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TESTS OF HYPOTHESES FOR THE OCCURRENCE OF POLYGYNY IN TERRITORIAL BIRDS USING THE RED-WINGED BLACKBIRD (*AGELAIUS PHOENICEUS*)

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ABSTRACT

Several hypotheses have been proposed to explain the occurrence of polygyny in birds. The purpose of this study is to test those hypotheses using data from a marsh-nesting population of the red-winged blackbird (*Agelaius phoeniceus*).

This study consists of two sections. The first section deals with theoretical aspects of the hypotheses and contains four chapters. In Chapter 1, I review all hypotheses and describe in detail their assumptions and predictions. In Chapter 2, I argue that the asynchronous settlement model cannot explain polygyny as stated and propose a new version of the model. In Chapter 3, I examine one assumption and four predictions of the sexy son hypothesis. Using examples, I demonstrate that the assumption and three predictions do not follow from the hypothesis. I argue that the the fourth prediction (mathematical model for the calculation of reproductive success of polygynous females) is flawed and propose a corrected version of the model. In Chapter 4, I review hypotheses that explain polygyny through "random" female settlement and propose a new ("status indifference") hypothesis. I conclude the first section by hierarchically classifying the plausible hypotheses by their key assumptions.

The second section of this study presents the results of field experiments that tested the key assumptions. In Chapter 5, I tested female preferences for unmated or monogamously mated males by offering newly settling females a choice of two adjacent territories, one defended by an unmated male and the other by a monogamously mated male. Male mating status was randomized with respect to the variation in territory quality and male quality. Early in the breeding season, significantly more females settled with the unmated males than with the mated males. Although a similar trend was evident late in the breeding season, the difference was no longer significant. The goal of Chapter 6 was to determine the consequences of polygamy on female reproductive success. After randomizing harem size with respect to territory and male quality, I found that 1) monogamous females fledged as many young as bigamous females; 2) nestlings on monogamous and bigamous territories were provisioned equally often by both parents; 3) on bigamous territories, asynchronous broods were provisioned by males significantly more frequently than synchronous broods; 4) Ten-day-old female nestlings on monogamous territories were better developed than their bigamous peers. The goal of Chapter 7 was to examine the effect of nesting synchrony between primary and secondary females on female reproductive success. Females on randomly selected territories were synchronized or asynchronized through clutch manipulations. Synchronous females suffered higher nesting losses than asynchronous females. Males provisioned asynchronous broods more frequently than synchronous broods, but the synchrony had no effect on female provisioning. Ten-day-old nestlings from synchronous broods were less developed than nestlings from asynchronous broods. The goal of Chapter 8 was to establish whether females exhibit preferences for selected habitat characteristics. On a broad spatial scale (choice of a nesting area within a marsh), univariate analyses established that female selection of nesting areas was non-random with respect to six characteristics. However, a multivariate analysis revealed that females settle non-randomly only with respect to water depth. Females preferred nesting areas located in deep water to those in shallow water. On the narrow spatial scale (choice of a nest site within a nesting area), females preferred dense clumps of vegetation surrounded by sparse vegetation.

In summary, the findings that 1) females prefer monogamy to bigamy, 2) monogamous females have higher reproductive success than bigamous females, and 3) asynchronous females have higher reproductive success than synchronous females, are consistent with hypotheses that assume net cost of polygyny to females, and contradict models that assume otherwise. Of these "cost" models, female preference for nesting areas located in deep water contradicts the asynchronous settlement model. The higher reproductive success of secondary asynchronous females as compared to that of secondary synchronous females also contradicts the defence of male parental investment model. Therefore, I conclude that the most plausible explanation for polygyny in this population of red-winged blackbirds is provided by either the polygyny threshold model or the sexy son hypothesis.

RÉSUMÉ

Plusieurs hypothèses ont été formulées pour tenter d'expliquer la polygamie chez les oiseaux. Le but de cette étude est de tester ces hypothèses à l'aide de données caractérisant une population de Carouges à épaulettes (*Agelaius phoeniceus*) colonisant les marécages.

Cette étude est divisée en deux sections. Dans le première section qui traite des aspects théoriques des hypothèses est divisée en quatre chapitres. Au premier chapitre, je revoie les hypothèses et je décris de façon détaillée leurs suppositions et leurs prédictions. Dans le deuxième chapitre, je discute le modèle "asynchronous settlement". Puisque le mécanisme proposé par ce modèle n'explique pas pourquoi les femelles devraient s'installer de façon polygame, je propose une nouvelle version de ce modèle. Dans le troisième chapitre, j'examine une supposition et quatre prédictions associées à l'hypothèse "sexy son". Je présente des exemples pour démontrer que la supposition ainsi que trois des quatres prédictions ne découlent pas de l'hypothèse, et que la quatrième prédiction (qui est une formule mathèmatique utilisée pour calculer le succès reproducteur de la femelle) est sont imparfaite. Dans le quatrième chapitre, je révise des hypothèses qui expliquent la polygamie par la colonisation au hasard ("random") des femelles. Je termine la section théorique en classant les hypothèses plausibles de façon hiérarchique basées sur leurs suppositions et leurs prédictions clés.

Le but de la deuxième section était de tester celles-ci en exécutant une série d'études de terrain. Dans le chapitre cinq, j'ai testé si les femelles démontraient une préférence pour des mâles sans conjoint ou avec un conjoint en offrant un choix de deux territoires adjacents aux femelles en voie de colonisation, soit un défendu par un mâle sans conjoint, et l'autre défendu par un mâle ayant un conjoint. Le statut des

mâles par rapport aux différences dans la qualité des territoires et la qualité des mâles-mêmes a été sélectionné de façon aléatoire. Tôt dans la saison des nids, un nombre significativement plus élevé de femelles se sont installées avec les mâles sans conjoint qu'avec ceux ayant un conjoint. Alors, qu'une tendance semblable était évidente plus tard dans la saison des nids, la différence n'était plus significative.

Le but du sixième chapitre était de déterminer quelles seraient les conséquences de la polygamie sur le succès reproducteur des femelles. Après avoir varié la taille des harems de façon aléatoire pour éviter les biais de qualité des territoires et des mâles, j'ai eu comme résultat que 1) les femelles monogames ont élevé plus di oisillons que les femelles bigames, mais cette différence est non-significative; 2) les oisillons qui n'ont pas encore quitté le nid ont été nourrit aussi souvent par un parent que l'autre sur les territoires monogames et bigames; et 3) sur les territoires bigames, les nichées asynchrones ont été nourries par les mâles plus souvent que les nichées synchrones.

Le but du chapitre sept était d'examiner l'effet de la synchronie des nichées entre les femelles primaires et secondaires sur le succès reproducteur des femelles. Les femelles de territoires choisiau hasard ont été synchronisées ou désynchronisées en manipulant les couvées. Les femelles synchronisées ont subt plus de pertes dans leur nichées que les femelles asynchrones. Les males ont nourri les nichées asynchrones plus fréquemment que les nichées synchrones, mais la synchronie n'a pas affecté le comportement nourricier des femelles. Les oisillons âgés de dix jours provenant de nichées synchrones étaient moins développés que ceux des nichées asynchrones.

Le but du huitième chapitre était d'établir si les femelles démontrent une préférence pour certaines caractéristiques d'habitat. A grande échelle (choix d'un site

de colonisation à l'intérieur d'un marécage), des analyses univariées ont démontré que le choix d'endroit de colonisation par les femelles n'était pas aléatoire pour six des sept caractéristiques d'habitat étudiées. Cependant, une analyse multivariée a démontré que les femelles s'installent seulement de façon non-aléatoire par rapport à la profondeur de l'eau. Les femelles préféraient les sites de colonisation dans l'eau profonde aux sites dans l'eau peu profonde. A petite échelle (choix d'un site de colonisation à l'intérieur d'une région de colonisation), les femelle préféraient des endroits caractérisés par des pousses de végétation dense entourées de végétation clairsemée.

Pour terminer, les résultats que 1) les femelles préfèrent la monogamie à la bigamie, 2) les femelles monogames ont un succès reproducteur plus élevé que les femelles bigames, et 3) les femelles asynchrones ont un succès reproducteur plus élevé que les femelles synchrones sont conformes aux hypothèses qui supposent un coût net de la polygamie chez les femelles, et contredisent les modèles qui supposent autres choses. De ces modèles de "coût", les femelles qui préfèrent les régions de colonisation dans l'eau profonde contredisent le modèle "asynchronous settlement". Le succès reproducteur plus élevé des femelles secondaires asynchrones comparé au succès des femelles secondaires synchrones contredit aussi le modèle "defence of male parental investment". Je conclus alors que l'explication la plus plausible pour l'observation de la polygamie chez les populations de Carouge à épaulettes est associée au modèle "polygyny threshold" ou par l'hypothèse "sexy son".

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GENERAL INTRODUCTION

Social polygyny, or the prolonged association and mating relationship between one male and several females (Searcy and Yasukawa 1995), is a rare mating strategy among birds, being exhibited by less than 5% of species (Lack 1968, Gill 1990). Because most bird species are monogamous, the occurrence of polygyny has long puzzled students of animal behavior. It is believed that males benefit from polygyny, because mating with multiple females increases their reproductive success. The benefits of polygyny to females are less clear. In many species, male territories contain limited resources necessary for reproduction, such as food. Breeding of multiple females on a single territory leads to competition for the resources and eventually to reduced reproductive success of the individual females. Because polygyny may reduce female reproductive success, it remains to be explain why females engage in such a mating strategy.

Historically, this puzzle has been explained by the excess of females in polygynous populations (e.g., Chapman 1928, Ryves and Ryves 1934, Skutch 1935, Kendeigh 1941, Mayr 1941, Wilson 1946, Williams 1952). However, many researchers have noticed that polygyny frequently occurs in species where the sex ratio is even or skewed in favor of males (Kluijver et al. 1940, Williams 1940, Fautin 1941, Armstrong 1955, Ali and Ambedkar 1956, 1957, Selander 1960, 1961, Carrick 1963, Verner 1964, Willson 1966, Zimmerman 1966, Holcomb and Twiest 1970). Wynne-Edwards (1959) suggested that polygyny is a form of social behavior that maintains population densities at an optimum size. However, Wynne-Edwards's arguments assumes that the social behavior is mainly shaped by group selection, a view criticized by many researchers (e.g. Orians 1969). Verner (1964) proposed an alternative explanation based on individual selection. This explanation was subsequently generalized by Orians (1969) and has become known as the polygyny threshold model.

Since 1964, a large number of new hypotheses have been proposed: some elaborate on the idea espoused by the polygyny threshold model, while other present new, distinct explanations. As a result, there are currently 18 distinct hypotheses and a number of their extensions and modifications.

The development of the theory has been followed by an equally intense effort to test the hypotheses with empirical data. The effort has concentrated mainly on several passerine species, such as the pied flycatcher (*Ficedula hypoleuca*; Alatalo et al. 1981, 1984), yellow-headed blackbird (*Xantocephalus xantocephalus*; Lightbody and Weatherhead 1987, 1988), red-winged blackbird (*Agelaius phoeniceus*; Weatherhead and Robertson 1977a,b; Orians 1980, Searcy and Yasukawa 1995), bobolink (*Dolichonyx oryzivorus*; Wittenberger 1978, Wootton et al. 1986) and house wren (*Troglodytes aedon*; Johnson 1992, Johnson et al. 1994). Despite this effort, however, there has been no systematic test of all hypothesis using a single study species (Searcy and Yasukawa 1989, 1995). Therefore, the goal of this study is to test all plausible hypotheses for polygyny using the red-winged blackbird as the study species.

The study species

The red-winged blackbird is perhaps the most abundant bird in North America, with population size estimated at 150 million individuals (Meanley and Royall 1976). Males are larger and more conspicuous than females: male plumage is jet black, with bright red upper coverts (epaluets), while female plumage is dusky brown, with white and black streakings of underparts (Yasukawa and Searcy 1995). The red-wing blackbird is a migratory species; birds from the northern populations migrate to southern United States and Middle America. The breeding phenology of redwings in my study area is as follows: males arrive from migration in mid March and soon afterwards start defending territories. Females arrive few weeks later. Nesting activities start in earnest in early May and last until July (in marshes) or August (in upland habitats). The nest is constructed by the female, who also incubates a clutch of 3-4 eggs. Feeding of young is shared by both parents, although the female contributes more than the male. Marsh-nesting females are usually single-brooded, although replacement broods are frequent. Polygyny is frequent in both marsh-nesting and upland-nesting populations. Polygamous males usually attract two females, although some males may attract up to five females at the same time. At the end of the breeding season, redwings congregate in roosts before returning south in late October.

One advantage of using the red-winged blackbird as a study species is that there is no intra-specific brood parasitism (i.e. females do not lay eggs in the nests of other females). Intra-specific brood parasitism has important consequences for one's ability to test the hypotheses. Most hypothese make a specific assumption about the effect of polygyny on female reproductive success. The hypotheses either assume that polygyny increases female reproductive success, or that it decreases the reproductive success, or that it does not have any effect at all. An accurate test of these assumptions therefore requires an accurate determination of female reproductive success. This is usually accomplished by counting the number of young fledged by a given female. However, the occurrence of intra-specific brood parasitism may substantially distort this measure of reproductive success, because (1) the female may lay eggs in nests of other females (in addition to her own nest), in which case her nest content underestimates her true reproductive success, or (2) other females may lay eggs in the nest of the focal female, in which case the nest content would overestimate the female's true reproductive success. The only way to correct for this distortion is to find all nests in the area where the female nests and to establish parentage of all young in the nests with a molecular techique (such as the DNA fingerpring).

Such large scale DNA fingerprinting studies have been carried out in three red-winged blackbird populations: one population was studied in Washington State, U.S.A. (Harms et al. 1991), one in eastern Ontario, Canada (Gibbs et al. 1990) and one in New York State, U.S.A. (Westneat 1993). Two studies detected no parasitism, while the third study estimated that 0.5% of nests were parasitised. Because the studies cover a large geographic area, and because they results are based on substantial sample sizes and are consistent between the studies, it can be safely concluded that intra-specific brood parasitism in the red-winged blackbird is negligible. The lack of the parasitism makes it possible to determine female reproductive success directly from the content of her nest and thereby makes the red-wing blackbird an attractive species for the testing of polygyny hypotheses.

Outline of the study

This study consists of two section. In the first section, I deal with the theoretical aspects of the hypotheses. In Chapter 1, I review all plausible hypotheses and describe in detail their assumptions and predictions. In Chapter 2, I discuss the mechanism proposed for the asynchronous settlement model. In Chapter 3, I examine one assumption and four predictions of the sexy son hypothesis. Finally, in Chapter 4, I examine hypotheses that explain polygamy through random female settlement and propose a new ("status-indifference") hypothesis. I conclude the first section by hierarchically classifying plausible hypotheses by their key assumptions and by outlining field experiments designed to test them.

