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# Female choice and Polygyny in Red-winged Blackbirds
## (*Agelaius phoeniceus*)

by

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Biology

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## Abstract

The purpose of this study was to test four predictions of the Polygyny Threshold Model (PTM) using data from a population of Red-winged Blackbirds (*Agelaius phoeniceus*). Testing the PTM is a two-step process. First, we must identify the ecological correlates of nesting success. Second, establish whether these variables influence the settlement of females and correlate with male harem size.

Predation was the major factor reducing the nesting success of Redwings. Redwing nesting success was positively correlated with mean male nest defense score for the nestling stage. The nesting success of Redwings also increased with increasing distance from the nearest Wren nest. The removal of males (1987), however, did not affect the nesting success of females and thus it was concluded that male nest defense was not an important determinant of nesting success.

Results of the tests of the four predictions yielded limited support for the model. First, harem size was negatively correlated with the number of Wren nests per male territory. Second, large harems preferentially attracted the first primary and secondary females. Third, the order in which males were chosen by primary and secondary females was positively correlated with the number of

Wren nests in their territory. The settlement of tertiary females was, however, independent of the number of Wren nests per male territory. Fourth, the order in which males were chosen by primary and secondary females was positively correlated while that of primary and tertiary females was not correlated. All significant Spearman rank correlation coefficients, however, were relatively low (<0.35) suggesting that only a small portion of the variance in harem size and female settlement could be explained by the PTM. It was suggested that this might be the result of (1) the poor correlation between date of female settlement and date of first egg, (2) that other male and/or territory features influence nesting success and female choice or (3) the inadequacy of the PTM in explaining female settlement and male harem size.

Future studies should investigate these possibilities.

# Abstrait

Le but de cette étude était de mettre à l'épreuve quatre prédictions du modèle du "seuil de la polygamie" à l'aide de données recueillies au sein d'une population de carouges à épaulette (Agelaius phoeniceus).

La prédation sur les oisillons et les oeufs fûrent les facteurs les plus importants limitant le succès reproducteur des carouges. Le succès des nids de carouge était directement relié à la distance au plus près nid de troglodyte des marais. Le succès des nids de carouge était aussi directement relié a la défense du nid par le male pendant le stage des oisillons.

Les résultats des tests des quatres prédictions du modèle du "seuil de la polygamie" supportent faiblement le modèle. Premièrement, la taille du harem des males carouges était inversement proportionelle au nombre de nids de troglodyte dans leur territoire. Deuxièment, la taille du harem était inversement reliée a l'ordre dans lequel les males fûrent choissis par les femelles primaires et secondaires. Troisièment, l'ordre dans lequel les males fûrent choisis par les femelles primaires et secondaires était directement corrélé au nombre de nids de troglodytes présent dans leur territoire. L'établissement des femelles tertiares était cependant indépendant du

nombre de nid de troglodyte dans le territoire des males. Quatrièment, l'ordre dans lequel les males fûrent choisis par les femelles primaires et secondaires était directement relié. L'établissement des femelles tertiaires était cependant indépendant des femelles primaires. De plus, toutes les corrélations de Spearman étaient relativement faibles (<0.35) suggérant que le modèle du "seuil de la polygamie" ne pouvait expliquer qu'un faible pourcentage de la variation existant dans la taille des harems des males et l'établissement des femelles. Il fût proposé que ces resultats pourraient découler de (1) la faible corrélation entre la date d'etablissement des femelles et la date a laquelle elles ont pondues leur premier oeufs, (2) la possibilité que d'autres variables que je n'ai considéré influencent l'établissement des femelles ou (3) l'incapacité du modèle à expliquer l'etablissement des femelles.

# General Introduction

Traditionally, mating systems have been divided in three categories depending on the number of mates males and females have and whether males and females form pair bonds (e.g. Barash 1978). A pair bond is defined as a behavioral affiliation between an adult male and a female associated with reproduction (Barash 1978). The duration of pair bonds is quite variable and can range from a single breeding season to an entire lifetime (Wilson 1975). The first mating system is monogamy and is characterized by an individual establishing a pair bond with a single member of the opposite sex. The second, polygamy, is characterized by an individual pairing and entertaining several simultaneous pair bonds with members of the opposite sex. Polygamy is further divided into polygyny and polyandry. Polygyny refers to a male mating with several females and polyandry to a female mating with several males. The third mating system is promiscuity and is characterized by an absence of pair bonds. In this mating system, males and females mate and disperse shortly thereafter leaving, in most instances, only the female to care for the offspring.

Approximately 91% of all bird species are monogamous with the majority of remaining species being polygynous (Lack 1966). The ecological factors that favor the occurrence and maintenance of

polygyny is a topic that has received considerable theoretical attention in the past 25 years (Verner 1964; Verner and Willson 1966; Orians 1969; Downhower and Armitage 1971; Elliot 1975; Wittenberger 1976; Altmann et al. 1977; Searcy 1979a; Weatherhead and Robertson 1979; Lenington 1980; Picman 1980a; Alatalo et al. 1981; Garson et al. 1981; Lightbody 1986; Yasukawa and Searcy 1986; Leonard 1987). Polygyny is expected to be advantageous to males because the number of offspring produced per male usually increases with harem size (Verner 1964; Orians 1969; Holm 1973; Weatherhead and Robertson 1977a; Leonard 1987). The evolution of polygyny may, thus, depend on its advantages to females (Orians 1969). Polygyny can be advantageous to females if the members of a harem cooperate in raising the offspring. There is, however, little evidence suggesting that harem mates cooperate in raising the offspring (Ward and Zahavi 1973; Alexander 1974; Picman 1980a; Picman et al. 1987) and most studies suggest that females compete and are aggressive toward each other (Scott 1942; Nero and Emlen 1951; Nero 1956; Orians and Christman 1968; Wiley 1973; Robel and Ballard 1974; O'Connor 1976; Morton et al. 1978; Lenington 1980; Power and Doner 1980; Gowaty 1981; Hurly 1982; LaPrade and Graves 1982; Yasukawa and Searcy 1982; Beletsky 1982; Hannon 1983, 1984; Hurley and Robertson 1984, 1985). Harem mates may compete for male parental care, nest sites and/or food. Hence, polygyny probably incurs negative effects on females and it is probably better for them to mate monogamously rather than polygynously (e.g. Wilson

1975; Barash 1978).

This raises the following question: If polygyny is disadvantageous to females why do some females mate polygynously? Several models have been proposed to explain the occurrence and maintenance of polygyny. First, polygyny is the result of female biased sex ratios (Skutch 1935; Mayr 1939; Armstrong 1947; Verner 1964; Wittenberger 1976). Female biased sex ratios would force some females to settle with already mated males. This explanation may be relevant to certain populations but is hardly universal. Polygyny has been reported in populations with even sex ratios (Williams 1940; Haigh 1968), and females often settle with mated males despite the presence of bachelors (Verner 1964; Picman 1980a; Leonard 1987). Selander (1965) further proposed that unbalanced sex ratios are a consequence rather than a cause of polygyny.

The second model proposes that males regulate population density by not mating when resources are scarce and by mating polygynously when resources are abundant (Wynn Edwards 1962). This model relies heavily on group selection arguments and has been severely criticized (e.g. Selander 1965; Crook 1965; Orians 1969). Several studies also suggests that all females coming to the breeding grounds obtain mates and that there are no floating populations of females (Nero 1956; Orians 1969; Holcomb 1973; but

see Hurley and Robertson 1985).

The third model proposes that females cannot assess the mating status of males and enter polygynous relationships unknowningly (Alatalo et al. 1981). Again, this model may be relevant to certain species, in particular the Pied Flycatcher (Fidecula hypoleuca), but does not appear generally applicable. Male Pied Flycatchers after mating with one female in one territory, move to a second more or less distant territory and attempt to attract a second female. If successful, they return to the primary female and leave the secondary female to raise the offspring almost unassisted. The polyterritorial behavior of male Pied Flycatchers may enable them to hide their mated status (Alatalo et al. 1981). Male polyterritorial behavior is, however, uncommon and, in most species, males defend a single territory. In such cases, it may be difficult for males to hide their mated status. This is particularly true when females are aggressive toward one another (see references listed above).

The fourth model, the Polygyny Threshold Model (PTM: Verner 1964; Verner and Willson 1966; Orians 1969), proposes that polygyny will be selectively maintained when females mating bigamously on high quality territories raise at least as many offspring as females mating monogamously on low quality territories (Figure 1). The term territory quality (Wittenberger

1976) refers to territory features (e.g. water depth, vegetation height/cover, location within a colony) influencing nesting success. The minimum difference between high and low quality territories necessary for polygyny to evolve was called the "polygyny threshold" (Figure 1). Although the influence of male features (e.g. age/breeding experience, nest defense, provisioning of young) on nesting success was recognized (Orians 1969), the model does not account for such differences and considers male and territory quality functionally synonymous. That is, females choosing high quality territories also choose high quality males. The term male quality (Wittenberger 1976) refers to male features influencing nesting success.

Weatherhead and Robertson (1979) proposed an expansion of the PTM. The model, called the Sexy Son Hypothesis, suggests that male and territory quality are not necessarily correlated and that females can offset the costs of polygyny by settling with high quality males. Weatherhead and Robertson (1979) argued that females might suffer a reduced immediate fitness by settling on a low quality territory with a "sexy" male but would ultimately gain an advantage through the production of "sexy sons" that would in turn attract large harems. This model has been severely criticized by Heisler (1981), Searcy and Yasukawa (1981) and Wittenberger (1981). Williams (1975) and Maynard Smith (1978) also suggested that the heritability of traits affecting fitness is low. Finally,

Kirkpatrick (1985) showed that forfeiting immediate for ultimate reproductive success is evolutionary unstable.

The Red-winged Blackbird (Agelaius phoeniceus) is a widespread North American passerine that breeds in both marsh and upland habitats. Males defend territories by a complex array of vocalizations and displays (Orians and Christman 1968) and are normally polygynous with harems up to 15 being reported by Orians (1980). The average harem size, however, of 33 populations from 18 localities is 3.0 (Standard Error=0.227; Appendix I).

