.e. accurate vs inaccurate females), vegetation density at actually chosen boxes did not significantly differ from that at simulated sites when 2 boxes were surveyed. Differences were significant, however, for simulations where females were allowed to visit 3 and 4 boxes before choosing the sparsest site. In these cases, females selected boxes in denser vegetation than predicted by these simulations (Table 3.2). The model suggests that real females restricted their choice to fewer than 3 boxes.

B-Area limited

In the last simulation females were allowed to sample boxes within a restricted distance from randomly determined boxes and then select what they could perceive as the sparsest sites. Table 3.4 gives the average number of simulated boxes visited when sampling was restricted to different distances.

There was no significant difference in vegetation density between the actually chosen and simulated boxes when females were allowed to select the best of all boxes present within 100 m and 200 m radius from randomly determined sites. However, a significant number of simulations indicated differences in vegetation density when females were allowed to sample the larger areas. In these cases, the actually selected boxes were in vegetation that was denser than predicted by the model. The results were similar for the two types of females simulated (accurate vs inaccurate, Table 3.2). This suggests that female house wrens restricted their choice to a relatively small area.

Table 3.2. Summary of results of computer simulations designed to test different female choice tactics. One hundred simulations were computed to test each of the hypothetical strategies. In the last column, vegetation density at real and simulated boxes is compared. Statistically significant differences (at P = 0.05) between boxes is indicated as sparser or denser relative to simulated boxes; ns = not significant.

Tactic	Subset	A[illegible]ssment [illegible]uracy*	No. of Simulations Different from the Actual Choice**	Conclusion	Vegetation Density
Random choice	---	---	69	rejected	sparser
Minimum criterion	---	---	25	rejected	sparser
Sequential	---	gross	35	rejected	denser
		fine	13	rejected	denser
Pool comparison area unlimited	2 boxes	gross	1	accepted	ns
		fine	4	accepted	ns
	3 boxes	gross	34	rejected	denser
		fine	40	rejected	denser
	4 boxes	gross	93	rejected	denser
		fine	98	rejected	denser
Pool comparison area limited	100 m	gross	0	accepted	ns
		fine	0	accepted	ns
	200 m	gross	1	accepted	ns
		fine	1	accepted	ns
	300 m	gross	12	rejected	denser
		fine	15	rejected	denser
	400 m	gross	17	rejected	denser
		fine	22	rejected	denser

*fine equals 1 dot, gross equals 6 dots.
** According to a Pratt's matched pair sign test at P = 0.05.

Table 3.3. Distance traveled by simulated females when allowed to sample a predetermined number of boxes. Significant differences between means, as determined by a Tukey's multiple range test (P = 0.01), are represented by different letters in parentheses.

Number of Boxes Visited	Mean Distance Traveled	SD	Range
2	203 (a)	43	137-304
3	634 (b)	65	483-765
4	979 (c)	117	833-1214

Table 3.4. Number of boxes visited by simulated females when allowed to sample all available sites within a predetermined distance from a randomly selected box. — Significant differences between means, as determined by a Tukey's multiple range test (P = 0.01), are represented by different letters in parentheses.

Distance (m)	Mean Number of Boxes Surveyed	SD	Range
200	1.8 (a)	0.1	1.6-1.9
400	2.5 (b)	0.2	2.1-2.9
600	3.2 (c)	0.2	2.8-3.5
800	3.6 (d)	0.2	3.4-4.2

DISCUSSION

Female house wrens did not mate randomly with regard to vegetation density at nest sites. This result is consistent with the idea developed in Chapter 2 that females exhibit a preference for sparse sites, presumably, because there they average higher success. As theory suggests (Janetos 1980), females judged boxes on a relative basis rather than against a fixed criterion. However, contrary to the generally accepted assumption that females compare all potential situations before making a decision, female house wrens apparently use a simpler strategy. In this species, female selection of nesting sites is best explained by the pool comparison tactic. I was unable, however, to discriminate between the area limited and area unlimited strategies. In either case, females restricted their choice to a small number of nesting sites (fewer than 3 boxes).

Similar results have been obtained for mottled sculpins, the only species for which strategies of female mate choice have been studied (Brown 1981). Female sculpins also weigh the relative quality of males but do not sample all males before choosing. Instead, they pick the first male that is better than the last one visited. In this case, the number of males visited is not known but is likely to be small. Furthermore, the theoretical work of Janetos

(1980) suggests that, in general, females should not sample more than 5 to 6 males.

Female house wrens may have restricted their choice to a small pool of boxes because of memory limitation. When memory capacity limits the number of situations a female could remember, two strategies could be adopted: (1) the sequential comparison tactic and (2) the area unlimited pool comparison tactic. The sequential tactic requires only that a female remembers the last two visited situations. Therefore, this tactic should be adopted when memory bcapacity is greatly limiting female choice (Wittenberger 1983). The sequential comparison tactic, however, did not provide an adequate explanation for female mate choice strategy in the house wren. In contrast, the area unlimited strategy provided a satisfactory explanation. This strategy, however, implies a slightly better ability to remember surveyed situations.