In the second section of this study, I describe the results of four field experiments. In Chapter 5, I examine female preferences for monogamous or unmated males. In Chapter 6, I describe the impact of polygamy, and in Chapter 7 the impact of nesting asynchrony, on female reproductive success. In Chapter 8, I analyze female nest site selection at two spatial scales. Finally, I summarize the experimental results and use them to discriminate among the hypotheses.

SECTION I: REVIEW OF HYPOTHESES

CHAPTER 1: CURRENT EXPLANATIONS FOR POLYGYNY

INTRODUCTION

The purpose of this chapter is to compile and review all reasonable hypotheses that have been proposed to explain the occurrence of polygyny in birds. I commence this review by presenting a list of hypotheses that have been proposed so far. Following that, I examine each hypothesis in detail. For each hypothesis, I list all assumptions that have been attributed to the hypothesis either by its original author, or by subsequent workers. The assumptions are labelled as "Assumption 1, Assumption 2, etc.", and each is referenced to its source of origin. For many hypotheses, however, the assumptions have not been explicitly stated. In such cases, I list all assumptions that are in my opinion necessary for the hypothesis to function. The list of the assumptions is followed by the statement of the hypothesis and then by a list of predictions.

Where applicable, I report assumptions and predictions that (1) have been shown by other authors to be false, or (2) I consider to be false. For the former, I will refer to the appropriate literature to explain why the assumptions or predictions are false. For the latter case, I will provide my own explanation.

LIST OF HYPOTHESES

At the present time, there are 18 distinct hypotheses described in the literature on polygyny. The hypotheses are listed below: I use an original name where available; where not, I propose an appropriate name. As some hypotheses are often called models (such as in the case of the "polygyny threshold" model), I will continue the convention and refer to such explanations as to models.

1."Male coercion" hypothesis

2."Globally skewed sex ratio" hypothesis

3."Locally skewed sex ratio" hypothesis

4."Neutral-mate-choice" hypothesis

5."True null" model

6."Random dispersion" hypothesis (5 mechanisms)

7."Female deception" hypothesis

8."Wynne-Edwards's" theory

9."Cooperative female choice" model

10."Polygyny threshold" model and its extension, the "Defence of male parental investment" model

11."Sexy son" hypothesis

12."Asynchronous settlement" model

13."No-cost no-benefit directed female choice" model

14."Davies's" hypothesis

The random dispersion hypothesis includes five separate mechanisms. They are combined under one heading here, but I discuss them separately when describing the hypothesis.

INDIVIDUAL HYPOTHESES

Male coercion hypothesis

This hypothesis is frequently invoked to explain polygyny in territorial mammals, most notably ungulates. "In territorial ungulates, males often physically interpose themselves between the territory boundary and a female or a group of females that is moving off; after displaying, the male attempts to 'herd' the female(s) back toward the territory center" (Searcy and Yasukawa 1989). In birds, this hypothesis is believed to explain polygyny only in the greater rhea, tinamous and several pheasants (Emlen and Oring 1977).

Skewed sex ratio hypothesis.

Perhaps the first description of this hypothesis can be traced to Ryves and Ryves (1934) and to Skutch (1935). Ryves and Ryves (1934), who studied breeding habits of Corn Buntings (Emberiza calandra), suggested that "Corn-Buntings definitely are ordained to be polygamous and ... to this end, Nature arranges for the production of females in considerable excess of males". One year later, Skutch (1935) wrote that "... among Red-winged Blackbirds and Meadowlarks, which normally appear to be monogamous, the occasional presence of an excess of females may result in polygamy. Among species in which the females are normally greatly in the majority, as with Oropéndolas (Gymnostinops montezuma and Zarhynchus wagleri) and Great-tailed Grackles (Cassidix mexicanus mexicanus), polygamy seams to be the rule."

As originally proposed, the hypothesis rests on the following assumptions:

Assumption 1: There are more females (willing to breed) than males (willing to breed) in the breeding population (Ryves and Ryves 1934, Skutch 1935).

Assumption 2: Female fitness decreases with increasing harem size (Searcy and Yasukawa 1995, p. 19).

If these assumptions are fulfilled, then late-settling females do not encounter any unmated males, because all males are already mated. Such females must mate polygamously if they are to breed at all during the current breeding season.

If the lack of unmated males is the only reason why females settle polygamously, then the second assumption makes sense - otherwise why would females avoid polygamy if polygamy is not costly to them? There may be, however, species where females mate polygamously for two different reasons. The majority of females may settle according to the "neutral-mate-choice" hypothesis, which assumes no relationship between female fitness and harem size (see below). However, if the sex ratio is unexpectedly shifted in favor of females, then early-settling females would still become polygamous according to the neutral-mate-choice hypothesis, but late settling females would fail to find any unmated mates and would be "forced" to settle polygamously. Contrary to the assumption, however, such females would not suffer the cost of polygyny, because their fitness is not affected by harem size. The unexpected shift in the sex ratio may occur for a number of reasons, such as: (1) primary sex ratio may deviate from unity by chance alone; (2) adult sex ratio may deviate from unity as a result of unusual environmental events. For example, in species with pronounced sexual size dimorphism, males may suffer greater mortality than females. During an unusually severe winter, males would suffer greater mortality than females and this would, in turn, create a surplus of breeding females during the next breeding season.

Search cost hypothesis

Stenmark et al. (1988) originally proposed the "search cost" hypothesis as a modification of the polygyny threshold model, but subsequent authors (i.e. Johnson 1992, Searcy and Yasukawa 1995) pointed out that the hypothesis can explain polygyny on its own. The essence of the hypothesis is as follows: if polygyny is costly to females, then a female should search for an unmated male. However, searching for a mate involves fitness costs. A searching female expands energy and time (Janetos 1980, Janetos and Blaine 1981, Wittenberger 1981b, Slagsvold 1986) and exposes herself to predators and parasites (Johnson 1991). The costs of searching are small for early-settling females, because such females are likely to encounter an unmated male soon. The costs may, however, be substantial for late-settling females, because such females search for unmated males when the majority of males are already mated. The search cost hypothesis postulates that there is a point during the searching process of late-settling females when the females would incur smaller fitness costs by settling with a mated male than by continuing to search for an unmated male.

The following assumptions of the hypothesis have been described in the literature:

Assumption 1: Female fitness decreases with harem size (i.e. there is a cost to polygyny; Stenmark et al. 1988).

Assumption 2: Females actively search for unmated males (Stenmark et al. 1988).

Assumption 3: Searching involves fitness costs (Stenmark et al. 1988).

In addition, I suggest that they hypothesis rests on the following assumptions:

Assumption 4: The cost of polygyny is greater than the cost of visiting and evaluating two males, but smaller than the cost of visiting and evaluating all males in the population.

Assumption 5: There is at least one unmated male in the whole population (if there were no unmated males, then this hypothesis would become the skewed sex ratio hypothesis, see above).

Assumptions 1,3 and 4 imply that a female maximizing her fitness should visit only a finite number of males. If, by chance alone, a female begins her search with a mated male, and encounters only mated males during her subsequent search, then the female would maximize her fitness by settling polygamously.

Neutral-mate-choice hypothesis

Lightbody and Weatherhead (1988) proposed the neutral-mate-choice hypothesis as an explanation for polygyny in the Yellow-headed Blackbird (Xantocephalus xantocephalus). The hypothesis was stated as follows: "females settle independently of each other and independently of variation in either male quality or territory quality. This occurs when females sharing territories neither compete nor cooperate (Lightbody and Weatherhead 1987) and when differences among males and territories either do not affect reproductive success or are unpredictable when females settle. ... In the neutral model, female mate choice is random, but it is an optimal behavior..." (Lightbody and Weatherhead 1987, p.21).

Based on this description, I suggest that the hypothesis rests on the following assumptions:

Assumption 1: Female behavior is adaptive, i.e. indifference confers higher fitness on a female than preference.

Assumption 2: Females settle independently of each other.

Assumption 3: Addition of a new female to a harem has no effect on the fitness of the resident female(s).

Assumption 4: Females settle independently of the variation in all features of male quality and territory quality. Note that Lightbody and Weatherhead (1988) wrote that "Females settle independently of the variation in either male quality or territory quality". This statement implies that females settle independently only with respect to one set of traits (either male quality or territory quality) and may choose the other set of traits. Therefore, it would be consistent with the assumption to observe that females choose males by their quality and settle independently of territory quality. It would be also consistent with the assumption to observe that females choose territories by their quality and settle independently of male quality. However, I believe that such an interpretation of the hypothesis is not what the authors intended. Rather, I believe that the authors meant to say that females should settle independently of all male and territory characteristics. I will take this interpretation to be correct and use it when testing the neutral-mate-choice hypothesis.

Assumption 5: Variation in male quality and territory quality does not affect female fitness.

If these assumptions are fulfilled, then polygyny occurs because some females settle (by chance alone) on territories of already mated males.

Several predictions of the neutral-mate-choice hypothesis have been published:

Prediction 1: "There is no correlation between reproductive success and settling order of the last females to settle" (Lightbody and Weatherhead 1988, p.23 and Table 1; Lightbody 1986, p.38).

Prediction 2: "There is no relationship between the reproductive success of earlier-settling females and later-settling females in harems of equal size (Lightbody and Weatherhead 1988, p.23 and Table 1; Lightbody 1986, p.39).

Prediction 3: "There is a weak positive correlation between the order of territories chosen by first females and the order of the same territories chosen by second females" (Lightbody and Weatherhead 1988, p.23 and Table 1; Lightbody 1986, p.40).

Prediction 4: "Harem size is positively correlated with territory area" (Lightbody and Weatherhead 1988, p.24 and Table 1; Lightbody 1986, p. 41).

Prediction 5: "Females settling in large harems achieve the same reproductive success as females settling at the same time in small harems" (Lightbody and Weatherhead 1988, p.24 and Table 1; Lightbody 1986, p. 40).

True null model

The true null model has been proposed as a non-adaptive alternative to the neutral-mate-choice hypothesis. Lightbody and Weatherhead (1988) described the model as follows: "females settle randomly even though interactions among females and variation in male quality or territory quality affect female reproductive success and can be predicted during settling....in the true null model, female mate choice is random and not optimal (i.e., not maximizing fitness)." (Lightbody and Weatherhead 1988, p. 21-22)

Based on this description, I suggest that the hypothesis rests on the following assumptions:

Assumption 1: Female behavior is not adaptive (see above).

Assumption 2: Females settle independently of each other.

Assumption 3: Addition of a new female to a harem affects fitness of the resident female(s). The addition may affect female fitness in any direction: it may increase the fitness, or it may decrease the fitness.

Assumption 4: Females settle independently of the variation in all features of male quality and territory quality. Note that Lightbody and Weatherhead (1988) did not specify with respect to what attributes females settle randomly. However, given that the true null model was meant as a non-adaptive alternative to the neutral-mate-choice model, and given that the neutral-mate-choice model postulates that females settle independently with respect to other females, male quality and territory quality, it can be safely assumed that females in the true-null model also settle randomly with respect to other females, male quality and territory quality.

Assumption 5: The variations in male quality and/or the variation in territory quality affect female fitness.

Assumption 6: Female mate choice is not an optimal behavior (i.e. it does not maximize fitness).

If these assumptions are fulfilled, then polygyny occurs because some females settle by chance alone on territories of already mated males.

No predictions of the model have been published.

Random dispersion hypothesis

Wootton et al. (1986) proposed the random dispersion hypothesis as an explanation for polygyny in the bobolink. The hypothesis was stated as: "some or all females settle randomly in homogeneous situations, producing a low level of polygynous pairings." (Wootton et al. 1986, p.). The authors proposed five mechanisms by which the random settlement can be achieved. Because each mechanism represents de facto a separate hypothesis, I will treat them individually.

Mechanism A) "Females cannot or do not choose territories or mates."
I explain in detail in Chapter 4 why this mechanism cannot explain polygyny.

Mechanism B) Females settle according to the polygyny threshold model, but some individuals make errors when evaluating the quality of territories. For example, if the real quality of a territory is 6 and females can evaluate it with precision of ± 1, then the perceived quality of the territory lies between 5 and 7 (Fig.1.1). Quality of a territory determines female fitness. An imprecise estimate of the quality translates into an imprecise estimate of the fitness. If the real quality of a monogamous option is higher than the real quality of a bigamous option, but there is an overlap in the perceived quality of the two options, then an erring female may underestimate the quality of the monogamous option and perceive it as worse than the bigamous option (Fig. 1.1). Alternatively, the erring female may overestimate the quality of the bigamous option, and perceive it as better than the monogamous option. In either case, the female would settle bigamously when in fact the bigamous option would yield lower fitness than the monogamous option.

Because this mechanism is based on the polygyny threshold model, it shares many assumptions with the polygyny threshold model (see below for a list of the assumptions). No predictions specific to this mechanism have been published.

Mechanism C) Females compare territory characteristics with those of their natal territories, and choose the territory with the most similar characteristics. The characteristics may include habitat quality, male quality, pairing status (i.e., monogamous vs. polygynous), and specific territory location.

<u>Mechanism D</u>) Females evaluate territories on the basis of their own previous breeding experience. Territories similar to those in which nests failed might be avoided, and territories similar to those in which young were fledged would be favored (it is not clear how females choose territories for their first breeding). As with previous cases, territories may be evaluated on the basis of habitat quality, male quality, pairing status (i.e. monogamous vs. polygamous) and specific territory location. Wootton et al. (1986) labelled mechanisms C) and D) the "experience-based-choice" hypothesis.

<u>Mechanism E</u>) Females choose a territory during the first breeding season by following either the polygyny threshold model or the "experience-based-choice" hypothesis. After making the territory choice once, they use this experience, exhibited by high fidelity to the site within the field, to choose territories in subsequent years.

Female deception hypothesis

This hypothesis was first proposed by Haartman (1969) and subsequently elaborated by several authors, such as Alatalo et al. (1981) and Alatalo and Lundberg (1990). The hypothesis states that males deceive females about their mating status by behaving as if they were unmated. This may occur either when males are polyterritorial (i.e. they defend two spatially disjunct territories) or when the vegetation on the territory is so dense that a new female fails to discover the presence of another female on the territory.

The female deception hypothesis rests on the following assumptions:

Assumption 1: Female fitness decreases with harem size (i.e. there is a cost to polygyny; Alatalo et al. 1981, 1982, 1984).

Assumption 2: Females actively search for unmated males.

Assumption 3: Settling females cannot detect whether a male is mated.

If these assumptions are fulfilled, then some females will settle with mated males because they perceive them as unmated.

Wynne-Edwards's theory

Proposed by Wynne-Edwards (1959, 1962), this theory has also been called the "group-selectionist" theory. Because there are other hypotheses that invoke group-selection as an evolutionary force, yet differ from this theory, I will refer to it as to the Wynne-Edwards's theory.