Polygyny in Redwings is generally believed to be the result of heterogeneity in quality of male territories as predicted by the PTM (Orians 1969, 1972, 1980; Holm 1973; Searcy 1979a; Lenington 1980; Yasukawa 1981; Yasukawa and Searcy 1986). A reassessment of this conclusion is necessary for three reasons. First, the three studies (Holm 1973; Weatherhead and Robertson 1977a; Lenington 1980) that directly tested the relationship between territory quality and harem size failed to find a significant correlation. Second, the assumption that male and territory quality are positively associated has never been tested. In fact, Eckert and Weatherhead (1987a) suggested that male and territory quality may not be associated in Redwings and that male quality may independently influence female choice of breeding situation (Wittenberger 1976). The term breeding situation refers to the combined affects of male and territory

quality on nesting success. Third, none of the previous studies of Redwing polygyny tested the predictions of the PTM concerning the settlement of females (Altmann et al. 1977; Garson et al. 1981).

The purpose of my study is to provide the first comprehensive test of the PTM for Red-winged Blackbirds. Testing the PTM is a two-step process. In Chapter I, I identify the male and territory correlates of nesting success and discuss the potential cues of female choice. In Chapter II, I test the major predictions of the model, including those concerning the settlement of females, and determine whether the PTM can be used to explain the occurrence and maintenance of polygyny in Redwings.

# CHAPTER I

## Ecological Correlates of Nesting Success in Red-winged Blackbirds

### INTRODUCTION

Trivers (1972) proposed that the sex with the greatest parental investment will be the most discriminating in mate choice. Trivers defined 'investment' as 'anything done by a parent to increase the chances of survival of existing offspring, at the expense of the parent's ability to invest in future offspring'. Eggs are more costly to produce than sperm and, in most species, females invest more in raising the offspring than males. Hence, females are assumed to be the most discriminating in mate choice.

Several studies attempted to identify the characteristics females might use to select mates (e.g. Verner 1964; Weatherhead and Robertson 1977a; Best 1977; Pleszcynska 1978; Wittenberger 1980; Askenmo 1980; Nagata 1986). In most bird species, males

defend territories and thus female choice of mate may be based on male and/or habitat features. Searcy (1979a) proposed that the factors influencing female choice of mate should also affect reproductive success. Hence, identification of the major causes of mortality and the ecological correlates of female reproductive success are necessary to determine the potential cues of female choice.

The Red-winged Blackbird is a polygynous resource defense (Emlen and Oring 1977) passerine. Numerous studies have shown correlations between territory features and Redwing nesting success. Yet, few generalizations can be made. Moreover, male attributes have seldom been considered. The following is a brief summary of the findings of these studies.

## Territory features

Goddard and Board (1967), Holm (1973) and Lenington (1980) suggested that nests built over deep water were more successful than those over shallow water. The relationship reported by Goddard and Board (1967), however, was not significant (Appendix II) while Lenington (1980) reported a significant association in only one of six marshes. Holm (1973) was unable to conclusively demonstrate that water depth influenced nesting success since deep marshes were associated with bulrush _Scirpus_ sp. and shallow ones with

cattail Typha lattifolia.

Lenington (1980) found a positive correlation between vegetation density and nesting success. Weatherhead and Robertson (1977a), however, showed the opposite while Caccamise (1977) failed to find any relationship between vegetation density and nesting success.

The influence of nest height on nesting success is also ambiguous. Meanley and Webb (1963), Holcomb and Twiest (1968) and Holm (1973) found that nesting success increased with nest height while Godard and Board (1967) and Weatherhead and Robertson (1977a) showed the opposite. Moreover, the positive relationships reported by Meanley and Webb (1963) and Holcomb and Twiest (1968) may have been due to difference in nest substrate rather than height (Francis 1971).

Lenington (1980) did not find any relationship between the success of a nest and the distance to the nearest edge of the marsh. Distance to edge has, however, been shown to be an important determinant of nesting success in Yellow-headed Blackbirds, Xantocephalus xantocephalus, (Richter 1984) and in Marsh Wrens, Cistothorus palustris, Leonard (1987).

Picman (1980a, b) showed that nesting success increased with decreasing distance to the nearest simultaneously active

conspecific while Caccamise (1977) reported the opposite.

Picman (1980a, b, 1983) reported that Redwing nesting success was negatively correlated with distance to the nearest Marsh Wren. This relationship has never been reexamined but merits additional consideration since both species often breed in the same marsh (Picman 1980a) and because Wrens may be responsible for a large number of Redwing nesting losses (Picman 1980a, b, 1983).

## Male characteristics

Males may influence nesting success in two ways. First, males can help in feeding the nestling. Second, they can defend the nest against predators. Patterson (1979), Fiala (1981), Searcy and Yasukawa (1982) and Muldal et al. (1986) showed that male provisioning of offspring significantly increased nesting success. The effect of male nest defense on nesting success is, however, unclear. Yasukawa et al. (1987) proposed that male nest defense influences nesting success but did not show any correlation between male nest defense and nesting success while Searcy (1979a) showed that male nest defense had no effect on nesting success. Male nest defense has, however, been shown to be an important determinant of nesting success in Stonechats, _Saxicola torquata_ (Grieg-Smith 1980), Kingbirds, _Tyrannus tyrannus_ (Blancher and Robertson 1982), and in American Goldfinches, _Spinis tristis_

(Knight and Temple 1986a).

The effect of male breeding experience on nest success is also unclear and open to speculation. Eckert and Weatherhead (1987b) showed that male Redwing feeding of nestlings was correlated with courtship behavior and Yasukawa (1979) observed that courtship behavior was correlated with male Redwing breeding experience. Yet, male breeding experience and nesting success have never been directly correlated.

The aim of this chapter is to: (1) determine the nesting success of Redwings and the major causes of mortality, (2) reassess the effect of habitat features on nesting success and (3) determine whether variation in Redwing nesting success can be explained in terms of male nest defense ability and/or breeding experience.

# MATERIAL AND METHODS

## Study site

This study was conducted from 1 May to 30 June 1983-1985 and 1987 in a homogenous cattail marsh located 15 km southeast of Ottawa, Ontario, Canada in the Mer Bleue conservation area. The study site was 9 ha in area in 1983 and 1984 but was increased to 10.5 ha in 1985 and to 11.5 ha in 1987. The area was divided into a grid of 20m X 20m squares, marked by 2 m high wooden stakes. Four passerine species, Red-winged Blackbirds, Marsh Wrens, Swamp Sparrows (_Melospiza georgiana_) and Common Grackles (_Quiscalus quiscula_) bred in the marsh.

## General field methods

Descriptive information on the breeding biology of Redwings was gathered from 1983-1985. In 1987, an experiment was designed to test the effect of male nest defense on nesting success.

Redwing males were captured using traps baited with cracked corn and decoy traps (Smith 1972), measured, banded with a CWS aluminum band and a unique combination of plastic colored leg

bands and released. Wing length (WL) was estimated with a ruler as in Godfrey (1976) to the nearest 0.5 mm. Bill and tarsus length respectively were measured with calipers as in Godfrey (1976) to the nearest 0.1 mm. Weight (W) was taken to the nearest 0.5 g with a 100g Pesola spring scale. Male physical condition was estimated by the following formula (Searcy 1979b):

$$\text{CONDITION INDEX} = (W / WL^3) \times 1000 \qquad \text{Equation (1)}$$

Females were captured using decoy traps (Smith 1972) and color banded in 1985 only.

Male territories were plotted weekly on calm, sunny days from 0600-1000 hours. Territory boundaries were mapped by plotting the location of song perches, flight paths and territorial disputes on a scale map of the study area. Territory boundaries were delimited using the minimum convex polygon technique. An Apple Graphics Tablet was used to calculate the area of male territories.

Twice a week the area was searched for nests by walking along 10-m interval transects located throughout the marsh. Nests found for the first time were plotted on a map and marked by placing a numbered label 1 m from the nest. Nest contents and 4 nest features were recorded:

(1) nest height relative to water level;
(2) vegetation density. This was achieved by counting the number of evenly spaced 1 cm red dots on a 50 cm stick placed on top of the nest. The count was taken from a 1 m distance west of the nest;
(3) height of the vegetation supporting the nest;
(4) water depth. Water depth was measured by estimating the water depth at 3 different points within a 1 m radius of the nest and recording the deepest measure. Water depth was measured in 1983 and 1985 only.

Male nest defense effort was measured in 1983 and 1984 by rating their reactions to a human observer searching for nests. Responses were taken when the observer was standing 1 m from an active nest. The scoring was done according to the following scheme:

(0) not seen or no visual and audible response;
(1) audible and/or visual response and bird >10 m from observer;
(2) audible and/or visual response and bird <10 m from observer;
(3) attack without physical contact with the observer;
(4) attack with physical contact.

On subsequent visits, only nest contents and male nest defense score were recorded. Nests were monitored until they failed or the young fledged.

## A) BREEDING BIOLOGY OF REDWINGS (1983-1985)

### Breeding success

Egg and nestling losses were categorized into predetermined classes of mortality. The classes were determined by changes in nest contents and in the physical condition of the nest between visits. **Egg abandonment** refers to clutches which remained unhatched beyond the normal incubation period (Orians 1961). **Unhatched eggs** refers to cases where one or two eggs remained unhatched while the others had hatched. Unhatched eggs includes infertile eggs and embryo mortality. **Egg predation** refers to mortality of total clutches and was often accompanied by partial or total nest destruction. **Nestling abandonment** includes cases where an entire brood was found dead without any of the nestling or the nest being disturbed. **Nestling predation** was characterized by the loss of an entire brood on a single day. Signs of nest tampering were usually evident. **Nestling starvation** comprised cases where a single nestling was found dead or disappeared while the remaining brood members and the nest appeared normal.

### Correlates of female reproductive success

A BMDP program for logistic regression was used to determine

the correlates of nesting success. Successful nests were defined as those fledging at least one offspring. This statistical technique was used because nesting success is a binary variable (failed or successful). A total of 17 independent variables were used. They included seven nest features:

(1) nest height,
(2) water depth,
(3) vegetation height,
(4) vegetation density,
(5) distance to the nearest edge of the marsh,
(6) distance to the nearest active Redwing nest on the date a female settled. Female settling date was estimated from the date the first egg was laid (Yasukawa and Searcy 1981 but see Lenington 1980).
(7) distance to the nearest Marsh Wren nest on the date a female settled,

four male nest defense scores;

(8) male defense during the building stage,
(9) male defense during the egg stage,
(10) male defense during the incubation stage,
(11) male defense during the nestling stage.

The scores were estimated by averaging all responses collected for

each nesting stage. Nesting stages were defined as Orians (1961). Responses were broken down according to nest stage because male response varies with the frequency of human visits to a nest (Knight and Temple 1986b) or with the nesting cycle (Smith 1950; Erpino 1968; Barash 1975; Curio 1975; D'arms 1978; Weatherhead 1979, 1982; Andersson et al. 1980; Grieg-Smith 1980; Patterson et al. 1980; Biermann and Robertson 1981; East 1981; Blancher and Robertson 1982; Roell and Bossema 1982; Merritt 1984; Shields 1984).