Alternatively, females may limit comparisons to few boxes if the benefits derived from comparing several alternatives are not great enough (Wittenberger 1983). In Chapter 1, I hypothesized that most of the variation in house wren reproductive success may be the result of random events. If this is so, we should expect benefits of comparing several boxes to be low and females to visit a restricted number of situations.

Although female house wrens may be free to move around and visit potential mates, finding distant unmated males may be difficult. Cues used by female wrens to locate unmated males remain to be determined but song seems to be the most obvious possibility for long distance identification (e.g. Marler 1977, Alatalo et al. (1982). However, air turbulence and reverberation from vegetation limit sound propagation (Wiley and Richards 1978, Richards and Wiley 1980). Therefore, it might be difficult for female wrens, in a relatively complex three dimensional habitat, to locate distant unmated singing males. To sample 3 males, simulated females had to travel over 600 m. When 4 males were compared, the traveled distance increases by about 350 m. It appears, therefore, that unmated males were fairly distant. Locating remote males may require more or less random searches, a process which could be time-consuming and, consequently, costly to females. The longer a female takes to make a decision, the greater are the chances that another female will select the best situation under consideration. Testing the above hypotheses requires further study.

Most cases of polygyny in birds may be explicable by the concept of a threshold in habitat quality (Verner 1964, Verner and Wilson 1966, Orians 1969). This hypothesis states that polygynous males provide compensatory benefits to females choosing them. In House Wrens, females apparently sample a limited number of candidates before choosing one to mate with. A female wren may accept her secondary status even though she might suffer a reduced reproductive success, if the chosen male was the best available candidate from the small pool sampled. Kendeigh (1941) and Freed (1986) reported that in their population, only 6 % of the males were polygynous. When polygyny is rare, however, it may not pay females to sample more prospects to avoid it (Alatalo, Lundberg and Stahlbrandt 1984). Hence, the small number of situations surveyed by females before pairing might account for the low incidence of polygyny in the house wren.

General Discussion

Current sexual selection theory holds that females choose mates on the basis of attributes that are important for their reproductive success. This prediction has received some support (e.g. Pleszczynska 1978, Wittenberger 1980). However, in most species, little information is available on specific criteria females use to select mates. But, knowledge of the cues used in female mate choice is critical to understanding the evolution of mating systems. In my work, I have conducted both descriptive and experimental studies to examine female mate choice in the house wren. My results suggest that reproductive success of female house wrens is influenced by the density of vegetation around their nesting cavities. The major cause of nesting mortality was predation by conspecifics. The high incidence of intraspecific predation presumably favors breeding in cavities with sparse surrounding vegetation because these sites allow more effective nest defense.

The concept of a threshold in habitat quality has been accepted as a general explanaition for the evolution of polygyny in passerines (Orians 1969), yet only one study supported the predictions of the model (Pleszczynska 1978).

In this model, female fitness is correlated with access to resources. A female may accept a secondary status if she receives compensatory benefits. The polygyny threshold model, as formulated by Orians (1969), assumes that females survey all opportunities before choosing. However, as pointed out by Janetos (1980), there might be several constraints on females and strategies that actually appear may at best approximate this assumption. The only field study that actually addressed the problem of mate choice strategies suggestes that female mottled sculpins may use a simpler strategy than the one of sampling all males. Female sculpins apparently pick the first male that is larger than the last one visited. Male size in this case is an indicator of parental ability (Brown 1981). Similarly, results of my study suggest that female house wrens restricted their choice to a limited number of candidates. Perhaps, in most species, one of the major assumptions of the polygyny threshold model does not hold and a more realistic model is needed for explaining the evolution of polygyny. For instance, Eliason (1986) found that the tendency of blackpoll warblers (Dendroica stiata) to return to a familiar site for breeding may constrain choice by experienced females. She argued that site fidelity can account for the low incidence of polygyny in her population. Bigamous mating in blackpoll warblers apparently result from the lack of unmated males near the former site of a returning female. Similarly, in house wrens, the low incidence of bigamy could potentially be explained by the limited number of boxes surveyed by females. Results of these studies, thus, suggest that, at least in some species, the evolution of the mating system will not be fully understood until female mate choice patterns are clarified.

General conclusions

(1) This study indicates that house wren reproductive success was greatly affected by predation. Wren attacks on conspecific nests appeared to be the most important source of nesting mortality.

(2) Nests placed in sparse vegetation were more likely to be successful than those placed in dense vegetation. The greater success of wrens in sparse vegetation may result from their more effective nest defense against conspecific intruders.

(3) Female house wrens preferentially selected boxes in sparse vegetation presumably because here they experience higher success.

(4) Male wing-length and vegetation density on territories were correlated with nestling weight but apparently did not influence female choice of a mate.

(5) Female house wrens apparently weighed the relative quality of a small number of boxes before choosing one. These results contradict the generally accepted assumption that females investigate all breeding opportunities before pairing.

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