Wynne-Edwards (1959) has proposed that "animals have become adapted, with varying success, to control their own population-densities, limiting them at the optimum level - this being the level that offers the best living to the largest number, ..." Animals are postulated to control their population-densities through a variety of mechanisms, one of which is polygamy. Wynne-Edwards explained the mechanism that leads to polygamy as follows: "polygamy could have evolved as a refinement of the homeostatic apparatus, effectively placing the control of fertilisation - the first step in actual progeniture - within the power of relatively few individuals. In the commoner of the two alternative forms of polygamy, where it is the dominant males that provide repeated matings (polygyny), it may be postulated that the pregnancy-rate could in this way more easily be held down to the optimal ceiling: the handful of participating males, being fully informed either of their own personal total or, where there is a communal lek, of the group-total of matings performed to date, could be conditioned to respond when the appropriate complement had been reached by becoming sexually inert."

According to Orians (1969), Wynne-Edwards's theory makes the following assumptions:

Assumption 1: Females are unable to mate because males withhold coition after a certain number of copulations have been achieved.

Assumption 2: Low-ranking males do not attempt to solicit copulations after the quota has been reached.

Assumption 3: Females are not receptive to the advances of low-ranking males.

Cooperative female choice model

This model was proposed by Altmann et al. (1977) and elaborated by Picman (1980a, 1988). The model is also known as the "female-cooperation" model (Lenington 1980), "beneficial female" model (Ritschel 1985) and "multiple-female-benefits" hypothesis (Johnson 1991).

The "cooperative female choice" model rests on six assumptions:

Assumption 1. (Male Quality). With each male plus his environment there can be associated a positive number $\underline{q}$ - the quality of his territory - that uniquely determines the fitness $F_n(q)$ of a female mating n-gamously with him.

Assumption 2. (Monotonicity). For any positive integer n, and any $\underline{q}$ and $\underline{q'}$ in the domain of F_n, $F_n(q) > F_n(q')$ if $q > q'$.

Assumption 3. (Female Competition). In any territory of quality q a certain number N(q) of females can live without competition, and in fact, $F_{n+1}(q) > F_n(q)$ for any $n < N(q)$. The function N is assumed to be non-decreasing, i.e., $N(q) \geq N(q')$ if $q \geq q'$.

Assumption 4. (Overlap). For any n (smaller than some upper bound N) there are two males with qualities q_1 and q_2 such that $F_{n+1}(q_2) > F_n(q_1)$.

Assumption 5. (No Polyandry). With each female is eventually associated, at least for the mating period or for some more extended period of time, only one male, her 'mate'.

Assumption 6. (Best Choice). There is a rank order for the females of a local population, such that, for any female f, the quantity $F_{n+1}(q)$ (where n denotes the number of higher ranking co-wives of f and q the territory quality of the mate of f) is a maximum; that is, for any other male, with quality q' and with n' mates of higher rank than f, $F_{n+1}(q) \geq F_{n'+1}(q'_1)$.

Comment on the meaning of two variables: Variable q is defined as the quality of a breeding situation. In Altmann et al. (1977, p. 399) words, it is intended to measure "the totality of the contribution made by the male to the fitness of his mates, either directly (genetically, through parental care, etc.) or indirectly, by any fitness-limiting resources to which his mates have preferential access, regardless of whether these resources are in a defended area". Variable $F_n(q)$ measures the fitness of a female mated n-gamously on a breeding situation of quality q.

If these assumptions are fulfilled, then females settle polygynously because they can achieve higher fitness by doing so than by settling monogamously. In contrast to the polygyny threshold model (see below), the fitness benefits are derived from group life, rather than from the superior qualities of the polygamous territory and the polygamous male. The benefits of group life may include the detection and avoidance of predators (Altmann 1974), group defense (Lazarus 1972), division of labor (Eisenberg 1966, Parsons 1966), group foraging (Murton 1971), sharing of information about the identity of predators and the location of food sources (Brown 1986, Greene 1987, Ward and Zahavi 1973) protection from adverse weather (Allee 1931) and mutual assistance in raising of young (Skutch 1955, 1961, 1976).

Polygyny threshold model

The polygyny threshold was first proposed by Verner (1964) and subsequently elaborated by Verner and Willson (1966). Verner and Willson (1966) described the model as "polygyny can be advantageous for females if, within the limited area from which a female is likely to select a mate, the difference between two males' territories is sufficient that a female is able to rear more offspring on the better territory, by herself, than she could rear on the poorer one even with the full assistance from the male. The difference between territories can be regarded as a 'polygyny threshold,' since it is likely that polygyny will be favored by natural selection whenever the difference exceeds a certain level. The parameters of a male's territory that might operate in this regard include all requisites of successful breeding (food, cover, space, nest sites, etc.)." Orians (1969) generalised the explanation into a graphic model (see Fig. 1-2) and expanded the definition of territory quality to include the quality of the male as well: "... females should evolve to be especially responsive to those morphological and/or behavioral traits of males which reflect their fitness" (Orians 1969, p.592).

The specific assumptions of the polygyny threshold model have been listed in the literature as follows:

Assumption 1: "Female makes a choice among available males" (Orians 1969, p.591). Garson et al. (1981) paraphrased this assumption as follows: "Females choose where they breed."

Assumption 2: “Females have perfect knowledge in the sense that they can assess territory quality and male mating status" (Davies 1989). Garson et al. (1981) stated this assumption as "Females can assess the mating status of males."

Assumption 3: "Females are free to settle where their expected reproductive success is greatest" (Davies 1989).

Assumption 4: "Acceptance of one mate generally precludes the acceptance of another mate". (Orians 1969, p. 591)

Assumption 5: "The failure to accept one mate will be followed by an opportunity to mate with other individuals with such a high probability that the loss in reproductive output resulting from rejection of a potential mate is, on average, less than the average gains that can be realized by obtaining a mate of superior fitness". (Orians 1969, p. 591)

Assumption 6: "Environment is variable in quality and mean reproductive success uncomplicated by density effects is correlated with this variation in quality" (Orians 1969, p.591). Davies (1989) stated this assumption as follows: "Males defend territories varying in quality (e.g. food, nest sites) which influence female reproductive success."

Assumption 7: "Average reproductive success decreases with harem size" (Orians 1969, p. 593). This assumption has been paraphrased by other authors as: "A primary female does benefit from the arrival of a secondary female" (Garson et al. 1981) and "There is a cost to females of sharing a territory" (Davies 1989).

Assumption 8: "Females are adapted to maximize their reproductive output on each occasion that they breed" (Garson et al. 1981).

Assumption 9: "A primary female breeds at least as successfully as the secondary female (if there is one) in her male's territory" (Garson et al. 1981).

Assumption 10: "The order in which individual males and their territories are ranked by their quality remains the same for the period during which females are settling" (Garson et al. 1981).

If these assumptions are fulfilled, then females settle polygynously because they can achieve higher fitness by doing so than by settling monogamously. In contrast to the cooperative female choice model (see above), the fitness benefits are from he superior qualities of the polygamous territory and the polygamous male, rather than from the advantages of group life.

The following predictions of the polygyny threshold model have been published:

Prediction 1: "Females mate with already mated males when unmated males are readily available and perceived by the female" (Orians 1969, p. 594-595).

Prediction 2: "The optimal choice distribution is stable, in the sense that if each female makes the optimal choice on the basis of the situation at the time of her arrival, then though her fitness may be drastically reduced by later additions to her harem, at no time will she have a better choice than her own mate" (Altmann et al. 1977).

Prediction 3: "For any two males, the one with the better territory will never have fewer females, and conversely, the one with fewer females will never be the one with a better territory" (Altmann et al. 1977, Davies 1989). This prediction has often been translated as "Territory quality and (or) male quality should be positively correlated with male mating status" (e.g. Garson et al. 1981). Davies (1989) explains why this translation is incorrect.

Prediction 4: "Within a single mating type - i.e. monogamy, bigamy, trigamy, etc. - the ordering of the males by the final fitness of their females will correspond exactly to the ordering by territory quality, with ties in the same place" (Altmann et al. 1977, p. 404; Davies 1989).

Prediction 5: "All the males having at least k mates have been ordered at least k times - by their first mates, by their second mates, etc. All these orderings must agree" (Altmann et al. 1977, p. 404).

Prediction 6: "Since the mate selection is assumed to be made on the basis of the territory quality of the males, the ordering of males by territory quality must agree with the order of their first mates, second mates, etc., and must, therefore, also agree with the mean order of their mates" (Altmann et al. 1977, p.405).

Prediction 7: "From the second and fifth prediction it follows that the ordering of the males by harem size must, apart from ties, also agree with the ordering by first mates, by second mates, etc., and thus with mean order" (Altmann et al. 1977, Garson et al. 1981)

Prediction 8: "Most-favoured male will have at least one more spouse than the least-favoured male" (Altmann et al. 1977).

Prediction 9: "Females of differing breeding status settling at the same time should achieve equal fitness gains" (Garson et al. 1981).

There are also five predictions that have been attributed to the polygyny threshold model by various authors, but that are not valid. The predictions are: 1)

"There should not be a negative correlation between average reproductive success per female and number of females mated with a given male, since females are assumed to enter polygynous matings only when it is advantageous for them to do so" (Orians 1969, p.595). 2) "The reproductive success should not decrease with increasing number of females per male" (Orians 1972, p.390). 3) "The average reproductive success of polygynous females should be as great, if not greater, than that of monogamous females" (Holm 1973, Harmeson 1974, Carey and Nolan 1975, Dhont 1987). 4) "Secondary females on high-quality territories should have reproductive success at least as high as monogamous females on low-quality territories" (Wittenberger 1976, Dhont 1987). 5) "The fitness gains achieved by females should be negatively correlated with their settling order, regardless of their chosen breeding status" (Garson et al. 1981). Davies (1989) explains why these five predictions do not follow from the polygyny threshold model.

The polygyny threshold model does not make any specific predictions about the effect of nesting asynchrony between primary and secondary females on female reproductive success. Recently, Slagsvold and Lifjeld (1994) proposed an extension of the polygyny threshold model which they call the "defence of male parental investment" model (DMPIM). The DMPIM postulates that fitness of primary females should increase with the laying interval between the primary and secondary female, while the fitness of the secondary female should decrease.

Sexy son hypothesis

This hypothesis was proposed by Weatherhead and Robertson (1979) as an alternative to the polygyny threshold model. According to this hypothesis, females assess male quality independently of territory quality and use both when choosing a mate. It is assumed that male quality is not correlated with territory quality owing to the prevalence of such behaviours as site dominance and site fidelity. Females make adaptive choices that involve a trade-off between the territory quality (which influences immediate reproductive success) and male quality (which influences long-term fitness). If the females choose male quality, and if the male offspring of the females inherit some of their fathers' attractive traits and in turn leave more offspring because they attract more females, then through these "sexy sons" their mother will eventually leave more descendants (Weatherhead and Robertson 1979).

Assumption 1: Territory quality and attractive male traits are not perfectly correlated.
Assumption 2: Attractive male traits are heritable.

Prediction 1: Order in which last females settle in each territory is not correlated to their reproductive success This assumption is discussed in more detail in Chapter 3.
Prediction 2: Reproductive success of earlier settlers has no relation to the reproductive success of later settlers (settling in different territories of equal harem size).
Prediction 3: Females settling in large harems have lower reproductive success than females settling at the same time in small harems.
Prediction 4: This prediction calculates the size of the initial loss in reproductive success that a polygamous female may tolerate. The mathematical expression used for this purpose is described in Heisler (1981).

Predictions 1,2 and 3 are discussed in more detail in Chapter 3.

Asynchronous settlement model

This asynchronous settlement model was proposed by Leonard (1990). At a superficial level, the asynchronous settlement model appears similar to the polygyny threshold model. However, the key difference between the two models is that in the polygyny threshold model, polygynous females are compensated for the cost of polygamy by breeding on good quality breeding situations, while in the asynchronous settlement model, females reduce the cost of polygyny by breeding asynchronously.

Assumption 1: "If females used asynchronous settlement as a means of reducing competition, then they would have to detect the presence of another female in a male's territory and determine its nestling stage."

Prediction 1: "Female reproductive success should be correlated positively with the number of days between successive females. This is because asynchrony between females decreases the costs of polygyny".

Prediction 2: "There is no expected relationship between male and territory quality and harem size." This is because male and territory quality may be either homogeneous or of no relevance to females.

Prediction 3: "The order in which first and second females settle should be (positively) correlated." This is for the following reason: if female settlement is staggered, the territories of the earliest females to settle should become available sooner than the territories of the females that settle later. Thus, second-settling females should settle first in the territories of the early females.

Prediction 4: "The order in which females settle should be correlated negatively with male pairing success. This is because the first territories settled would be opened to subsequent females sooner than other territories."

Prediction 5: "Secondary females and monogamous females settling at the same time should have equal fitness. Because males and territories are similar and female success is related to the timing of settlement, a female settling in a territory with an incubating female should do as well as a female settling in the territory of a bachelor male."

Prediction 6: "The ASM does not require a relationship between female reproductive success and the order in which territories are settled. That is, if each territory is settled only after the resident female is incubating, then females in all territories should do equally well."

The mechanism of this hypothesis, as well as all assumptions and predictions are discussed in detail in Chapter 2.

No-cost no-benefit directed female choice model

This model was proposed by Searcy and Yasukawa (1989). The model states that female fitness does not change with increasing harem size, but that females choose mates according to the breeding situation quality. Although this hypothesis has not been elaborated, polygyny presumably occurs because females have no preference for monogamous vs. polygamous breeding situations, or if they have preferences, they do not exhibit them.

Assumption 1: Female fitness does not change with harem size.

Assumption 2: Females choose mates according to breeding situation quality.

Davies's hypothesis

Davies (1992) proposed that females evaluate habitat quality, but they do not evaluate male quality or a male's pairing status. As a result, two females select a habitat patch that is defended by a single male, and thereby become polygamous. Davies does not make any assumptions about the effect of such behavioral rules on female fitness.

Assumption 1: Females evaluate habitat quality.

Assumption 2: Females do not evaluate male quality.

Assumption 3: Females do not choose mates on the basis of their mating status (i.e. unmated vs. mated).

To conclude this overview of the individual hypotheses, one explanation (mechanism A of the random dispersion hypothesis) cannot explain polygyny at all (see Chapter 4 for details), while another four hypotheses are unlikely to explain polygyny in the red-winged blackbird. These four hypotheses are the male coercion hypothesis, the globally skewed sex ratio hypothesis, the locally skewed sex ratio hypothesis and the female deception hypothesis. The male coercion hypothesis is unlikely to apply for reasons explained in Searcy and Yasukawa (1989). The globally and locally skewed sex ratio hypotheses are unlikely explanations because there are unmated males capable of breeding available throughout the breeding season in many populations (e.g. Orians 1969) including the population investigated in this study (S. Pribil, unpublished data). The female deception hypothesis is unlikely to apply for two reasons: 1) male red-winged blackbirds are monoterritorial, and 2) it is relatively easy for a new female to detect the presence of a resident female on the territory.