The independent variables also included five male physical characteristics;

(12) wing length,
(13) tarsus length,
(14) bill length,
(15) weight,
(16) condition index,

and

(17) male breeding experience. The number of years a male acquired at least one mate in the study area was used to estimate his breeding experience.

When 17 correlations are computed at a significance level of 0.05,

the probability of obtaining at least one spurious correlation is

$$1-(0.95)^{17} = 0.582$$

The probability of obtaining at least one spurious correlation out of 17 at a significance level of 0.01 is

$$1-(0.99)^{17} = 0.157$$

Hence, to reduce the probability of obtaining spurious significant correlations, significance levels were set at 0.01 in the logistic regression analyses.

## B) EXPERIMENTAL MANIPULATION OF MALE NEST DEFENSE (1987)

In 1987, the effect of male nest defense on nesting success was tested by removing resident males after females completed their clutches. The nest defense effort of the female and of the new male defending the territory were scored according to the scheme used in 1983 and 1984.

Seventeen males were removed from their territories using decoy traps (Smith 1972) and traps baited with cracked corn. The removed birds were housed in the University of Ottawa Animal Care

Facility and later released. Seven males were removed on 13 May, 4 on 21 May, 1 on 23 May, 2 on 24 May, 1 on 31 May, 1 on 2 June and 1 on 4 June. A total of 23 females were "widowed". Twenty of 23 (87%) females were incubating and in the other 3 cases, the eggs were hatching on the day the male was removed.

## RESULTS

### Nesting success

Nesting began in late April or early May, depending on the year, and extended to early July. A total of 361 active Redwing nests was found of which 122 (34%) fledged at least one young. Table 1 shows the nesting success and sources of Redwing nesting mortality. Predation was the most important cause of nesting failure (64% of all nesting losses) with egg predation being more important than nestling predation (Table 1). Most successful nests (64%; 78/122) suffered partial losses. These losses were the result of unhatched eggs and nestling starvation.

### Potential predators of Redwing nests

In 1985, Picman's "camera setups" (1987a) were used to identify the potential predators of Redwing nests. During this study, artificial nests baited with a Blue Breasted Quail (<u>Coturnix</u> <u>coturnix</u>) egg were placed in the marsh where Redwings bred. The artificial nests were placed along a 200 m transect at 20 m intervals. A break cable attached to the egg at one end and to a camera 1 m away at the other took pictures of predation

events at experimental nests. Only 2 terrestrial predators, Raccoons, Procyon lotor, and Short-tailed Weasels , Mustela erminea, and 1 avian predator, Marsh Wrens, were observed taking or breaking eggs at these nests. Raccoons (64 pictures) were more important than Weasels and Wrens combined (23 pictures each).

## Correlates of nesting success

Table 2 shows that only two variables were significantly associated with Redwing nesting success. First, Redwing nesting success was positively correlated with distance to the nearest Wren nest (Table 2). Second, the reproductive success of females increased with increasing mean male nest defense score for the nestling period (Table 2). It is noteworthy that male nest defense scores for the egg and incubation stages were significantly correlated with that of the nestling stage (building: Spearman $r=0.022$, $n=59$, $p>0.400$; egg: Spearman $r=0.385$, $n=49$, $p<0.005$; incubation: Spearman $r=0.418$, $n=71$, $p<0.001$).

## Experimental manipulation of male nest defense

Twenty eight of 50 (56%) control nests (male not removed) were successful (fledged at least one young) but only 8 of 23 (35%) experimental nests (male removed following clutch completion) were successful. The nesting success of control and experimental,however, nests were not significantly different (X2 Yates=1.99, $P>0.10$).

# DISCUSSION

## Factors affecting nesting success

Egg and nestling predation were the major factors reducing the reproductive success of Redwings in this study (Table 2). This result is consistent with that of Orians (1961), Holcomb and Twiest (1968), Robertson (1972, 1973), Caccamise (1976, 1977, 1978), Dolbeer (1976), Picman (1977a, b, 1980a, b, c, 1983), Weatherhead and Robertson (1977a), Searcy (1979a) and Eckert and Weatherhead (1987b). Moreover, Raccoons, Marsh Wrens and Short-tailed Weasels appear to be responsible for most nesting losses. Mammalian predation on nests of marsh-nesting species has been documented or discussed by Allen (1914), Hamilton (1940), Stollberg and Hine (1952), Sargeant et al. (1973), Knight et al. (1985) and Leonard (1987). The negative effect of Marsh Wrens on the reproductive success of sympatric Blackbirds has been documented or discussed by Allen (1914), Orians and Willson (1964), Burt (1970), Picman (1977a, b, 1980a, b, c, 1983), Runyan (1979), Bump (1983), Picman et al. (1987) and A. Isabelle (unpublished data).

## Correlates of nesting success and potential cues of female choice of mate

Searcy (1979a) proposed three criteria to identify the potential cues of female choice of mate. First, factors influencing female choice should influence nesting success. Table 2 shows that the proximity of Wrens and male nest defense meet this criterion. The removal of males in 1987, however, suggests that male nest defense effort has no effect on nesting success. This supports a similar finding by Searcy (1979a). Moreover, because the manipulation of a variable is a more powerful test than a correlation, I conclude that male nest defense has no effect on female nesting success and should not influence female choice. Yasukawa et al. (1987) showed that although male nest defense effort may influence nesting success it affected female choice of mate in only one of the three habitats they studied (deep marsh). Studies showing the negative effect of Wrens on the reproductive success of co-occurring Blackbirds have been listed in the previous paragraph.

It is noteworthy that the distance to the edge of the marsh and water depth at the base of the nest were negatively correlated with the number of Wren nests in the male territory settled (distance to edge: Spearman $r=-0.231$, $n=148$, $p<0.005$; water depth: Spearman $r=-0.255$, $n=112$, $p<0.005$). Several studies show that nesting success is positively correlated with distance to edge and water depth (e.g. Richter (1984) and A. Isabelle (unpublished data) in Yellow-Headed Blackbirds, *Xantocephalus xantocephalus*, and

Leonard (1987) in Marsh Wrens. Moreover, most of these studies used distance to edge and/or water depth as a relative measure of accessibility of territories to terrestrial predators. Females settling in the deep marsh far from the edge of the marsh may thus avoid both Wren and mammalian predation.

Second, characteristics influencing female choice must be assessable prior to mating (Searcy 1979a). Three lines of evidence suggest that the location of Wrens might have been predictable. First, Wrens build large, conspicuous dome-shaped nests. Second, the number of Wren nests per male territory was negatively correlated with distance to edge and water depth at the base of the nest (see previous paragraph). Third, the location of Wren nests appeared to be predictable between years (Table 3).

Third, characteristics influencing female choice of mate must be variable (1979a). From Table 2 it appears that the proximity of Wren nests varies within the study area.

In summary, the proximity of Wrens is the only variable scored that meets Searcy's (1979a) requirements for cues affecting female choice of mate. It is interesting the proximity of Wren nests can be linked to predation. This should not be surprising as predation is the major factor reducing the reproductive success of most marsh-nesting populations of Redwings.

# CHAPTER TWO

## Polygyny in Redwings:

## A Test of the Polygyny Threshold Model

### INTRODUCTION

Polygyny is expected to be advantageous to males because the number of offspring produced per male usually increases with harem size (Verner 1964; Orians 1969, 1972, 1980; Holm 1973; Weatherhead and Robertson 1977a; Leonard 1987). Because of interfemale competition and reduced male parental care, polygyny is ,however, expected to incur costs and be disadvantageous to females (Orians 1969).

Verner (1964), Verner and Willson (1966) and later Orians (1969) proposed a model to explain how females can offset the costs of polygyny. The model was termed the Polygyny Threshold Model (PTM) and suggests that high quality territories compensate females for their polygynous status (Figure 1). That is, polygyny is maintained because females mated bigamously on high quality territories can raise at least as many offspring as monogamously

mated females on low quality territories (Figure 1). The minimum difference between high and low quality territories necessary for polygyny to be maintained was termed the "polygyny threshold" (Figure 1). Although the influence of male quality on female reproductive success was recognized (Orians 1969), the model does not account for such differences and considers male and territory quality functionally synonymous. That is, females choosing high quality territories also choose high quality males.

The PTM is the most widely accepted explanation for the evolution of resource defense polygyny (Emlen and Oring 1977) in passerines (Verner and Willson 1966; Orians 1969, 1972, 1980; Holm 1973; Altmann et al. 1977; Pleszcynska 1978; Searcy 1979a; Garson et al. 1981; Yasukawa and Searcy 1986).

Altmann et al. (1977) and Garson et al. (1981) reviewed the PTM and proposed predictions that can be used to test the model.

I) Territory quality should be positively correlated with male harem size (Altmann et al. 1977; Garson et al. 1981). In this study, the harem size of male Redwings should be negatively correlated with the number of Wren nests in their territory This is because the most "attractive" territories should be those with few or no Wren nests.

II) Male pairing success (harem size) should be negatively correlated with the order in which males are chosen by primary, secondary, tertiary and etc. females (Altmann et al. 1977; Garson et al. 1981). Large harems are presumably associated with high quality territories and should acquire the first primary, secondary, tertiary and so on females.

III) Territory quality should be negatively correlated with the order in which males are chosen by primary, secondary, tertiary and etc. females (Altmann et al. 1977). High quality territories should attract the first primary, secondary, tertiary and so on females. In this study, territories with no or few Wren nests should acquire the first primary, secondary and tertiary females. Again, this is because the most "attractive" territories should be those with few or no Wren nests.

IV) The order in which males are chosen by primary females should be positively correlated with the order in which males are chosen by subsequent females (Altmann et al. 1977). That is, the first females should choose the "best" breeding situations and these choices should also be the "best" for later settling females if they are to be compensated for the costs of polygyny.