Of the remaining 13 explanations, Wynne-Edwards's theory is difficult to test with empirical data because of the challenge associated with measuring the strength of group selection. Likewise, I will not test mechanisms C, D and E of the random dispersion hypothesis, because of the practical difficulty of following individual females over prolonged periods of time (i.e. between years). The remaining 9 hypotheses, however, provide plausible explanations for blackbird polygyny. In the following three chapters, I will examine several of those hypotheses in detail and propose a new hypothesis. At the end of the first section, I will hierarchically classify all plausible hypotheses by their key assumptions and outline field experiments that could test those and thereby discriminate among the alternatives.

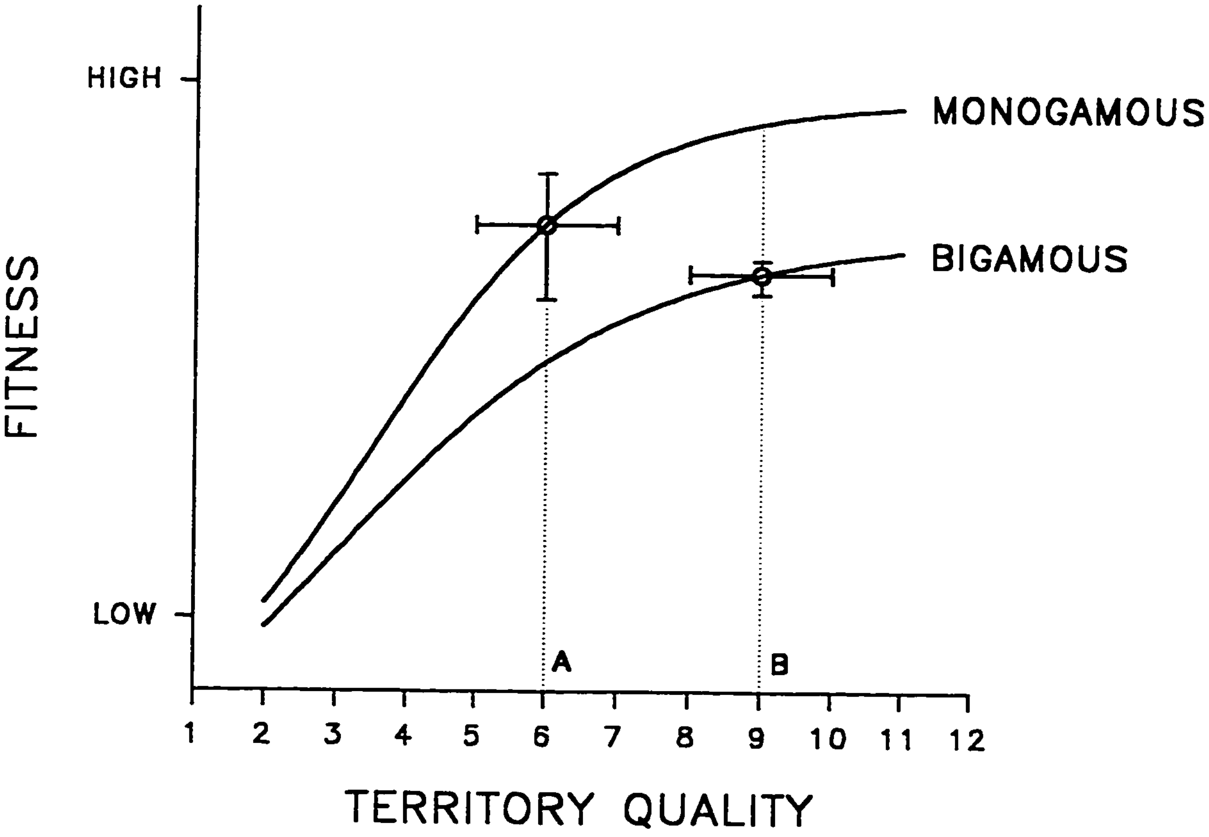


Figure 1.1: Graphic representation of mechanism B of the random dispersion hypothesis. The curve marked "monogamous" describes how the fitness of a monogamously mated female increases with territory quality. The curve marked "bigamous" describes how the fitness of a secondary bigamous female increases with the territory quality. Females make errors in evaluating territory quality and the errors are translated into inaccurate estimates of expected fitness. For example, if a female underestimates the quality of territory A and overestimates the quality of territory B, then her perceived fitness gain of being monogamous may be lower than the perceived gain of being polygamous. Such female would settle polygamously when in fact she could achieve higher fitness by settling monogamously.

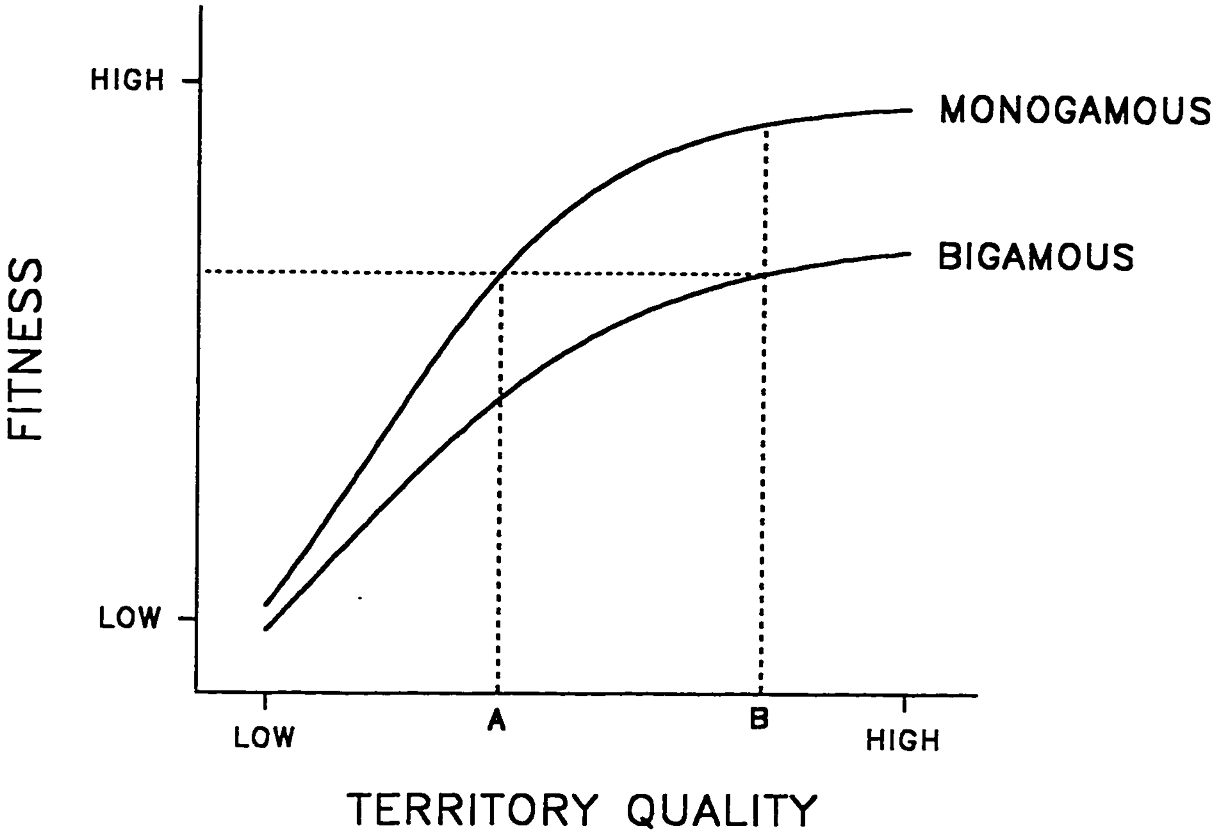


Figure 1.2: Graphic representation of the polygyny threshold model. The curve marked "monogamous" describes how the fitness of a monogamously mated female increases with territory quality. The curve marked "bigamous" describes how the fitness of a secondary bigamous female increases with the territory quality. The territory quality is a a combination of the quality of the male and of his territory. The cost of polygyny is the vertical difference between the "monogamous" and "bigamous" curves.

CHAPTER 2: A NEW INTERPRETATION OF THE ASYNCHRONOUS SETTLEMENT MODEL

INTRODUCTION

The polygyny threshold model, which is considered by many as the most plausible explanation for polygyny in territorial birds, assumes that a settling female makes relatively complex decisions when choosing a breeding situation: (i) the female must evaluate the quality of available males and their territories, (ii) the number of resident females present on those territories, and (iii) the combined impact of those females on her reproductive success. Then, on the basis of this information, the female chooses that breeding situation where she can achieve the highest fitness.

Recently, Leonard (1990) proposed an appealing alternative, the "asynchronous settlement" model (ASM). This model requires less complex behaviors than the polygyny threshold model, and for that reason is perhaps more feasible. However, the mechanism by which polygyny occurs in the ASM is not clearly described. In fact, if one is to rely on the written explanation, rather than on the perceived intent of the author, the described mechanism cannot give rise to polygyny at all. Here, I propose to clarify and refine the mechanism in a manner that I believe is consistent with the original intention.

The outline of this contribution is as follows. I will first describe the salient points of the polygyny threshold model, because this model is most similar to the ASM and hence most difficult to distinguish. I will then describe the version of the ASM as proposed by Leonard (1990), identify two key problems of that model that need clarification and suggest ways of resolving them. Following that, I will propose a new version of the model, and compare its assumptions and predictions to those of the original version. I will conclude by comparing the new version of ASM with the polygyny threshold model and state assumptions and predictions that can separate these two models, as well as those that cannot be used for that purpose.

THE POLYGYNY THRESHOLD MODEL

The polygyny threshold model was proposed by Verner (1964), and subsequently elaborated by Verner and Willson (1966) and Orians (1969). The main idea behind the model can be summarized as follows: polygyny occurs when the variation in the quality of breeding situations (males and their territories) is sufficiently large so that a female can achieve higher reproductive success when polygamously mated on a good-quality breeding situation than when monogamously mated on a poor-quality breeding situation. Thus, despite the fact that polygyny is costly to females, females settle polygynously because they are fully compensated for the cost of polygamy by the high quality of the chosen breeding situation.

In addition to being compensated for the cost of polygyny, females may reduce the initial cost through several mechanisms. One mechanism described in the original version of the polygyny threshold model is especially pertinent here, because it is very similar to the mechanism proposed by the ASM. The mechanism was described by Orians (1969, p.594) as follows: "Even if the male also cares for the offspring, in which case the number of other females he already has is a major factor in female choice, there are conditions which tend to minimize the reduction in reproductive success attendant upon polygynous matings. For example, if the successive females of a male are staggered in their breeding so that the periods of dependence of their offspring overlap little or not at all, more support from male could be available (Verner 1964). This should give selective advantage to two different forms of female behavior. The first is the attempt to exclude additional females from the territory of the male until such time as the overlap in dependency periods of the young would be minimized, and second, the avoidance by newly arriving females on territories in which a prior female was just beginning to breed."

This mechanism allows females to reduce the initial cost of polygamy by settling asynchronously. However, as the cost is not reduced completely, females are postulated by the model to settle polygamously only if they are compensated for the remaining cost by settling on high-quality breeding situations.

THE ASYNCHRONOUS SETTLEMENT MODEL: ORIGINAL VERSION

The asynchronous settlement model makes only one explicit assumption: a female must be able to detect the presence of another female in a male's territory and determine the other female's nesting stage. If females can do so, then the model postulates that females reduce the cost of polygamy by nesting asynchronously, and this, presumably, leads to polygamy (Leonard 1990, p.452). As asynchrony is postulated to reduce, but not eliminate, the cost of polygyny, females must be compensated by other mechanisms if they are to settle polygamously at all (otherwise, all females would settle monogamously because they would avoid the remaining cost of polygyny). As no compensating mechanism is proposed elsewhere in the model, one presumes that females are compensated by the variation in territory quality, as proposed by the polygyny threshold model. This assumption is supported by prediction

1 of the ASM, which allows females to choose territories by their quality (Leonard 1990, pg.454), but subsequently contradicted by prediction 5, which states that female reproductive success is not related to the order of their settlement (if females were choosing territories by their quality, then there should be a negative correlation; see Lightbody and Weatherhead 1988).

As is evident, two key aspects of the ASM need clarification: (1) what is the mechanism that gives rise to polygyny (i.e., how are females compensated for the cost of polygyny)?; and (2) what is the relationship between female settlement and the variation in territory quality and male quality (i.e., do females choose breeding situations by their quality)?

THE ASYNCHRONOUS SETTLEMENT MODEL: NEW VERSION

I suggest that the original intention of the author was to state that the cost of polygyny is completely eliminated through asynchronous settlement. When the cost is eliminated, there are no differences between polygamous and monogamous breeding situations and consequently there are no fitness advantages for settling one way or another. Under such circumstances, some females may settle with already mated males, and thereby become polygamous. As there is no need to further compensate females for the cost of polygamy (they are already fully compensated), there is no need for females to evaluate and discriminate among several breeding situations on the basis of their quality.

This version of the model rests on five assumptions. Three assumptions (1,2,4) have been implied by the original version of the model, but only one (3) was explicitly stated.

Assumption 1: The fitness costs of mating polygamously (e.g., costs due to competition for limiting resources such as food, male parental care, etc.) outweigh the benefits (e.g., mutual nest defence by females in a harem). Hence, there is a net fitness cost to polygyny (henceforth "cost of polygyny").

Assumption 2: As the asynchrony between the primary and the secondary female increases, the cost of polygyny declines, eventually reaching zero. The stage of the nesting cycle where the cost reaches zero is herein defined as the "temporal polygyny threshold", because it is the temporal threshold beyond which polygyny may occur.

This assumption describes the effect of asynchrony on the cost of polygyny when the asynchrony is experimentally manipulated (compare to prediction 1 below). The cost of polygyny need not decline in a linear fashion (Fig. 2.1), nor is there a requirement that all individual fitness components be affected (Fig. 2.2).

Assumption 3: Females can detect the presence of another female in a male's territory and determine the female's nesting stage.

Assumption 4: Females do not or cannot evaluate and choose territories or males by their quality. This does not necessarily mean that female settlement is non-random with respect to the variation in territory quality or male quality, only that the non-random pattern of settlement is not the result of female preferences for such variables. Consider, for example, that polygyny is costly because there is a limited supply of food on territories and females compete for it. If one was to follow females that are sampling potential breeding situations and compare the amount of food on territories that females rejected to the amount of food on territories that females selected, one would find that the rejected territories have consistently lower supply of food than the selected territories. The observed pattern is not, however, due to female preference for territories with a large supply of food, but rather due to female preference for territories where the resident female is asynchronous.

This assumption sets the ASM apart from the polygyny threshold model. According to the polygyny threshold model, the cost of polygyny is reduced, but not eliminated, through asynchronous settlement. Females settle polygamously because they are compensated for the remaining cost by choosing high-quality breeding situations. If the ASM did not make this assumption, then some females could settle polygamously not because the cost of polygyny would be eliminated through asynchrony, but because the remaining cost would be compensated by the good quality of the chosen breeding situation. Polygyny in such females would result from a mechanism that is identical to that proposed by the polygyny threshold model, and as a result there would be no difference between the ASM and the polygyny threshold model.

The original asynchronous settlement model led to six predictions. Four predictions have not been affected by my interpretation of the model. Their original versions, as described by Leonard (1990), are:

Prediction 1: "The order in which first and second females settle should be correlated. That is, if female settlement is staggered, the territories of the earliest females to settle should become available sooner than the territories of the females that settle later. Thus, second-settling females should settle first in the territories of the early females."

Prediction 2: "The order in which females settle is negatively correlated to male pairing success. Again, this is because the first territories settled would be opened to subsequent females sooner than other territories."

Prediction 3: "Secondary females and monogamous females settling at the same time should have equal fitness." The original justification for this prediction was as follows: "Because males and territories are similar and female success is related to the timing of settlement, a female settling in a territory with an incubating female should do as well as a female settling in the territory of a bachelor male." This justification was apparently meant to apply to the marsh wren (Cistothorus palustris), the species for which the asynchronous settlement model was originally proposed. For other species, where the temporal polygyny threshold occurs at other stages of female nesting cycle, the justification should perhaps be as follows: Because males and territories are similar in quality, and because secondary females settle only when the cost of polygyny is eliminated, a female settling with an already mated male should do as well as a female settling with a bachelor.

Prediction 4: "Asynchronous settlement model does not require a relationship between female reproductive success and the order in which territories are settled. That is, if each territory is settled only after the resident female is incubating, then females in all territories should do equally well." This prediction is true in principle, but may be difficult to test in field experiments. In many species of birds, there is a well established relationship between individual reproductive success and the time of the season: individuals that breed early have higher reproductive success than individuals that breed late. The seasonal decline in reproductive success has been attributed to several causes, for example: (1) there is a seasonal deterioration in the quality of the environment (e.g. seasonal decline in availability of food); or (2) old (and more productive) females nest earlier than young (and less productive) females. Regardless of the exact causes, the decline may give raise to a negative correlation between the order of female settlement and female reproductive success. Since the negative correlation may occur even if females avoid the cost of polygyny by settling asynchronously, the negative correlation (uncorrected for the effect of decline) should not be used to reject the asynchronous settlement model.

The original version of the ASM makes two additional predictions, both of which have been affected by my interpretation of the model. In the following section, I will first state the original prediction, then the new prediction, and then explain the reason for the difference.

Prediction 5: The original version stated: "If asynchrony between females decreases the cost of polygyny, then there should be a relationship between female success and settlement pattern. Female reproductive success should be correlated positively with the number of days between successive females." (Leonard 1990). This prediction appears similar to assumption 2 (above), as it relates female reproductive success to asynchrony. The important difference between this prediction and assumption 2 is that the assumption examines the effect of asynchrony on the reproductive success when the asynchrony is experimentally manipulated, while this prediction relates asynchrony to reproductive success when females are allowed to choose their preferred degree of asynchrony. Since females settle polygamously only after the cost of polygamy declines to zero (i.e. after asynchrony reaches the temporal polygyny threshold), all females suffer zero cost of polygamy and there is no variation among females in this variable. There may be, however, variation in the degree of asynchrony between females, because some females settle sooner after the temporal polygyny threshold is reached than others. Consequently, there should be no relationship between the cost of polygamy and the observed degree of asynchrony.

The relationship is illustrated in Fig. 2.1 by the portion of the line to the right of the temporal polygyny threshold.

Until now, I have assumed that a secondary female can determine the nesting stage of a primary female with little or no error. This may be a reasonable assumption if the temporal polygyny threshold coincides with some obvious changes in the primary female's nesting activity, such as with the onset of incubation or feeding. However, if the temporal-polygyny-threshold falls in the middle of the female's incubation period, then the secondary female may commit a large error when estimating the nesting stage of the primary female and as a result: (1) start nesting too early (i.e. before the temporal polygyny threshold); or (2) start nesting too late (i.e. after the threshold). Females that err by settling too late suffer no penalty, because the cost of polygyny remains at zero after temporal threshold. The same is not true for females that err by settling too early. Such females pay the cost of polygyny because the cost is still higher than zero. Because monogamous females achieve higher fitness than polygamous females that err in the wrong direction, natural selection should strongly act to make the erring conservative (i.e. to underestimate the degree of asynchrony). However, if the erring is unavoidable, one may find that there is a weak (but statistically significant) relationship between the degree of asynchrony and the reproductive success. This is because there would then be two types of females: (1) females that settle too late (their reproductive success is independent of asynchrony); and (2) females that settle too early (their reproductive success is inversely related to asynchrony). Combined, both types would produce an inverse relationship between the two variables.

Until now, I have also assumed that there is no seasonal decline in the reproductive success of females. Since the seasonal decline has been established for many populations of birds (Forslund and Pärt 1995), it may be worthwhile to examine its effect on this prediction of the model. As an example, consider that a large proportion of females is asynchronous well past their temporal polygyny threshold (e.g. the threshold is short relative to the length of nesting cycle and there is a high renesting rate due to predation on the young). If these conditions are fulfilled, one may find that the degree of asychrony is inversely related to the reproductive success. This is because females that renest immediately will do so earlier in the season (and are likely to be more synchronous with the primary females) than females that wait and renest late in the season (Fig.2.3).

As is apparent from these three examples, the observed relationship between asynchrony and reproductive success may be neutral, positive or negative. For this reason, no particular prediction can be made unless the effects of all confounding variables are precisely determined.

<u>Prediction 6</u>: Original version: "Because male and territory quality may be either homogeneous or of no relevance to females, there is no expected relationship between male and territory quality and harem size." By "no expected relationship", the author means that the relationship may be positive or negative, but the direction cannot be determined (Leonard, pers. comm.). This prediction is correct, because (as will be shown below) the relationship may vary from negative to neutral to positive depending on the specific male/territory attributes involved. Yet because the range of possible outcomes is so wide, the prediction is of little heuristic value because it cannot be falsified. In the following, I will provide examples where the relationship is negative, neutral and positive, and then propose a more specific version of this prediction.

Example 1: Consider male attributes or territory attributes that are related to the tenure of the primary female, such as the abundance of insect food on a territory. If such attributes are measured after the primary females settle, but before the secondary females arrive, then the territories of the early-settling primary females should contain less food than the territories of late-settling primary females. However, because secondary females should settle first on the territories of the early-settling females (see prediction 1), one would find a negative correlation between the abundance of food and the subsequent harem size.

Example 2: By analogy to example 1, consider measuring the nest-defence behavior of resident males. Since intensity of the behavior usually increases with the progress of the nesting cycle, then the mates of the early-settling primary females should be the best defenders, while the mates of the latest primary females should be the worst defenders. As a result, one would find a positive correlation between the intensity of the nest-defence behavior and the subsequent harem size.

Example 3: Consider, however, that (1) the attributes are measured either before the first primary female settles, or (2) after the last territory reaches the temporal polygyny threshold; or (3) that the attributes are not related to the tenure. Since females do not evaluate and choose attributes of territory quality and male quality (see assumption 4), and since such attributes are not related to the degree of asynchrony, the observed pattern of settlement of secondary females should not be related to the variation in such attributes. Hence, such attributes should vary independently of harem size.

I propose to restrict prediction 6 to attributes defined in example 3. For these attributes, the prediction would then state that there is no relationship (i.e. no correlation) between male and territory quality and harem size. Although this may appear to be a minor and cosmetic adjustment, its consequences are far-reaching. This is because prediction 6 represents perhaps the most feasible and accurate way of discriminating between the asynchronous settlement model and the polygyny threshold model. Of the four assumptions and six predictions considered so far, only assumptions 4 and predictions 4 and 6 can discriminate between the two models. Assumption 5 requires experimental manipulation of territory/male quality, while prediction 4 is weak. In contrast, prediction 6 requires no experimental manipulation and is strong and easily testable.

COMPARISON BETWEEN THE ASYNCHRONOUS SETTLEMENT MODEL AND THE POLYGYNY THRESHOLD MODEL

The polygyny threshold model represents perhaps the most closely related alternative to the ASM. For this reason, it would be worthwhile to emphasize the differences between the two models and describe how the differences were affected by my interpretation of the ASM. To facilitate the comparison, the predictions of both models are summarized in Table 2.1. As is evident from the table, both models postulate the same outcome for predictions 1,2,3 and 5. However, the models differ in the outcome of predictions 4 and 6, as I indicated above, prediction 4 is weak, because the seasonal decline in reproductive success would alter its outcome in the direction predicted by the polygyny-threshold model. Prediction 6, which relates harem size to the variation in those male/territory attributes that are not affected by asynchrony, however, can separate both models. The polygyny threshold model predicts that good-quality breeding situations should attract large harems, while the asynchronous settlement model predicts that there should be no significant relationship between the quality of breeding situations and their harem size. Because this prediction does not require any experimental manipulation of the variables, it should provide a relatively easy and plausible way of discriminating between the two models.

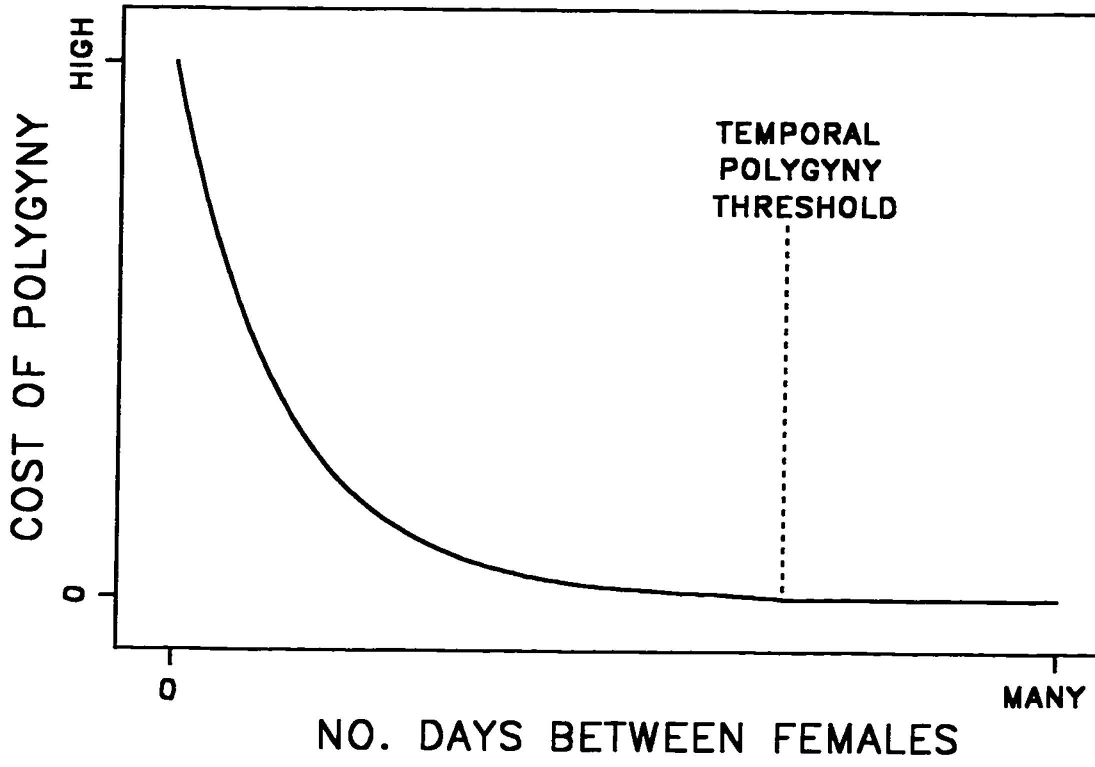


Fig. 2.1. The effect of nesting asynchrony between the primary and secondary female on the cost of polygamy to the secondary female. In this example, polygyny is costly because females share male parental care (i.e. male provides for both broods according to their need from hatching to fledging). Note that the cost of polygyny declines non-linearly. This is because male feeding is relatively more important just before fledging, when the demand is the greatest and when the female already provisions young at the maximum rate and cannot substitute for the male, then just after hatching, when the demand is low and the female can easily attend to all needs alone. The temporal polygyny threshold indicates when the cost of polygyny reaches zero.

Fig. 2.2. The effect of nesting asynchrony between the primary and secondary female on two fitness components of the secondary female: a) number of young fledged, b) survival of young to reproduction (as determined by the weight of fledglings), and (c) female fitness, as determined by the combined contribution of a) and b).