The Red-winged Blackbird appears to be an ideal species to

test the PTM. First, males are normally polygynous (Appendix I) and the pairing success of males within populations is highly variable (Payne 1979; Searcy and Yasukawa 1983). Second, the nesting success female Redwings appears to be influenced by habitat features (e.g. Brenner 1966; Goddard and Board 1967; Holcomb and Twiest 1968; Holm 1973; Robertson 1972, 1973; Weatherhead and Robertson 1977a, b; Searcy 1979a; Lenington 1980; present study Chapter 1). And third, the territorial behavior of males enables us to estimate territory quality. In spite of this, earlier tests of the PTM considering only territory quality have failed to produce conclusive results (e.g. Holm 1973; Weatherhead and Robertson 1977a, b; Lenington 1980). Holm (1973) showed that harems were larger in cattail than in bulrush territories but failed to demonstrate that nest support (cattail vs bulrush) influenced fledging success. Weatherhead and Robertson (1977a, b) and Lenington (1980) were unable to show any relationship between territory size and harem size. Two explanations can be given to account for these results. First, although all studies recognized that predation was the most important factor reducing Redwing reproductive success, none considered the effect of Marsh Wrens on female Redwing fitness and choice of breeding situation. This may be an important variable because Wrens often breed in the same marsh as Redwings (Picman 1980a) and may be responsible for a large number of nesting losses in co-occurring Blackbird (Allen 1914; Orians and Willson 1964; Picman 1977, 1980a, b, c; Runyan 1979; Bump 1983; Picman et al. 1987; A. Isabelle unpublished data;

present study Chapter I). Second, previous tests of the PTM in Redwings considered only one of the five predictions listed above (Prediction I). A more direct test of the model, however, consists in testing the predictions concerning the settlement of females (Predictions II, III, IV). These predictions may also be more reliable than correlations between male and territory quality because they do not rely on our ability to measure features that are important to females (Predictions II, and IV).

The aim of this Chapter is to (1) determine the effect of one aspect of territory quality (proximity of Wrens) and and (2) provide the first comprehensive test of the Polygyny Threshold Model for the species by testing the four predictions previously listed.

## MATERIAL AND METHODS

This study was conducted from 1 May to 30 June 1985 in a homogeneous cattail marsh located 15 km south east of Ottawa, Ontario, Canada in the Mer Bleue conservation area. See Chapter I for a description of the study site and field methods.

Territory quality has been defined as any territory feature that influences nesting success (Wittenberger 1976). Distance to the nearest Marsh Wren nest was the only nest feature to correlate with Redwing nesting success (Chapter I). I thus estimated territory quality by counting the number of Wren nests present on male territories on 1 June of each year. Most female Redwings had settled by this date.

The maximum number of simultaneously active Redwing nests on a territory was used to estimate male harem size. Female pairing date was estimated from the date the first egg was laid (Yasukawa and Searcy 1981 but see Lenington 1981). Successful nests were defined as those fledging at least one offspring.

Statistical tests are one-tailed because each correlation is a test of a directional prediction. Significance levels were set at 0.05 because only one or two correlations were calculated per prediction.

# RESULTS

**PREDICTION I:** Territory quality should be positively correlated with male pairing success (Altmann et al. 1977; Garson et al. 1981). In this study, the number of Wren nests per male territory should be negatively correlated with harem size.

Figure 2 shows that harem size was negatively correlated with the number of Wren nests per male territory as predicted by the PTM.

**PREDICTION II:** Harem size should be negatively correlated with the order in which males are chosen by primary, secondary, tertiary and etc. females (Altmann et al. 1977; Garson et al. 1981)

Figures 3 and 4 show that harem size was negatively correlated with the order in which males were chosen by primary and secondary females, respectively. It was impossible to test this prediction for tertiary females because only 3 males were tetragamous during the study.

**PREDICTION III:** Territory quality should be negatively correlated with the order in which males are chosen by primary, secondary, tertiary and etc. females. (Altmann et al. 1977). In this study, territories with no or few Wren nests should acquire the first primary, secondary and tertiary females.

Figure 5 shows that the order in which male Redwings were chosen by primary females was positively correlated with the number of Wren nests on their territory.

Figure 6 shows that the order in which male Redwings were chosen by secondary females was positively correlated with the number of Wren nests on their territory.

Figures 7 shows that the number of Wren nests per male territory did not influence the settlement of tertiary females.

**PREDICTION IV:** The order in which males are chosen by primary females should be positively correlated with the order in which males are chosen by secondary, tertiary and etc females. (Altmann et al. 1977)

Figure 8 shows that the settlement order of primary and secondary females were positively correlated. The settlement order of primary and tertiary females, however, were not correlated (Figure 9).

## DISCUSSION

Four predictions of the PTM were tested using data from three breeding seasons of Red-winged Blackbirds. All predictions were supported to some extent.

As predicted by the PTM, large harems and high quality territories also attracted the first primary and secondary females (Predictions II and III). As predicted, the settlement order of primary and secondary females were positively correlated (Prediction IV). The settlement order of tertiary females, however, was not correlated with territory quality and the settlement of primary and tertiary females also were not correlated. Two explanations can be proposed to account for the behavior of tertiary females. First, the ranking of breeding situations by territory quality changed during the period females settled. That is, territories that were of high quality to primary and secondary females were perceived as low quality by tertiary females. This seems unlikely as, on average, only 8 days separated the settlement of primary and tertiary females. Second, tertiary females are young, inexperienced females possibly unable to accurately assess the quality of breeding situations. This is possible, as Crawford (1977) showed that the last Redwing females to settle are mostly yearlings. The assumption that yearling females cannot accurately assess breeding situations remains to be verified.

In this study, female settlement and female order within a harem were estimated using the date the first egg was laid. Lenington (1980) and Teater at al. (1987 in press), however, suggest that there might only be a weak correlation between date of female settlement and date of first egg. Although this result is interesting, it is questionable for marsh-nesting blackbirds since Lenington's study was based on a relatively small size and Teater et al. 's (1987 in press) based on an upland population of Redwings. Nevertheless, the possibility that date of settlement and date of first egg are not correlated exists and must be considered.

Could a poor correlation between date of female settlement and date of first egg affect the results of this study?

If the date of first egg is a poor index of female settlement this might lead to errors in the assignment of female ranks within harems (primary, secondary, tertiary, etc). It is, however, believed that the weak relationship between date of female settlement and date of first egg only reduced the value of the Spearman rank correlation coefficients computed in tests of Predictions II, III and IV.

In summary, although the results from this study failed to falsify the model, they provide only limited support for the PTM.

This conclusion is based on two points. First, the settlement of tertiary females was independent of the number of Wren nests per male territory and the settlement of primary and tertiary females were not associated as predicted by the model. Second, all significant Spearman rank correlation coefficients were relatively low (<0.35) suggesting that only a small portion of the variance in harem size and female settlement could be explained by the PTM. This might be the result of (1) the poor correlation between date of female settlement and date of first egg, (2) that other male and/or territory features influence nesting success and female choice or (3) the inadequacy of the PTM in explaining female settlement and male harem size. Future studies should thus keep these problems in mind and attempt to resolve them.

# GENERAL CONCLUSIONS

1) Data from three breeding seasons of Red-winged Blackbirds were used to: (1) determine the potential cues of female choice in Redwings and (2) test four predictions of the Polygyny Threshold Model.

2) Predation was the major source of nesting failure and egg predation was more important than nestling predation.

3) The potential predators of Redwing nests included Raccoons, Short-tailed Weasels and Marsh Wrens.

4) Searcy (1979) proposed that cues affecting female choice should (1) influence nesting success, (2) be assessable prior to mating and (3) be variable. First, both the distance to the nearest Marsh Wren nests and male Redwing nest defense were negatively correlated with nesting success. The removal of males, however, suggested that male nest defense has no effect on nesting success. Because the manipulation of variable provides a more powerful test than a correlation, I concluded that male nest defense was not an important determinant of

nesting success in Redwings. Second, the number of Wren nests per male Redwing territory appeared to be assessable prior to mating. Third, the number of Wren nests per male Redwing territory also appeared to be variable in the population studied.

5) All four predictions of the PTM tested were supported to some extent. First, harem size was negatively correlated with the number of Wren nests per male territory. Second, large harems preferentially attracted the first primary and secondary females. Third, the order in which males were chosen by primary and secondary females was positively correlated with the number of Wren nests in their territory. The order in which males were chosen by tertiary females was, however, independent of the number of Wren nests per male Redwing territory. Fourth, the order in which males were chosen by primary and secondary females was positively correlated while that of primary and tertiary females was not correlated.

7) Although the results from this study failed to falsify the model, they provide only limited support for the PTM. This conclusion is based on two points. First, the settlement of tertiary females was independent of the number of Wren nests per male territory and the settlement of primary and tertiary females were not associated as predicted by the model. Second, all significant Spearman rank correlation coefficients were

relatively low (<0.35) suggesting that only a small portion of the variance in harem size and female settlement could be explained by the PTM. It has been suggested that this might be the result of (1) the poor correlation between date of female settlement and date of first egg, (2) that other male and/or territory features influence nesting success and female choice or (3) the inadequacy of the PTM in explaining female settlement and male harem size.

Figure 1. Polygyny Threshold Model. The top curve shows the relationship between territory quality and the fitness of primary females. The lower curve shows the relationship between territory quality and the fitness of secondary females. The model predicts that the first female (f1) to arrive to the breeding ground should settle in territory T2 if she is to maximize her reproductive output. The second female (f2) may either mate bigamously in T2 or monogamously in T1 since the expected fitness is the same in both cases. That is because territory T2 compensates the female for her secondary mating status. Distance "a" is the "polygyny threshold" and is the minimum difference between high and low quality territories, T2 and T1 respectively, necessary to favor bigamous matings by females (slightly modified from Orians 1969).