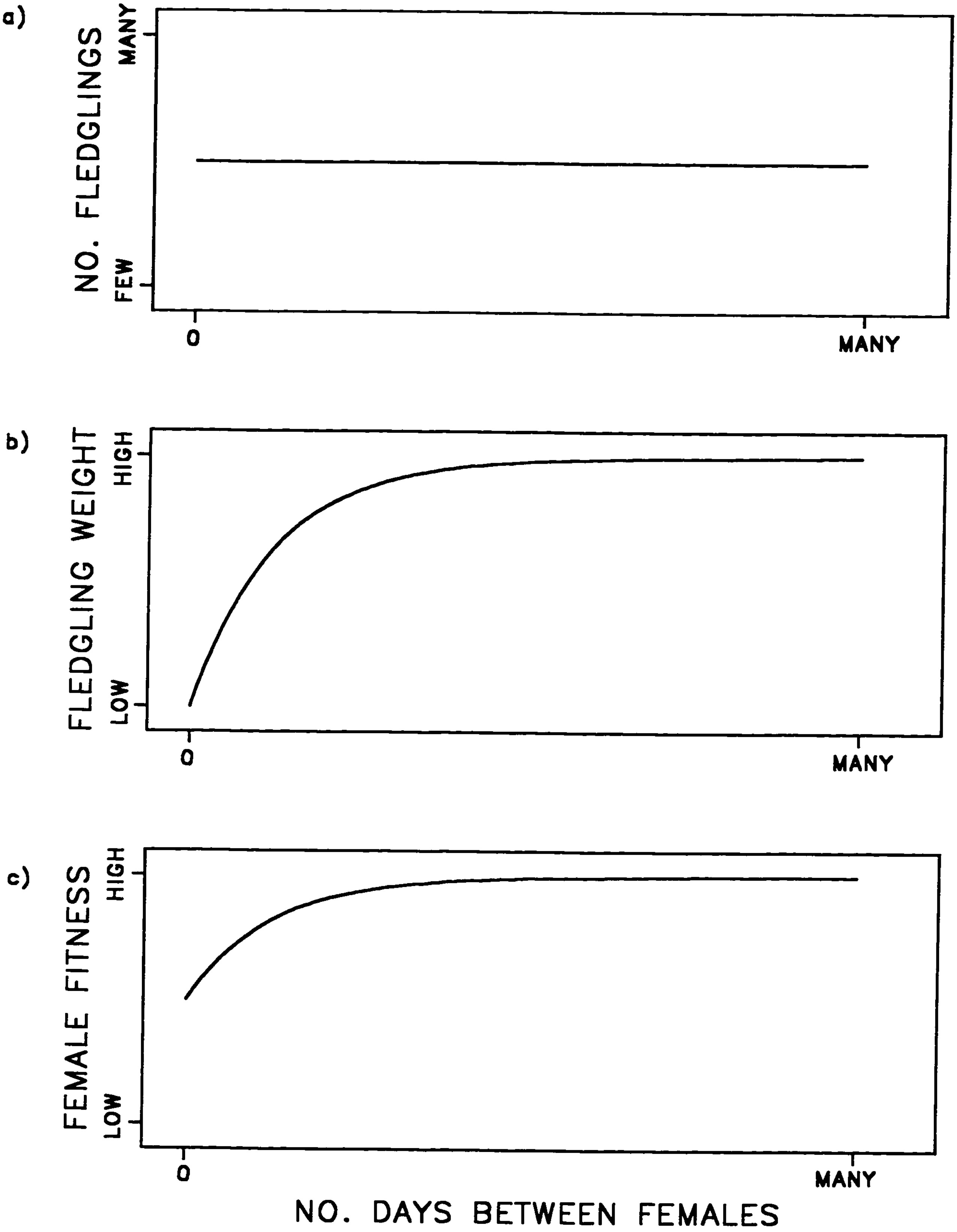
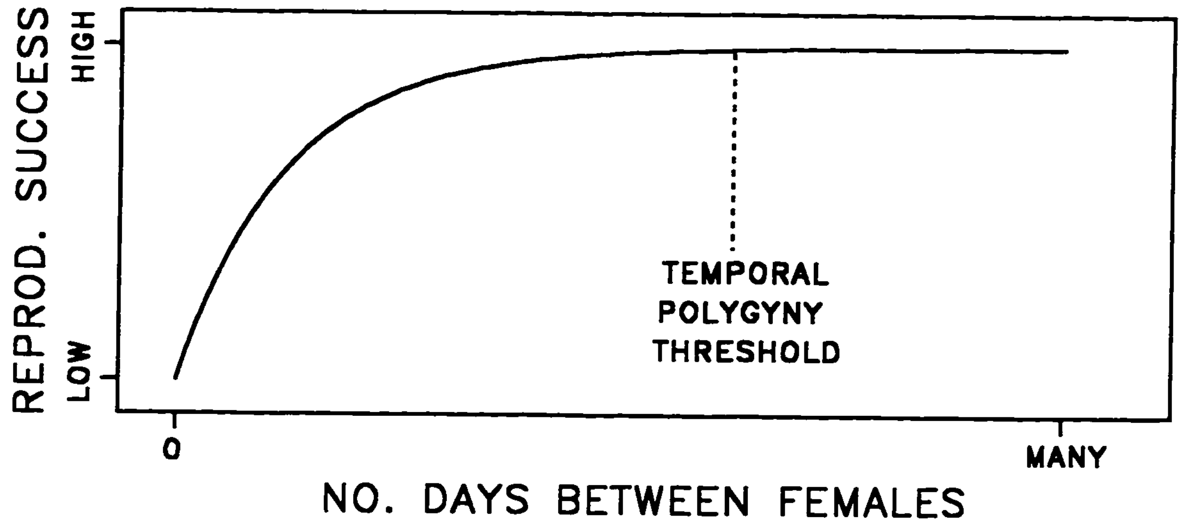
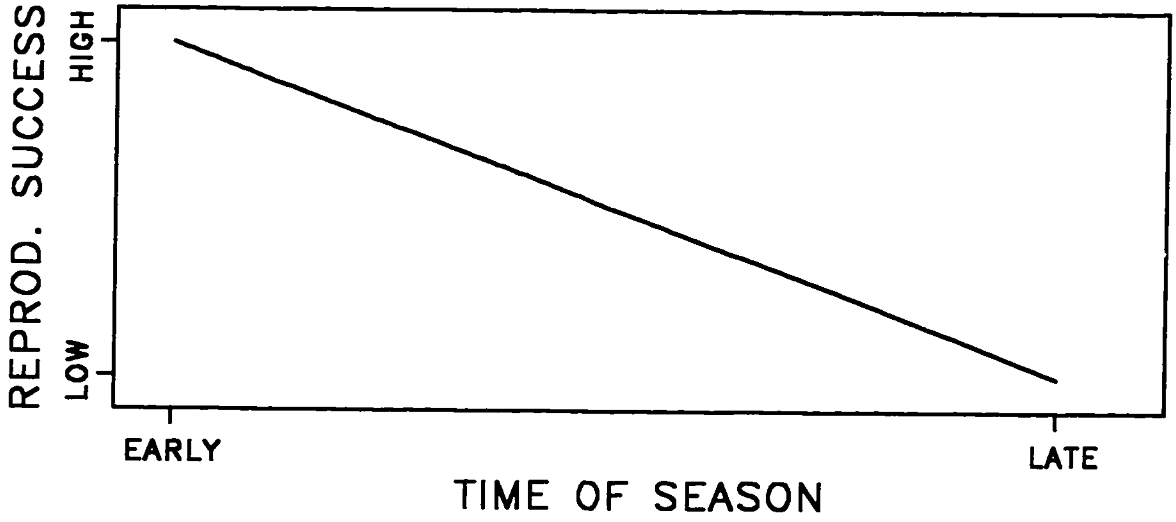

a)
NO. FLEDGLINGS
MANY
FEW
0
MANY
b)
FLEDGLING WEIGHT
HIGH
LOW
0
MANY
c)
FEMALE FITNESS
HIGH
LOW
0
MANY
NO. DAYS BETWEEN FEMALES

Fig. 2.3. The effects of nesting asynchrony and the time of season on the reproductive success of the secondary female: a) female reproductive success as determined by the degree of nesting asynchrony between the primary and secondary female; b) reproductive success as determined by the seasonal decline in environmental quality; c) reproductive success as determined by the combined effects of a) and b). Note that if most polygamous females are asynchronous past the temporal polygyny threshold, then there is an inverse relationship between the degree of asynchrony and the reproductive success.

a)


REPROD. SUCCESS
HIGH
LOW
TEMPORAL
POLYGYNY
THRESHOLD
0
MANY
NO. DAYS BETWEEN FEMALES

b)


REPROD. SUCCESS
HIGH
LOW
EARLY
LATE
TIME OF SEASON

c)

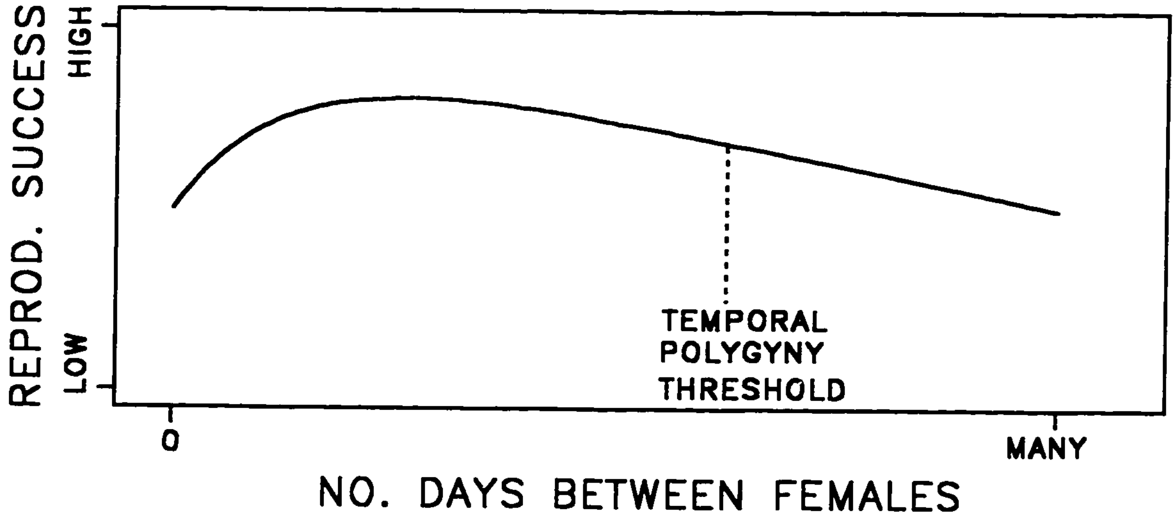

REPROD. SUCCESS
HIGH
LOW
TEMPORAL
POLYGYNY
THRESHOLD
0
MANY
NO. DAYS BETWEEN FEMALES

Table 2.1. Summary of predicted outcomes of the polygyny threshold model (PTM) and the original and new versions of the asynchronous settlement model (ASM).

prediction	PTM[1]	ASM	
		original version	new version
1) Order of settlement of primary vs. secondary female	positive correlation	positive correlation	positive correlation
2) Order of settlement vs. male pairing success	negative correlation	negative correlation	negative correlation
3) Fitness of monogamous vs. secondary females settling at the same time	same	same	same
4) Order of settlement vs. female reproductive success	negative correlation	no correlation[2]	no correlation[2]
5) Degree of asynchrony vs. female reproductive	positive or no correlation	positive or no correlation	positive, negative or no correlation
6) Male/territory quality vs. harem size	positive correlation	no predicted relationship	no correlation[3]

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[1] Predictions stated by Altmann et al. (1977), Lightbody and Weatherhead (1988)

[2] correlation may be negative, see text

[3] valid when male/territory quality is not affected by the degree of asynchrony

Chapter 3: COMMENTS ON ONE ASSUMPTION AND FOUR PREDICTIONS OF THE SEXY SON HYPOTHESIS.

INTRODUCTION

Since its inception in 1979, the sexy son hypothesis has generated much discussion and controversy (e.g. Searcy and Yasukawa 1981, Weatherhead and Robertson 1981, Wittenberger 1981a, Wagner 1994, Weatherhead 1994). The discussion has centered on two aspects of the hypothesis: on the theoretical foundations upon which the hypothesis is based, and on the applicability of the hypothesis to various species of birds, especially to the red-winged blackbird.

The original description of the sexy son hypothesis (Weatherhead and Robertson 1979) consists of two parts: (1) a short verbal description of the mechanism by which polygyny is deemed to arise; and (2) quantitative model to verify the mechanism. The quantitative model is not a genetic model, but rather a mathematical expression that calculates the number of a female's surviving grandchildren as a function of the female's mating status. The purpose of this expression was to show that polygynous females may tolerate initial loss in reproductive success because this loss is recouped in the subsequent generation through the higher mating success of their sons. Weatherhead and Robertson (1979) calculated the size of the initial loss, and then compared the calculated value to that observed in several populations of birds. Since the observed loss was always lower than the calculated one, the authors considered this to be corroborating evidence for their hypothesis.

Their mathematical formula was later found to contain several logical inconsistencies (Wittenberger 1981, Heisler 1981). To correct the inconsistencies, Heisler (1981) proposed a new mathematical formula to calculate the expected number of grandchildren. The improved formula confirmed the qualitative expectations of the original sexy son hypothesis, and provided a new set of values for the initial loss in reproductive success. The values were subsequently used by field workers to test the sexy-son hypothesis in a wide variety of polygynous species. However, as I will show later in this chapter, Heisler's formula still contains a flaw. The flaw concerns the interval over which female fitness is calculated: when the time interval is corrected, the initial loss is increased almost two times over that previously allowed.

The controversy surrounding the theoretical basis of the hypothesis did not, however, end with Heisler's formula. In 1985, Kirkpatrick proposed two genetic models that simulate the joint evolution of attractive traits and female preferences for such traits, as envisioned by the sexy son hypothesis. In the first model, male attractiveness is assumed to be a continuous trait with polygenic inheritance. In the second model, the trait is assumed to be discrete, with a two-locus haploid system of inheritance. Kirkpatrick (1985) found that both models yielded similar quantitative results. The models demonstrated that female preference for attractive traits cannot be maintained in a stable evolutionary equilibrium, and that "the only alternative evolutionary outcome to this equilibrium is an unstable runaway process in which the population follows a maladaptive evolutionary trajectory with declining population fitness, possibly leading to extinction" (Kirkpatrick 1985).

These conclusions of the Kirkpatrick's models were subsequently questioned by Curtsinger and Heisler (1988). Using a diploid genetic model, these authors demonstrated using counterexamples that the generalizations of Kirkpatrick's models are not valid. In the diploid model, attractive male traits, and female preferences for such traits, can evolve from low initial frequencies and be maintained at a stable evolutionary equilibrium. Curtsinger and Heisler also discussed the sensitivity of their model and those of Kirkpatrick to the type of genetic inheritance assumed. Although the type of inheritance and the technique used may explain the differences between the models, it is not clear which type of inheritance should be preferable (e.g. diploid vs. polyploid) and hence which conclusion is more plausible. Thus, although the theoretical foundation of the sexy son hypothesis may be partly established, it does not rest upon firm ground yet.

In addition to the controversy surrounding its theoretical foundation, the sexy son hypothesis stirred much debate about its applicability to many species of birds. With few exceptions, most authors have argued that the hypothesis cannot explain polygyny in their particular species: Searcy and Yasukawa (1981) in the red-winged blackbird, Johnson (1992) in house wrens (Troglodytes aedon), Catchpole et al. (1985) in the great reed warbler (Acrocephalus arundinaceus), Alatalo et al. (1981) and Alatalo and Lundberg (1986) in the pied flycatcher (Ficedula hypoleuca), Lightbody and Weatherhead (1988) in the yellow-headed blackbird (Xantocephalus xantocephalus) and Korpimäki (1989) in the Tengmalm's Owl (Aegolius funereus). There were, however, exceptions to this rule: Burley's (1986) carefully designed experiments with captive zebra finches (Taeniopygia guttata) and Gustafsson et al.'s (1995) experimental manipulations of parental effort in the collared flycatcher (Ficedula albicollis) provided solid support for the main tenets of the hypothesis. The evidence for or against the hypothesis can be divided into two categories: First, evidence based on the comparison of the calculated loss in reproductive success (obtained from Heisler 1981) to that observed in natural populations. As I indicated above, the calculated loss may be underestimated, and this may affect the conclusions of the studies that have used it. Second, evidence that comes from empirical tests of the various assumptions and predictions of the hypotheses, specifically from those that attempt to discriminate between the sexy son hypothesis and its most similar alternative, the polygyny threshold model. Here, I will discuss one assumption and three predictions of the hypotheses that have been, in my opinion, misunderstood. All have been tested in the literature and their consistency with the experimental results have been used to reject (or support) the sexy son hypothesis. I will compare the assumption to the requirements of the hypothesis, and point out that the assumption is incomplete because it leaves out one important set of male traits. I will then examine an alternative version of this assumption that has been proposed by other authors, and demonstrate by examples that their version does not reflect the requirements of the sexy son hypothesis. I will also examine the predictions and provide examples to illustrate that the predictions are not universally valid, i.e. their outcome depends on the nature of traits that constitute male attractiveness.

I will start this chapter by reviewing the differences between the sexy son hypothesis and the polygyny threshold model. Following that, I will discuss one assumption, each of the three predictions, and finally the mathematical formula used to calculate the loss in reproductive success. I will conclude by discussing the impact of my findings on our ability to experimentally discriminate between the sexy son hypothesis and the polygyny threshold model.