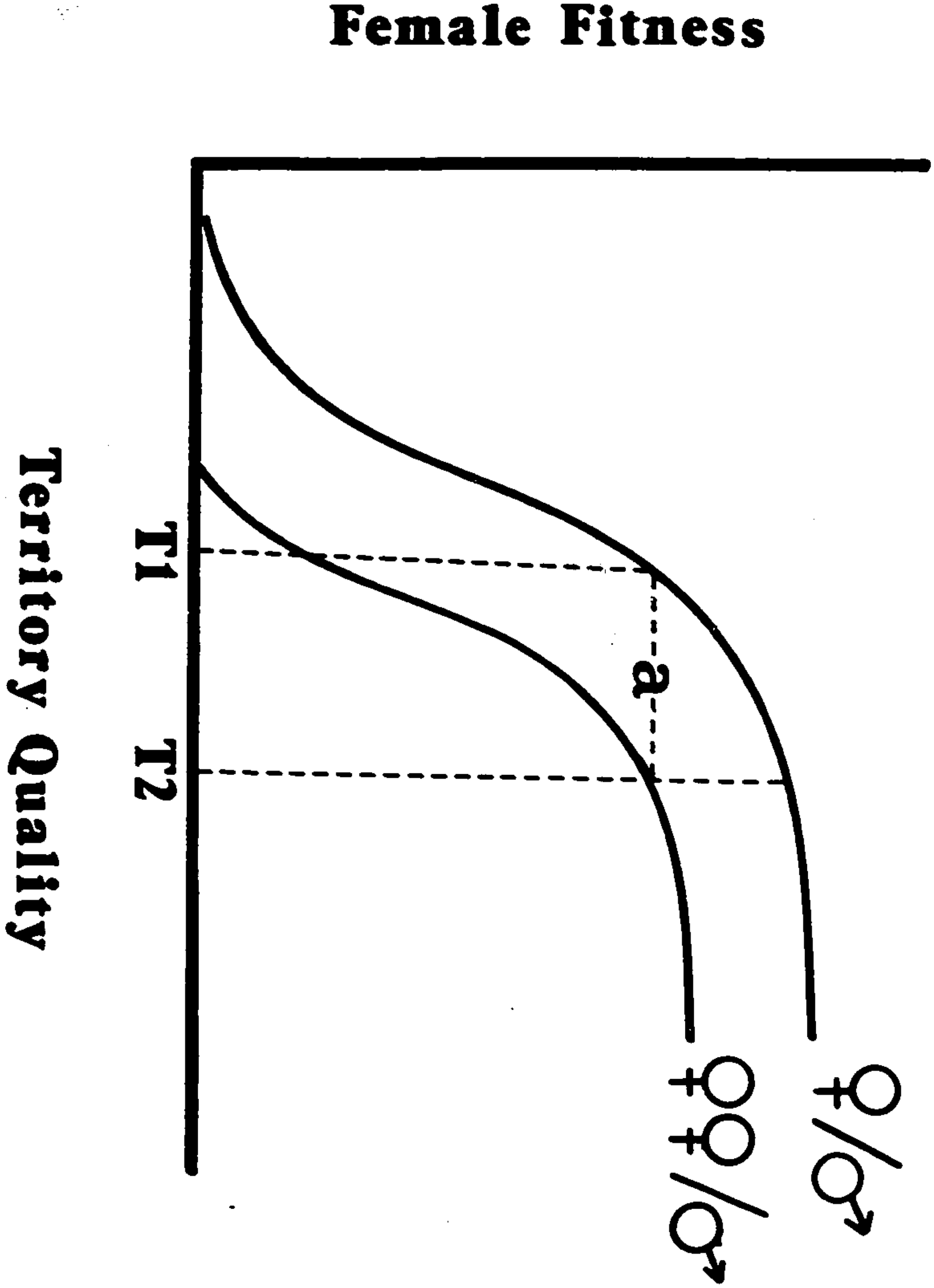

Female Fitness
Territory Quality
T1
T2
a
♀/♂
♀♀/♂

Figure 2. Harem size of male Redwings versus the number of Wren nests per male Redwing territory (Prediction I).

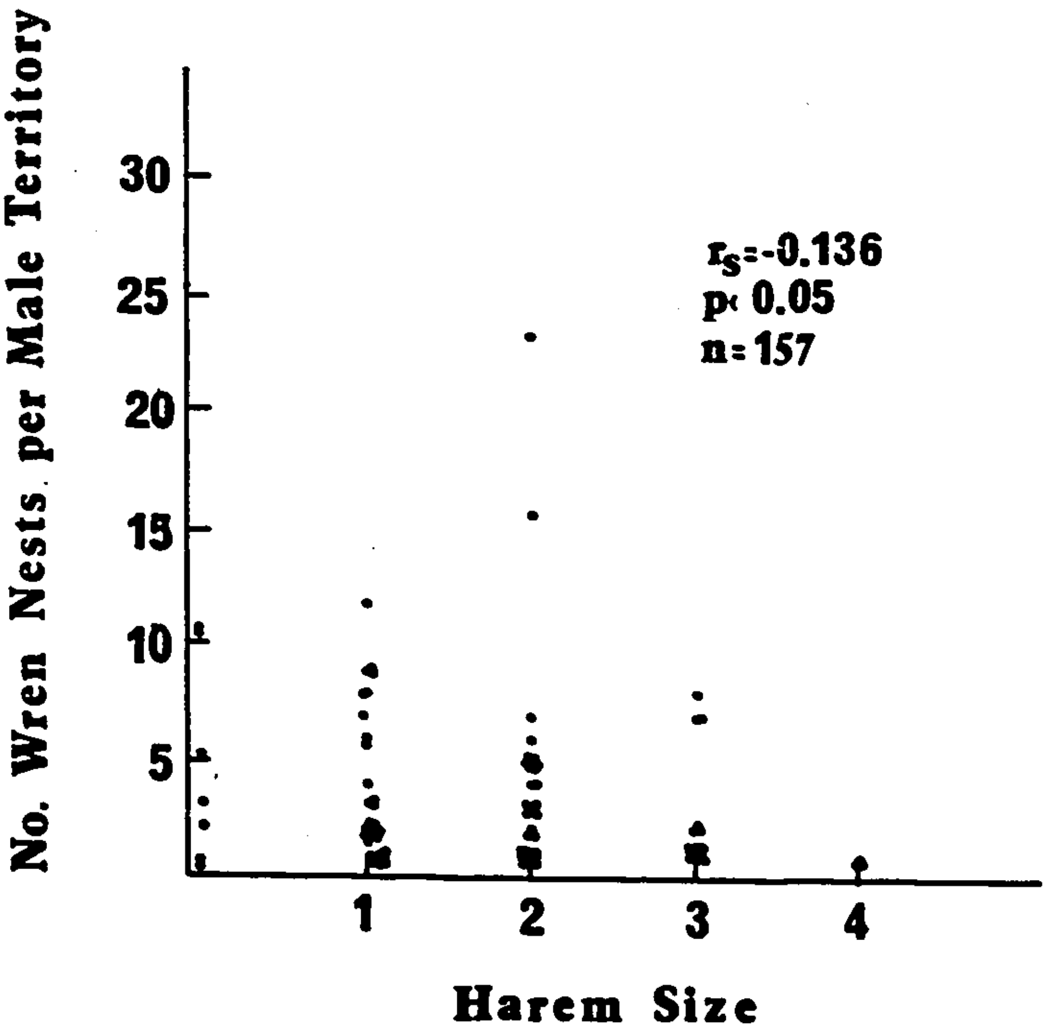

No. Wren Nests per Male Territory
30
25
20
15
10
5
1
2
3
4
Harem Size
$r_s$=-0.136
p< 0.05
n=157

Figure 3. Harem size of male Redwings versus the order in which male Redwings were chosen by primary females (Prediction II).

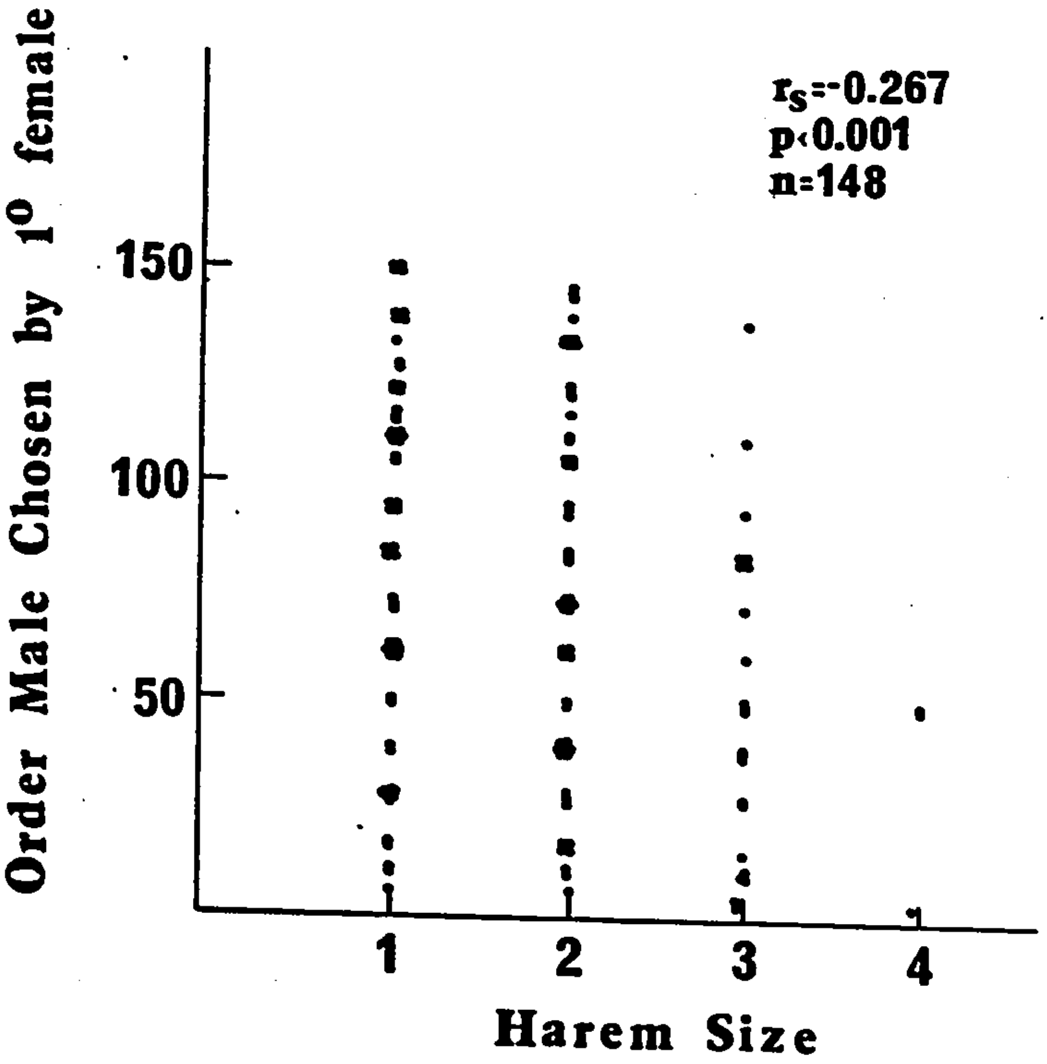

$r_s = -0.267$
$p < 0.001$
$n = 148$
Order Male Chosen by 1° female
150
100
50
1
2
3
4
Harem Size

Figure 4. Harem size of male Redwings in relation to the order in which male Redwings were chosen by secondary females (Prediction II).