THE SEXY SON HYPOTHESIS

The sexy son hypothesis has been proposed as an extension of the polygyny threshold model. Both hypotheses explain why female birds mate polygamously despite the fact that (1) the presence of other females in a harem reduces their reproductive success; and (2) monogamous breeding options are available to them. Both hypotheses offer similar explanation: polygyny occurs when the variation in the quality of breeding situations is sufficiently large so that a female can achieve higher fitness when polygamously mated on a good-quality breeding situation than when monogamously mated on a poor-quality breeding situation (Verner 1964, Verner and Willson 1966, Orians 1969, Weatherhead and Robertson 1979). The hypotheses differ in their definition of female fitness. The polygyny threshold model defines female fitness as her reproductive success (RS). The sexy son hypothesis extends this definition to include not only female RS, but also the mating success of her sons (mating success of sons, or MSS). This latter component is especially important in polygynous species where males vary in their ability to attract mates. According to the sexy son hypothesis, females consider both components independently when sampling and evaluating potential breeding situations: they evaluate how many young they can raise, and they also evaluate the attractiveness of resident males and how this attractiveness will affect through inheritance the mating success of their sons. Both components (RS and MSS) contribute to female fitness, and sampling females settle in those breeding situations where their total fitness is maximized.

ASSUMPTION 1

One important prerequisite of the sexy son hypothesis is that the variation in attributes that determine female reproductive success is not perfectly associated with the variation in attributes that determine male attractiveness. This prerequisite was stated in the original description of the sexy son hypothesis as: "males with individual attributes most attractive to females are not necessarily those with the best quality territories" (Weatherhead and Robertson 1979). The individual male attributes were subsequently defined as those male traits that are heritable and that females use when choosing mates (henceforth "attractive" traits). The characteristics that constitute "best-quality territories" are not defined, but one can presume that they involve those territory characteristics that affect female reproductive success and that females evaluate when choosing territories (henceforth "territory quality").

When the requirements of the sexy son hypothesis are compared to the assumption described in Weatherhead and Robertson (1979), it is obvious that one important set of traits is left out from the description. The set involves non-heritable male traits that affect female reproductive success. Because such traits are not heritable, they cannot be passed from fathers to sons and, therefore, cannot affect MSS. Hence, females should not consider them when evaluating how the attractiveness of her mate will affect the attractiveness of her sons to other females. On the other hand, the traits affect female reproductive success, and hence females should use them to evaluate potential breeding situations. I propose that such traits be combined with other territory characteristics into one category of "reproductive" attributes, and that the assumption be amended to state that "the variation in traits that affect MSS is not perfectly correlated with the variation in attributes that affect female RS."

Catchpole et al. (1985) proposed a version of this assumption that requires that "the variation in male traits should not be correlated with the variation in territory characteristics." The category of male traits is not restricted to "attractive" traits (as defined above), but rather includes all male traits that can be quantified. Similarly, the category of territory characteristics is not restricted to "territory quality". By not restricting the assumption to specific male traits and specific territory characteristics, this assumption may be tested with male traits that are not "attractive", or with territory characteristics that do not constitute "territory quality". By testing the assumption with inappropriate attributes, one may (1) erroneously reject the assumption when the assumption may more properly be supported; or (2) support the assumption when the assumption should be more properly rejected. To provide an example, consider a species where the sexy son hypothesis does not apply. Suppose that one selects territory characteristics that are easy to measure, but that have no effect on either male or female reproductive success. Since the characteristics are unimportant to males, males are unlikely to consider them when evaluating the quality of prospective territories, or when competing for the territories with other males. Consequently, these territory characteristics are unlikely to be correlated with male characteristics. The lack of correlation is consistent with the assumption, and thus appears to support the sexy son hypothesis, when in fact the sexy son hypothesis should not apply at all in this case.

In conclusion, the broad and all-inclusive definition of male traits and territory characteristics employed in this version of assumption 1 may produce unreliable conclusions. Future studies should test this assumption only by comparing male traits that affect MSS to male traits/territory characteristics that affect female RS.

PREDICTION 1

Lightbody and Weatherhead (1988) tested the polygyny threshold model, the sexy son hypothesis and the neutral-mate-choice hypothesis in the yellow-headed blackbird. For each hypothesis, they proposed five predictions and then tested the predictions with data on female reproductive success and the pattern of their settlement. Here, I will discuss three predictions that were tested for the sexy son hypothesis.

The first prediction states that there should be no relationship between female reproductive success and the order in which the last females in each territory settle. As this prediction is not present in the original description of the sexy son hypothesis, Lightbody and Weatherhead (1988) had to derive it from the first principles of the hypothesis. The logic behind this derivation is described on p. 22: if females choose males solely on the basis of expected reproductive success, then the order of settlement would be negatively correlated with female reproductive success. However, if females settle according to the sexy son hypothesis, then the negative correlation is broken because some females sacrifice their reproductive success for mating with an attractive male.

Although, intuitively, this reasoning makes sense, it is not clear whether the lack of a correlation holds true for all possible types of attractive traits. The attractive traits may be (1) arbitrary, i.e. they do not affect female reproductive success; (2) functional (they affect reproductive success) and shareable (i.e. all females within a harem benefit from the trait to the same degree); or (3) functional and non-shareable (e.g. some females always benefit more than other females). In addition, the association between attractive traits and reproductive attributes may vary from complete independence to a moderately-strong correlation. Here, I will show with examples that the lack of a significant correlation is not generally valid, and that, depending on the situation, the correlation can be significant and either negative or positive.

Consider a hypothetical population of five females that settle on the territories of five males according to the polygyny threshold model. In the example, female reproductive success is determined by a single feature of territory quality. Because each female selects the territory where her expected reproductive success is the highest, the order of female settlement is perfectly correlated with their expected reproductive success (Fig. 3.1).

Consider now three examples where females settle according to the sexy son hypothesis. In the examples, male quality (represented by a single attractive trait) contributes to female fitness and females assess it independently of territory quality.

Example 1: In this example, the contribution of the attractive trait (as measured by the mating success of sons, or MSS) to female fitness is small in comparison to the contribution of the territory quality (as measured by reproductive success). Because the attractive trait is of little importance, the ranking of breeding options by the expected fitness is determined mostly by the variation in reproductive success, and less by the variation in MSS (Fig. 3.2). As a result, the order of female settlement is negatively correlated with the expected reproductive success, and the order in which the last female in each territory settles is negatively correlated with the female's expected/realised reproductive success (Fig. 3.2).

This conclusion holds true for all types of attractive traits (i.e arbitrary, functional shareable, functional non-shareable) and for all plausible types of association (i.e. independence, moderate positive or negative correlation) between the variation in the attractive trait and the variation in the territory quality.

Example 2: Here, the contribution of MSS to female fitness is substantial, and the attractive trait varies independently of the variation in the territory characteristics. Consider first that there is little variation in the MSS as compared to the variation in reproductive success. Because the ranking of breeding situations is determined mostly by the variation in reproductive success, the order of settlement (of the last females in each territory) is again negatively correlated with the expected/realised reproductive success (Fig. 3.3). Suppose now that the variation in MSS is increased. As the variation increases, MSS becomes more and more important in determining the ranking of breeding situations, and the correlation between the order of settlement and the reproductive success becomes increasingly weaker. Although the underlying negative relationship should persist, it should become progressively more difficult to detect it with increasing variation in MSS even with large sample sizes.

Example 3: In this example, there is little variation in either the MSS or reproductive success. The attractive trait is an arbitrary trait, and varies inversely with the territory characteristics (Fig 3.4). In addition, the level of polygyny is restricted by the number of available nesting sites (this regularly occurs in territorial, cavity-nesting species). Because the level of polygyny is restricted, the overall pattern of female settlement will proceed from the highest fitness to the lowest fitness, and thus from the lowest reproductive success to the highest reproductive success. Consequently, the order of female settlement is positively correlated with their expected reproductive success and likewise, the order in which the last females in each territory settle is positively correlated with their expected/realised reproductive success (Fig.3.4). Note that this relationship holds even as the restrictions on the variability of MSS and reproductive success are loosened, provided there is sufficient sample size to detect it. Note also that this relationship may hold for some functional attractive traits, provided that fitness declines as reproductive success increases. These four examples illustrate that the order in which the last female in each territory settles may be either negatively correlated, positively correlated or independent of female reproductive success. The examples also illustrate that the predicted outcome depends on two variables: (1) the type of attractive trait; (2) the underlying correlation between the attractive traits and territory characteristics. Future studies should consider both variables when making a prediction about the order of female settlement and the reproductive success.

PREDICTION 2

The second prediction states that there should be no relationship between the reproductive success of early and late settlers settling in same-sized harems. Because this prediction is a corollary of prediction 1, I will employ the same arguments as described in the previous sections. Consider examples 1 to 3 above, but restrict the analyses to harems of the same size. In examples 1 and 2, early settling females have higher reproductive success than late settling females (Figures 3.2 and 3.3), while in example 3 early settling females have lower reproductive success than late settling females (Fig. 3.4). Again, these examples illustrate the importance of (1) the type of attractive trait, and (2) the correlation between the attractive trait and territory characteristics, and the need for considering both variables when making a prediction.

Before concluding the discussion of predictions 1 and 2, I would like to point out a practical difficulty with testing both predictions by field experiments. In many species of birds, old females start nesting earlier in the season than young females. Old females also achieve higher reproductive success than young females, perhaps due to their greater experience (Wootton et al. 1986, Forslund and Pärt 1995). As a result, one may find a negative correlation between the order of female settlement and their reproductive success that is entirely age/experience-related, and not related to either the polygyny threshold model or the sexy son hypothesis. One possible way to circumvent this problem is to restrict the analyses to females of the same cohort, but one must be aware of the fact that the decline may be related to experience rather than age, and that even within a single cohort experienced females may settle earlier and have higher reproductive success than naive females.

PREDICTION 3

The third prediction states that the last females settling in large harems should have lower reproductive success than last females settling at the same time in small harems (Lightbody and Weatherhead 1988). This prediction is based on the assumption that females settling at the same time achieve equal fitnesses. The validity of this assumption has been questioned by several authors (e.g. Altmann et al. 1977, Wittenberger 1979, Vehrencamp and Bradbury 1984), and it appears that given "some reasonable assumptions about female decision rules, about limits to the number of territories examined, and about statistical distributions of territory quality, females choosing mated males usually have lower mean fitness than females simultaneously choosing unmated males" (Alatalo and Lundberg, pers. comm., cited in Searcy and Yasukawa 1989). Even if this assumption turns out to be incorrect, it is possible to revise the prediction and to state that "if two territories (large-harem vs. small-harem) are ranked by females as being of the same quality (i.e.fitness), then a female settling in the large-harem territory should produce fewer young than a female settling in the small-harem territory." There may be a practical difficulty in determining how territories are ranked by females, but this difficulty does not alter the outcome of the prediction.

The prediction is illustrated in Fig. 3.5. Here, male attractiveness is an arbitrary trait that is weakly correlated with territory quality, and the territory quality is the only attribute that determines female RS. Consider two breeding situations, A and B, that would provide a settling female with equal fitness. Territory A is defended by a bachelor, whereas territory B is defended by a monogamously mated male. Since territory A is initially of worse quality than territory B, and since both breeding situations would provide a new female with similar fitness, the RS of a female settling on territory B (larger-harem) would be lower than the RS of a female settling on territory A (smaller-harem).

However, this situation may be changed by simply changing the nature of male attractiveness. If male attractiveness is an arbitrary trait that varies independently of territory quality, as in Fig. 3.6, then males A and B are, on average, of similar attractiveness. Since breeding situations A and B provide equal fitness, and since males A and B are equally attractive, a female settling in A (smaller-harem) would produce as many young as a female settling in B.

It is also possible that male attractiveness is an arbitrary trait negatively correlated with territory quality (e.g. tail length in the golden-headed cisticolas, Cisticolas exilis, Cockburn 1990). If that is the case, then a female settling in territory A (small-harem) would achieve lower reproductive success than a female settling in territory B (Fig. 3.7).

These three examples demonstrate that the outcome of the prediction depends on the nature of the male attractiveness and on the relation between male attractiveness and territory quality.

PREDICTION 4

The original version of the third prediction stated that last females settling in large harems should have lower reproductive success than last females settling at the same time in small harems. This prediction is graphically illustrated in Fig. 3.6, where the last female settling in a small harem (monogamous female) achieves the same fitness as the last female settling in a large harem (secondary bigamous female), yet the bigamous female fledges fewer young than the monogamous female. According to the sexy son hypothesis, the bigamous female is compensated for her initial loss of reproductive success by the higher mating success of her son, so that her final fitness is identical to that of the monogamous female.

The maximum loss of reproductive success tolerated by a polygynous female was mathematically modelled by Heisler (1981) for various population parameters. In Heisler's model, a population of females consists of two mating types: polygynous and monogamous. Polygynous females differ from monogamous females in two respects: (1) polygynous females fledge fewer young than monogamous females; and (2) sons of polygynous females attract more mates than sons of monogamous females. The model calculates the number of descendants of the monogamous and polygynous females over the course of several generations. Ideally, the calculation would be carried out over as many generations as possible. This is because the compensation occurs over the course of many generations, albeit to a progressively decreasing degree. However, because such a model would have to assume a specific mode of inheritance and because the compensation is the greatest during the first generation, Heisler limited her model to the first one and a half generation. In the model, the number of descendants (grandchildren) is calculated for monogamous and polygynous females separately. The calculations can be visualised as consisting of three steps: First, the model calculates the number of offspring (children) that survive to reproduce. In the second step, this number is multiplied by the number of mates that each offspring attracts. In the third step, the term derived in the preceeding two steps is multiplied by the number of young that each mate produces (which is the number of grandchildren of the original female). Specifically, the number of grandchildren produced by a monogamously mated female (F_m) and the number of grandchildren produced by a polygynously mated female (F_p) is calculated as:

$$F_m = c\left(\frac{s}{1 + s}\right)\left[b_{pn}cxk + b_{nn}c\,\frac{(1 - sfk)}{s(1 - f)}\right]$$

$$+\ c\left(\frac{1}{1 + s}\right)\left[cxsfk + c(1 - sfk)\right] \qquad [1]$$

$$F_p = cx\left(\frac{s}{1 + s}\right)\left[b_{pp}cxk + b_{np}c\,\frac{(1 - sfk)}{s(1 - f)}\right]$$

$$+\ c\left(\frac{1}{1 + s}\right)\left[cxsfk + c(1 - sfk)\right] \qquad [2]$$

where the variables are:

f = proportion of males who are polygynous;

s = the breeding sex ration (total number of adult males divided by the total number of adult females);

k = the number of mates per polygynous male ("harem size");

c = the number of surviving young per monogamously mated female;

x = the number of surviving young per polygynously mated female divided by the number of surviving young per monogamously mated female;

b_{ij} = the probability that a male is of mating type i, given that his father was of mating type j. Male mating types are either p=polygynous or n=nonpolygynous.