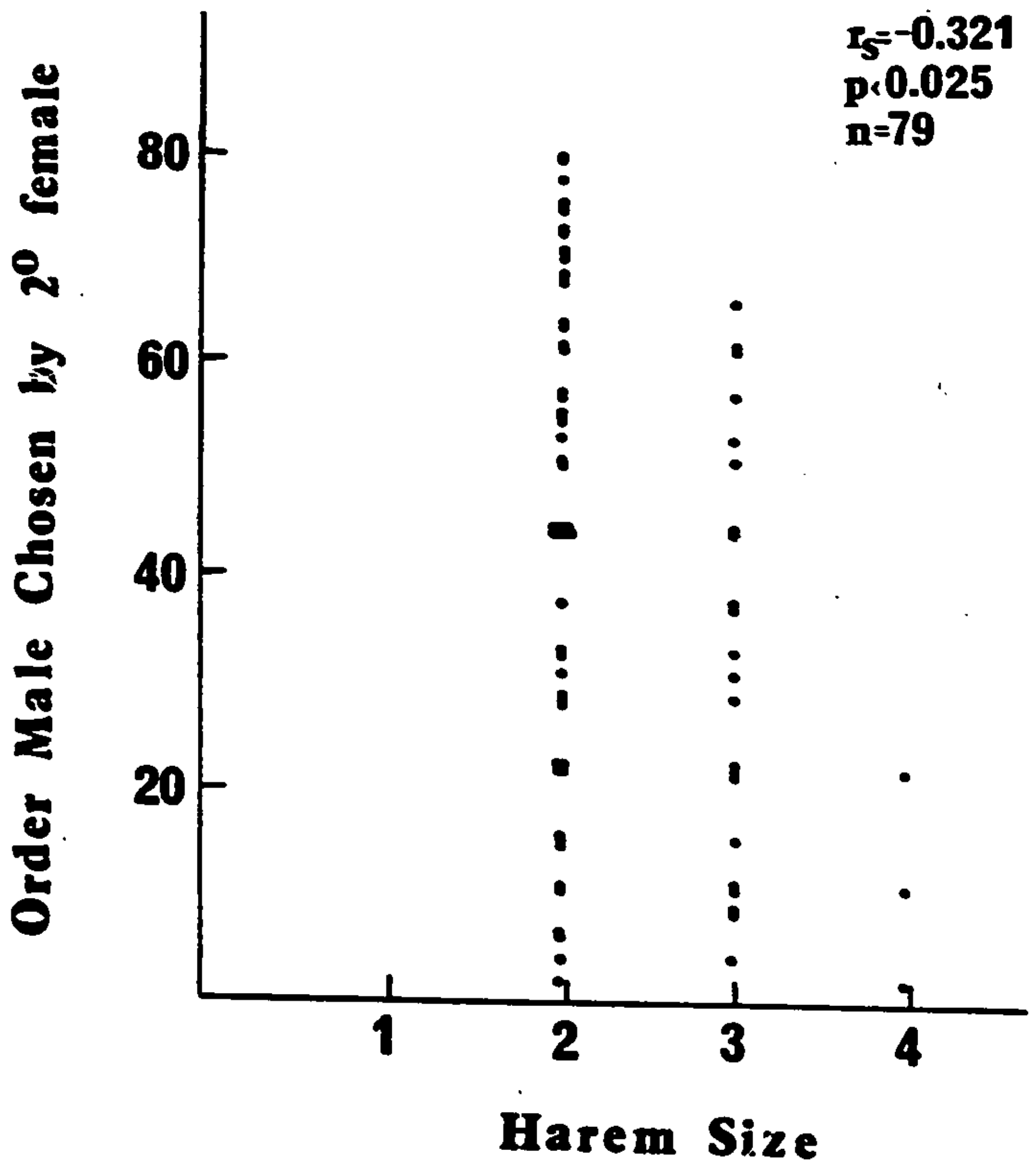
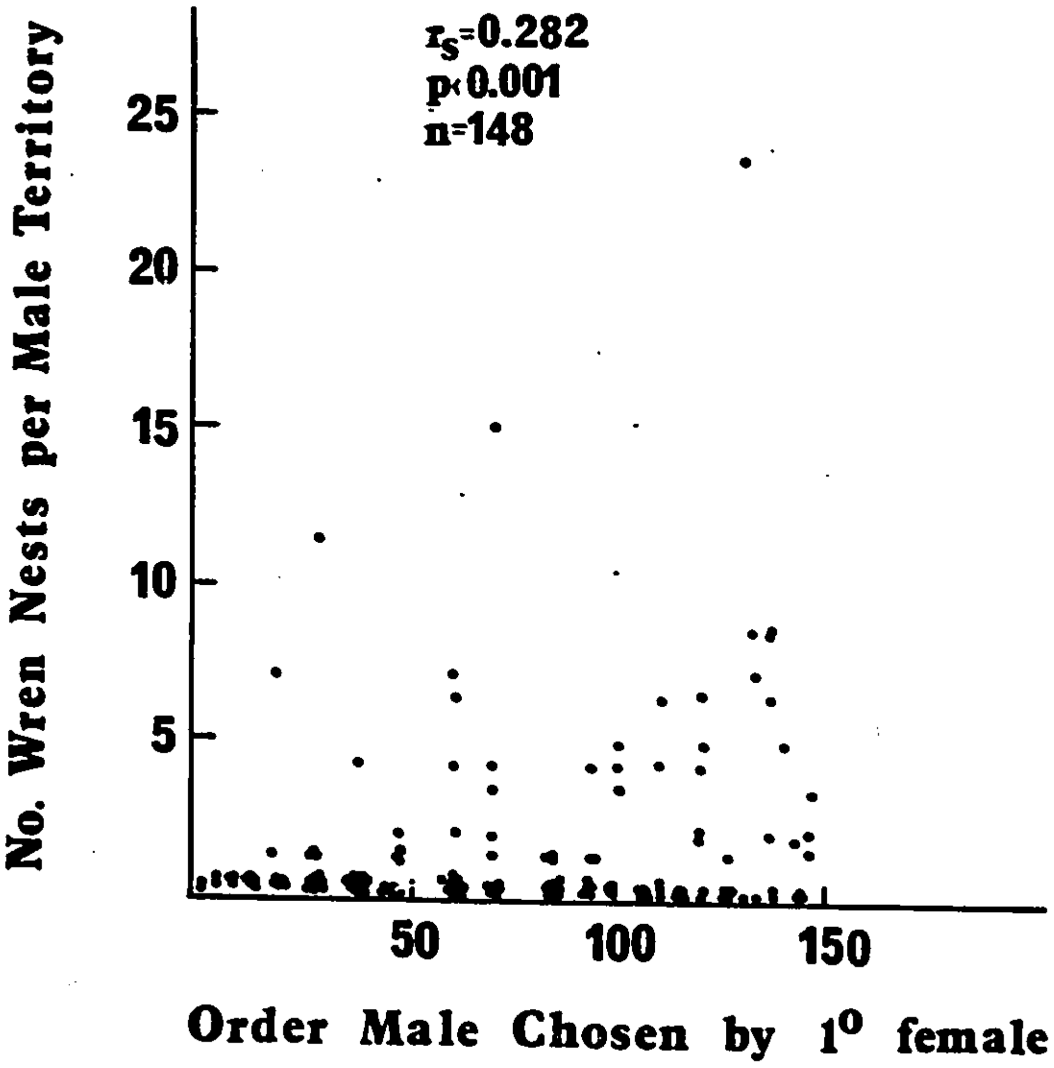

$r_s = -0.321$
$p < 0.025$
$n = 79$
Order Male Chosen by $2^0$ female
80
60
40
20
1
2
3
4
Harem Size

Figure 5. Number of Wren nests per male Redwing territory versus the order in which male Redwings were chosen by primary females (Prediction III).



$r_s = 0.282$
$p < 0.001$
n=148
25
20
15
10
5
50
100
150
No. Wren Nests per Male Territory
Order Male Chosen by 1° female

Figure 6. Number of Wren nests per male Redwing territory versus the order in which male Redwings were chosen by secondary females (Prediction III).

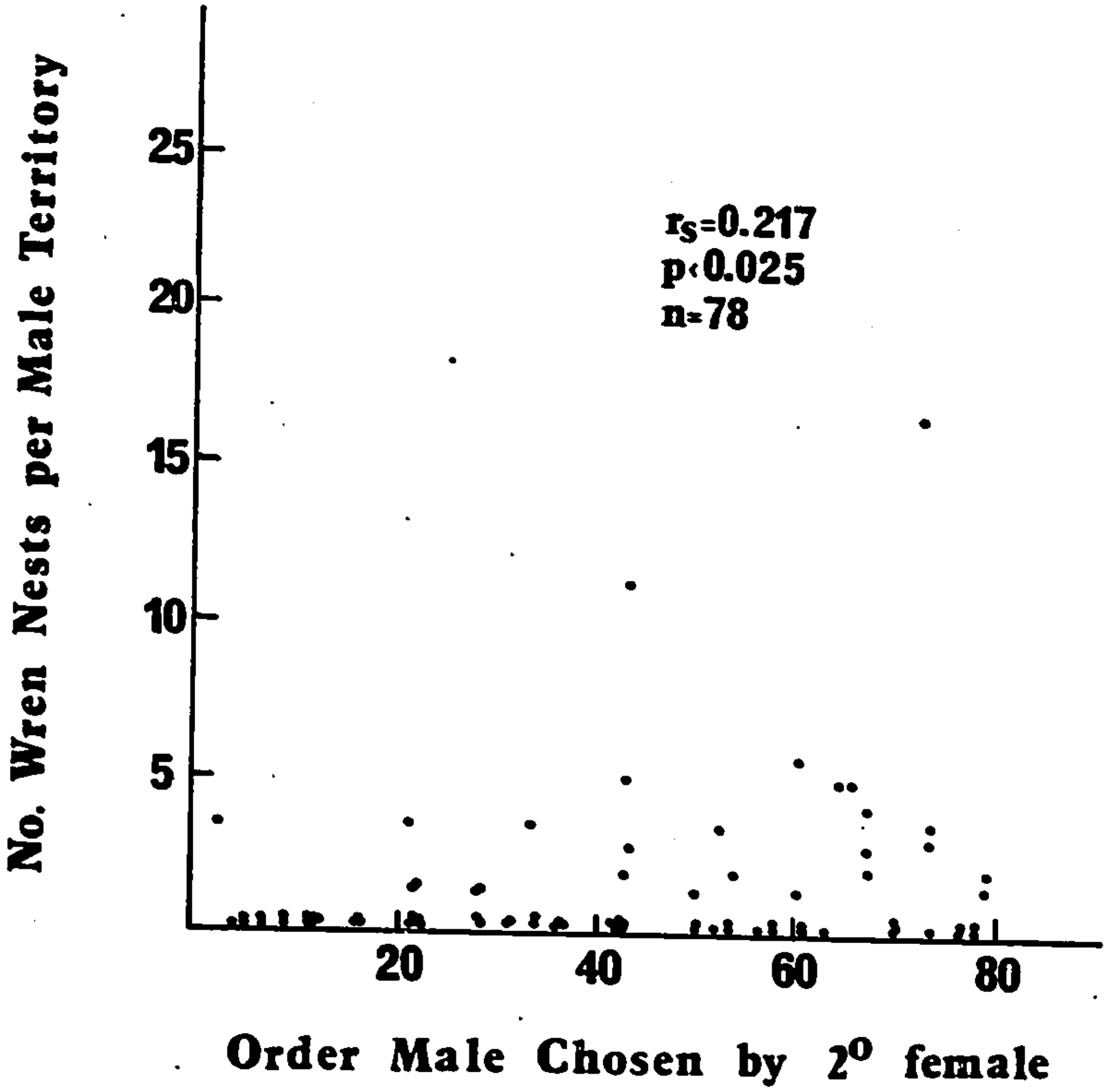

No. Wren Nests per Male Territory
25
20
15
10
5
20
40
60
80
Order Male Chosen by 2° female
$r_s$=0.217
p<0.025
n=78

Figure 7. Number of Wren nests per male Redwing territory versus the order in which male Redwings were chosen by tertiary females (Prediction III).

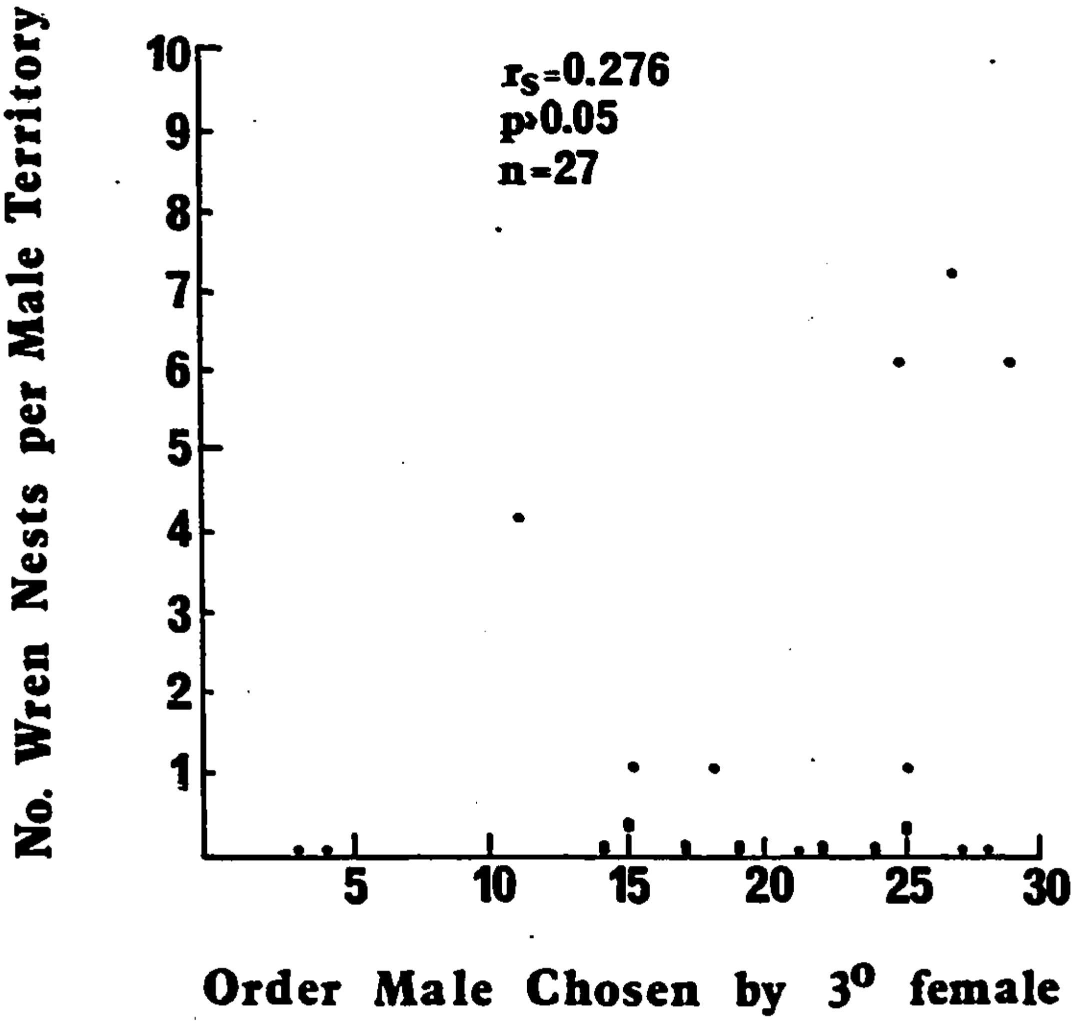
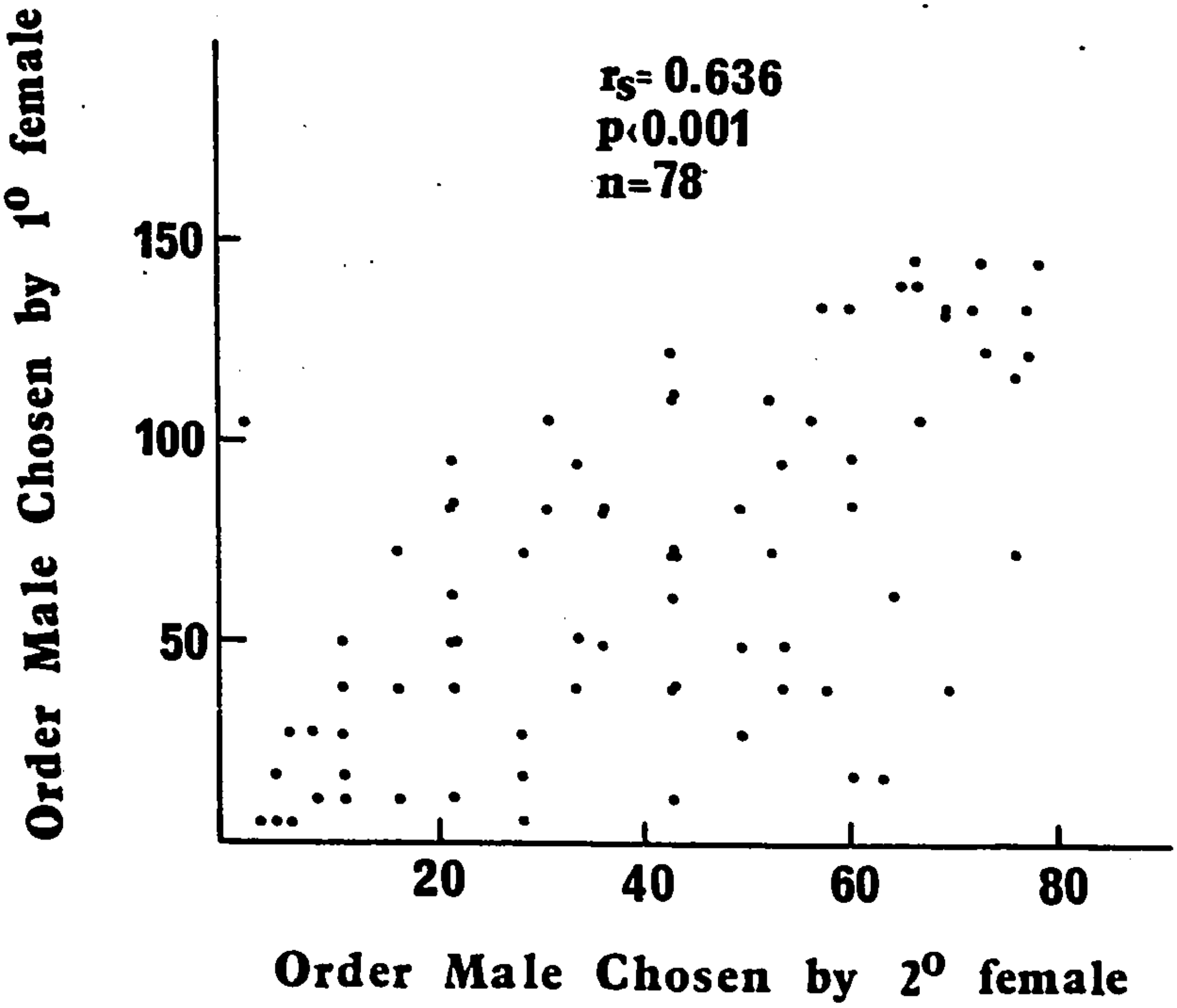

No. Wren Nests per Male Territory
10
9
8
7
6
5
4
3
2
1
5
10
15
20
25
30
$r_s = 0.276$
$p > 0.05$
$n = 27$
Order Male Chosen by 3° female

Figure 8. Order in which male Redwings were chosen by primary females versus the order in which male Redwings were chosen by secondary females (Prediction IV).



$r_s$= 0.636
p<0.001
n=78
150
100
50
20
40
60
80
Order Male Chosen by 1° female
Order Male Chosen by 2° female

Figure 9. Order in which male Redwings were chosen by primary females versus the order in which male Redwings were chosen by tertiary females (Prediction IV).

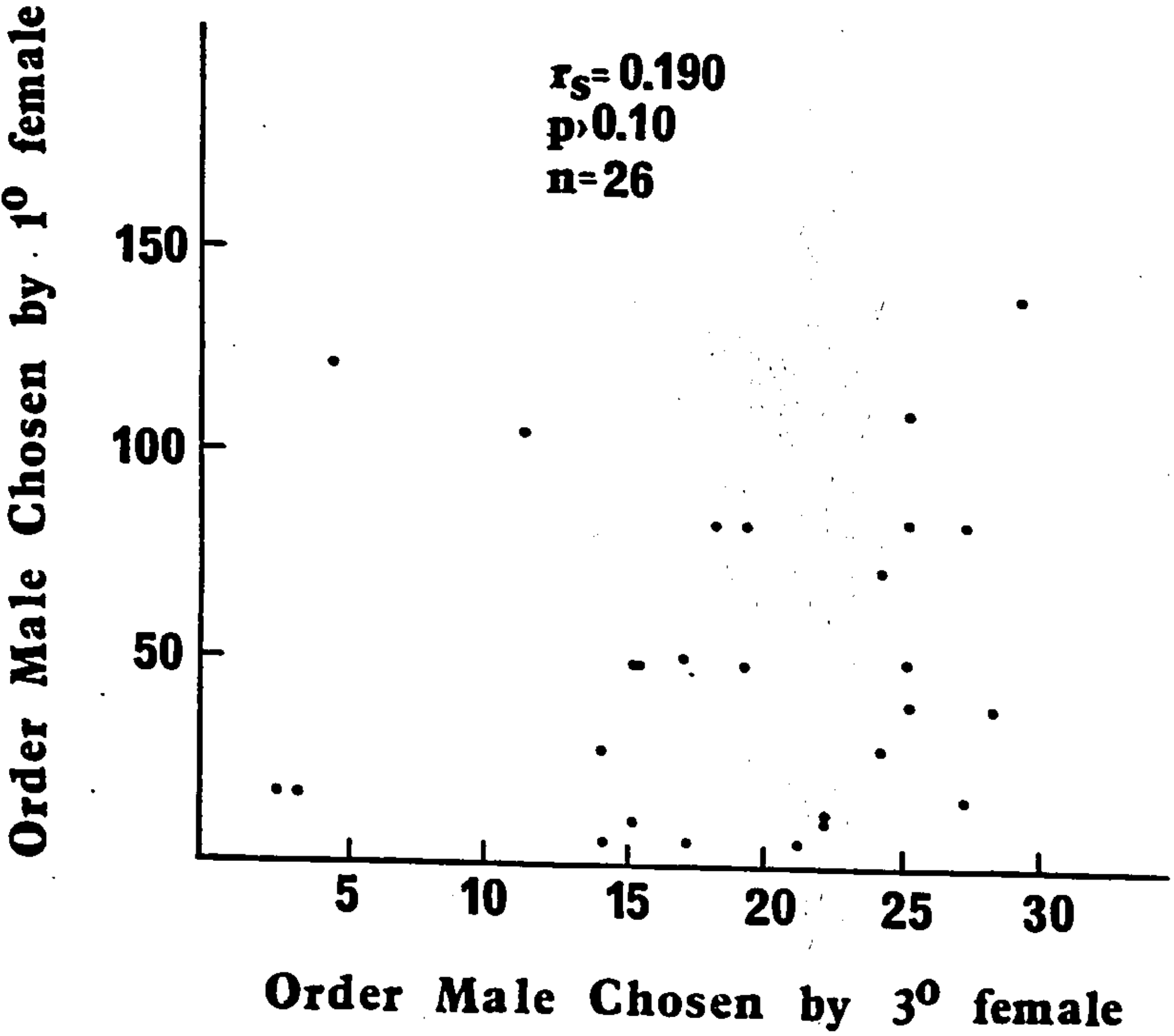

$r_s = 0.190$
$p > 0.10$
$n = 26$
150
100
50
5
10
15
20
25
30
Order Male Chosen by $1^0$ female
Order Male Chosen by $3^0$ female

Table 1. Redwing nesting success and sources of Redwing nesting mortality. 83 eggs and 97 nestlings had an unknown fate.

| | |
|---|---|
| **NESTING SUCCESS** | |
| Number of eggs laid | 1150 |
| Number of eggs hatching (%) | 654 (58) |
| Number of nestlings fledging (%) | 321 (58) |
| % eggs producing fledglings | 31 |
| **MORTALITY** | |
| 1. Egg | |
| abandonment (%) | 79 (12) |
| unhatched (%) | 47 (7) |
| predation (%) | 288 (45) |
| total egg mortality (%) | 414 (64) |
| 2. Nestling | |
| abandonment (%) | 13 (2) |
| predation (%) | 124 (19) |
| starvation (%) | 99 (15) |
| total nestling mortality | 236 (36) |

Table 2. Correlates of Redwing nesting success.
One-tailed test (d.f. 1).

| Variable | Unstandardized Logistic Regression Coefficient | X2 | Probability |
|---|---|---|---|
| Vegetation Height | 0.003 | 0.625 | 0.429 |
| Vegetation Density | 0.084 | 3.279 | 0.070 |
| Water Depth | 0.005 | 1.336 | 0.239 |
| Nest Height | 0.005 | 0.218 | 0.641 |
| Distance to Edge | 0.005 | 2.034 | 0.154 |
| Distance to Nearest Redwing nest | 0.006 | 1.130 | 0.105 |
| Distance to Nearest Marsh Wren Nest | 0.001 | 6.324 | 0.010 |
| Male Nest Defense | | | |
| -nest building | -0.014 | 0.147 | 0.702 |
| -egg | 0.058 | 4.961 | 0.026 |
| -incubation | 0.051 | 4.968 | 0.026 |
| -nestling | 0.105 | 11.101 | 0.001 |
| Male Wing Length | -0.011 | 1.922 | 0.166 |
| Male Bill Length | -0.042 | 1.742 | 0.187 |
| Male Tarsus Length | -0.021 | 0.828 | 0.363 |
| Male Weight | 0.010 | 1.456 | 0.228 |
| Male Physical Condition Index | $0.179 \times 10^{8}$ | 2.792 | 0.095 |

Table 3. Association of Marsh Wren nests for all possible pairs of years. The study area was broken down into 51 arbitrary quadrats (40 m X 40 m) and the number of Wren nests for each quadrat in each year counted. The number of Wren nests per arbitrary quadrat for all possible pairs of years were then related using a Spearman rank correlation. The distribution of Wren nests on 1 June 1983, 1984 and 1985 were used for this analysis. n=51.

| | 1983 | 1984 | 1985 |
|---|---|---|---|
| 1983 | ***** | | |
| 1984 | 0.497<br>$p<0.0005$ | ***** | |
| 1985 | 0.359<br>$p<0.01$ | 0.741<br>$p<0.0005$ | ***** |

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# Appendix I

Mean harem size, territory size and nesting success of Red-Winged Blackbirds in various marshes throughout North America.

| Locality | Mean harem size | Mean territory size (m2) | % successful nests | Source |
|---|---|---|---|---|
| **CANADA** | | | | |
| British Columbia | 2.8 | - | - | Runyan (1979) |
| " | 4.7 | 9202 | 18.9 | Picman (1980) |
| " | 4.5 | 8996 | 28.7 | " |
| " | 4.1 | 9923 | 38.0 | " |
| " | 4.2 | 7188 | 45.0 | " |
| Ontario | 2.6 | 1060 | 33.9 | Weatherhead and Robertson (1976) |
| " | 1.9 | - | - | Weatherhead and Eckert (unpublished data) |
| " | 1.7 | 1380 | 30.0 | present study |
| " | 1.6 | 1380 | 60.0 | " |
| " | 1.6 | 1298 | 46.0 | " |
| Quebec | 2.9 | - | - | Weatherhead et al. (1980) |
| **UNITED STATES** | | | | |
| California | 3.7 | 668 | - | Orians (1961) |
| " | 2.8 | 981 | - | " |
| " | 2.7 | - | - | Collier (1968) |
| Connecticut | | - | 40.0 | Robertson (1977) |
| Illinois | 2.6 | - | 40.7 | Smith (1943) |
| | 1.8 | 700 | - | Lenington (1980) |
| | 4.0 | 300 | - | " |

Appendix I (continued)

| | | | | |
|---|---|---|---|---|
| Maryland | 1.6 | 1180 | 38.0 | Meanley and Webb (1963) |
| " | 2.2 | 1090 | 65.0 | " |
| " | 2.4 | 867 | 46.0 | " |
| " | 2.6 | 590 | 69.0 | " |
| " | 1.6 | 2023 | 55.0 | " |
| " | 1.7 | 2569 | 53.0 | " |
| New Jersey | - | - | 63.0 | Caccamise (1977) |
| New York | 3.3 | 1068 | - | Howard (1977) |
| " | 1.9 | 1052 | 47.1 | Case and Hewitt (1963) |
| " | 2.2 | 1337 | 22.0 | " |
| Oklahoma | 1.9 | 364 | 51.8 | Goddard and Board (1967) |
| Pennsylvania | 2.0 | - | 57.7 | Brenner (1966) |
| " | 2.1 | - | 36.1 | " |
| " | 1.0 | - | 36.8 | " |
| " | 0.4 | - | 50.0 | " |
| " | 0.9 | - | 52.6 | " |
| Washington | 5.4 | 2316 | - | Orians (1980) |
| | 3.6 | 1740 | - | " |
| | 7.6 | 513 | - | " |
| | 3.0 | 432 | 45.7 | Holm (1973) |
| | 2.7 | 646 | 39.0 | " |
| Wisconsin | 2.0 | 330 | - | Nero (1956) |
| **COSTA RICA** | 3.7 | 2361 | 21.5 | Orians (1973) |
| | 1.3 | 1101 | - | " |

# Appendix II

Table 5 from Goddard and Board (1967) relating Redwing nesting success to water depth at base of nest.

| Water Depth (cm) | % successful nests | N |
|---|---|---|
| 0-10 | 23.2 | 155 |
| 11-20 | 29.2 | 65 |
| 20+ | 43.5 | 23 |

Spearman r=0.105, n=221, p>0.05.

# Appendix III

Return rates of male Redwings for 1983-1985.

| Year | Number of males banded | Number of males returning from previous year (%) | Number of males returning in following year (%) |
|---|---|---|---|
| 1983 | 52 | ----- | 34<br>(65) |
| 1984 | 45 | 34<br>(76) | 38<br>(84) |
| 1985 | 48 | 38<br>(79) | ----- |

Appendix III (Continued)

Return rates of males from the previous year in both 1984 and 1985 were nearly 50% larger than that reported by Picman (1981; 46%) and Beletsky and Orians (1987; 52%). Moreover, 42 of the 76 (55%) males breeding in the study area were present in 2 consecutive years and 26 of 76 (37%) were present in all 3 years. Two males held territories in 1983 and 1985 but not in 1984.

Moreover, all (70/70) territories defended by the same male in consecutive years overlapped. The extent of site fidelity in this population is slightly larger than that reported by Searcy (1979b; 34/39 (87.2%) of territories defended by the same male in consecutive years overlapped), Beletsky and Orians (1987; 84/107 (78.5%) of territories overlapped) and Picman (1987b; 94% of territories overlapped). Moreover, 26 of 28 (93%) territories defended by the same male in 1983 and 1985 overlapped.