Because monogamous and polygynous females are to achieve the same fitness, equation F_m can be set equal to equation F_p, producing the following quadratic expression:

$$0 = 2sfk\,(1 - f)x^2 + (2 - 4sfk + r)(1 - f)x - (1 - sfk)\,[r/sk + 2(1 - f)] \qquad [3]$$

In the model, the first generation begins when the original females start reproducing and ends when their offspring begin to reproduce (but after they mate). The second generation would begin when the offspring begin to reproduce and end when their offspring (i.e. grandchildren of the original females) begin to reproduce (but after the grandchildren mate). Because the model does not include a term describing the mating success of the grandchildren, it describes less than two generations, but more than one generation. Consequently, I will refer to the generation length of the model as 1.5

generations.

The fact that the model calculates the number of descendants over a fraction of the generation time (e.g. over 1.5 generations) rather than over an integer multiple of the generation time (e.g. over 1,2 or 3 generations) is likely to affect the accuracy of the model. During each generation, there are two key events that affect the number of descendants: (1) nesting period; and (2) the period of mate attraction. During the nesting period, the number of descendants produced by polygynous females declines relative to the number of descendants produced by the monogamous females, because polygamous females suffer the cost of polygamy (i.e. they compete with other females in a harem for limited resources and therefore produce fewer young). During the period of mate attraction, the number of descendants produced by polygynous females increases relative to the number of descendants produced by monogamous females, because the sons of polygynous females (who have inherited from their mothers the gene(s) that makes polygynous females polygynous) attract more mates (and dispense the gene to a larger number of offspring) than the sons of monogamous females.

These two events are repeated every generation. If the frequency of polygyny is to remain constant in a population, then the fitness of polygynous females must equal unity (e.g. the number of descendants must neither increase nor decrease over a prolonged period of time). This means that the number of descendants that polygynous females loose (relative to monogamous females) during the event 1 must equal to the number of descendants that they gain (relative to monogamous females) during the event 2. In Heisler's model, however, the number of descendats was calculated over 1.5 generations, which means that two events 1 were set equal to one event 2. In other words, two declines in the number of descendants were set equal to one increase in the number of descendants (e.g. in equations 3). This means that the value of variable x (which measures the decline in the number of descendants of polygynous females relative to the decline in the number of descendants of the monogamous females) was underestimated.

This inaccuracy of the model can be corrected by removing the third term from equations F_m and F_p. The third term multiplies the first and second term by the reproductive success of the daughters and sons. When the third term is removed, the equations calculate the changes in the number of descendants from the beginning of reproduction of the original females to the beginning of reproduction of their sons/daughters. The removal of the term therefore reduces the generation time to one generation and this removes the inaccuracy described above. The corrected equations are:

$$F_m = c\left(\frac{s}{1 + s}\right)\left[b_{pn}k + b_{nn}\frac{(1 - sfk)}{s(1 - f)}\right] + c\left(\frac{1}{1 + s}\right)\left[sfk + (1 - sfk)\right] \qquad [4]$$

$$F_p = cx\left(\frac{s}{1 + s}\right)\left[b_{pp}k + b_{np}\frac{(1 - sfk)}{s(1 - f)}\right] + c\left(\frac{1}{1 + s}\right)\left[sfk + (1 - sfk)\right] \qquad [5]$$

When these equations are set equal, one obtains the following mathematical expression:

$$0 = s(xfk + r + x - fk - 1)(1-f) + (x - xf - r/k + f - 1)(1-sfk) \qquad [6]$$

which, when solved for x as a function of the remaining variables, yields:

$$x = 1 + r(1/k - s)/[(s + 1)(1 - f)] \qquad (7)$$

The effect of variation in parameters r,s,f and k on the value of x is illustrated in Figure 3.8. This figure, which is directly comparable to Figure 1 in Heisler (1981), demonstrates that the corrected value of x is lower than the value calculated by the original model for most combinations of the parameters. In Table 3.1, I compiled data on the population parameters s,f and k for 8 polygynous species of birds. For each species, I calculated the value of x using the corrected equation (7) and also using the original equation derived by Heisler (1981). For all species, the corrected value of x was lower than the value calculated by the original model. The difference varied from 0.09 to 0.165, which means that a polygynous female may fledge up to 0.164 young fewer (for every young fledged by a monogamous female) than it was originally believed. Given that x can vary only between 0 and 1, the difference of 0.164 young is substantial.

In conclusion, future studies that use the Heisler's model to test the sexy son hypothesis should calculate the value of x from equation 7 above.

HOW TO DISCRIMINATE BETWEEN THE SEXY SON HYPOTHESIS AND THE POLYGYNY THRESHOLD MODEL?

Since the sexy son hypothesis is an extension of the polygyny threshold model, there are only few assumptions and predictions that can be used to discriminate between the two hypotheses, and even fewer that can be feasibly tested in field experiments. Predictions 1 to 3 have been believed to have this discriminatory power (Table 3.1). According to the polygyny threshold model, the first prediction stated that there should be a negative correlation between the order in which the last females in each territory settle and their reproductive success (Table 3.1). As I have shown above, the sexy son hypothesis predicts that the correlation may be negative, neutral or positive. Thus, the first prediction cannot be used to reject the sexy son hypothesis, because the empirical data will always be consistent with the prediction. The only way to use this prediction to discriminate between the hypotheses is to reject the polygyny threshold model on the basis of positive or neutral correlations.

The second prediction compares the reproductive success of earlier settlers vs. later settlers in harems of the same size. The polygyny threshold model states that earlier settlers should have higher success than the latter settlers. As I have shown, the outcome predicted by the sexy-son hypothesis includes higher, equal or lower relationship. Again, this prediction cannot be used to reject the sexy-son hypothesis, and thus the only way to differentiate it from the polygyny threshold model is to reject the latter on the basis of lower or no relationship.

The third prediction compares reproductive success of females settling in large harems to the reproductive success of females settling at the same time in small harems. The polygyny threshold model predicts that there should be no difference in the reproductive successes of the females, while the sexy son hypothesis predicts that females in large harems should have lower success than females in small harems. As I indicated in Figures 3.6 and 3.7, there are other outcomes possible under the sexy son hypothesis, such as equal or higher success of females settling in large harems.

Since the sexy son hypothesis allows for all possible outcomes, this prediction cannot be rejected with empirical data and the only way of discriminate the sexy son hypothesis from the polygyny threshold model is to reject the latter alternative.

In its present form, the three predictions discussed above lack the power to discriminate between the two hypotheses. It should be possible to reformulate the predictions for particular male traits and use those to differentiate between the hypotheses.

Table 3.1: Comparison of seven polygynous species with respect to their population parameters s,f,k and x. The parameter x is the minimum number of young that a polygynous female must fledge for every young fledged by a monogamous female. The value of x was calculated from equation 10 in Heisler (1981) and from equation 7 in Chapter 3. Heritability was set at $r = 1$.

					x	
Species	Reference	s	f	k	Heisler's study	This study
Pied Flycatcher[1]	Alatalo et al. (1981)	1	0.143	2	0.798	0.708
Great reed Warbler[2]	Catchpole et al. (1985)	0.905	0.263	2	0.783	0.712
Blue Tit[3]	Kempenaers (1994)	0.824	0.206	2.037	0.823	0.770
Northern Harrier[4]	Simmons (1988)	0.830	0.15	2.430	0.794	0.731
House Wren[5]	Johnson et al. (1994)	1	0.10	2	0.810	0.722
Tengmalm's Owl[6]	Korpimäki (1989)	1.401	0.044	2	0.772	0.607
	Korpimäki (1991)	1.361	0.093	2.081	0.751	0.589
European Starling[7]	Pinxten and Eens (1990)	0.64	0.33	2.19	0.851	0.833

1 *Ficedula hypoleuca*, 2 *Acrocephalus arundinaceus*, 3 *Parus caeruleus*, 4 *Circus cyaneus*, 5 *Troglodytes aedon*, 6 *Aegolius funereus*, 7 *Sturnus vulgaris*.

Table 3.2: Three predictions of the polygyny threshold model (PTM) and the sexy son hypothesis (SSH).

Prediction	PTM	SSH literature	SSH this study
Order in which the last females in each territory settle vs. reproductive success	negative correlation[1]	no correlation[1]	negative, positive or no correlation
Reproductive success of earlier vs. later settlers of earlier settlers in same-sized harems	higher success of earlier settlers[1]	no relationship[1]	lower, equal or higher success of earlier settlers
Reproductive success of females settling at the same time in different-size harems	equal[1]	lower in large harems than in small harems[1]	lower, equal, or higher in small harems

[1] Lightbody and Weatherhead (1988)

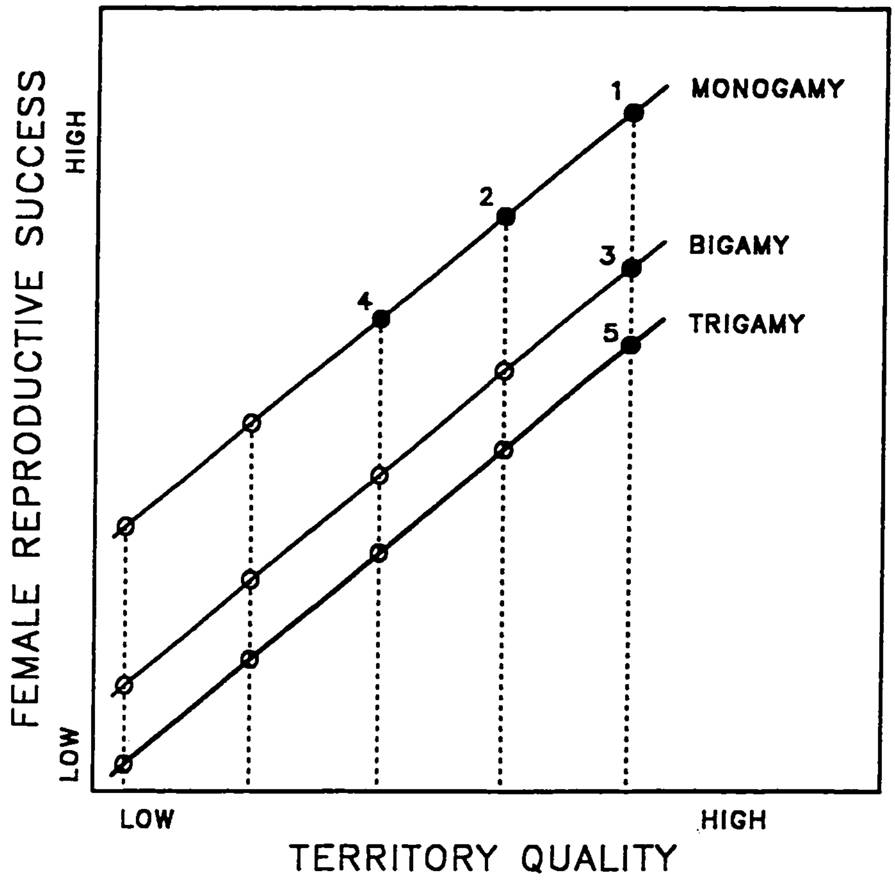


Figure 3.1: Settlement of females according to the polygyny threshold model. Five females settle on five territories. Female reproductive success is determined by a single feature of territory quality. The position of each territory along the "territory quality" axis is indicated by the dashed line. Solid lines indicate how the female reproductive success increases with territory quality: MONOGAMY represents the relationship for monogamous females, BIGAMY for both (i.e. primary and secondary) females, and TRIGAMY for all three trigamous females. Full circles indicate breeding options selected by the females, numbers describe the order in which females settled.

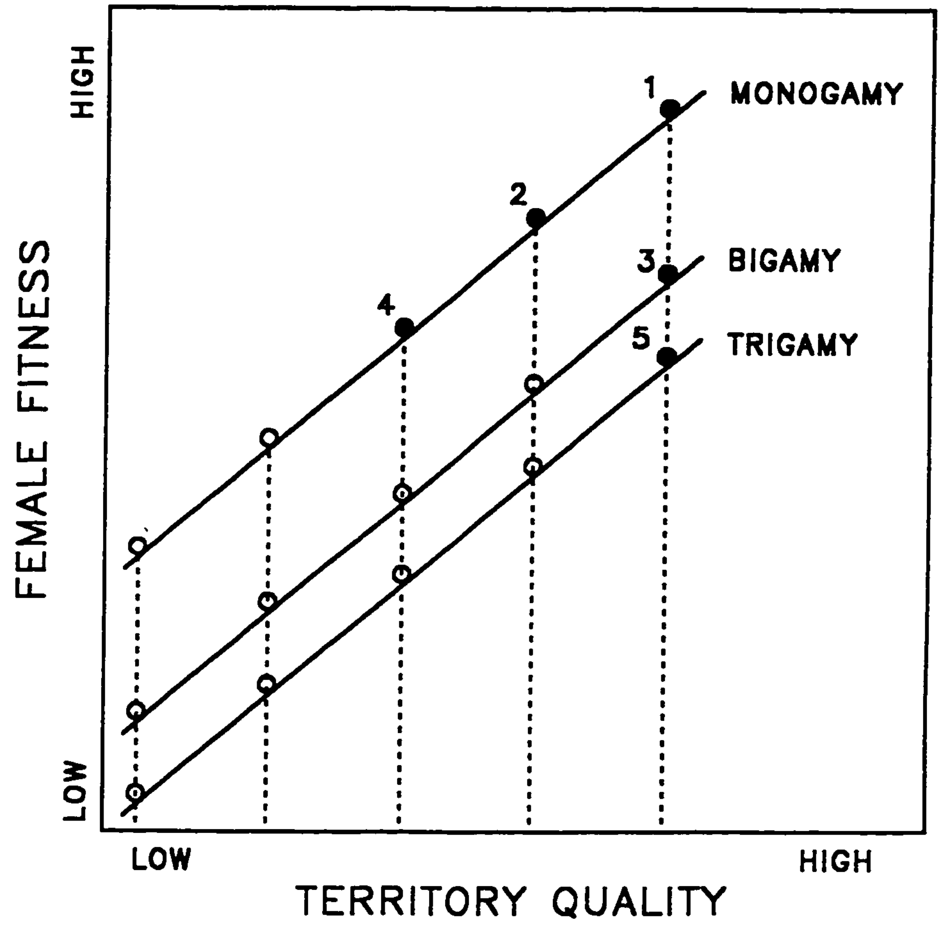


Figure 3.2: Settlement of females according to the sexy son hypothesis. Female fitness consists of two components: reproductive success, and the attractiveness of her mate. Male attractiveness is an arbitrary trait that varies independently of the variation in territory quality. The fitness contribution of male attractiveness is indicated by the vertical distance between the solid lines and the open/full circles. The fitness contribution of the reproductive success is indicated by the vertical distance below the solid lines. The fitness contribution of the attractiveness is small in comparison to the contribution of the reproductive success. Explanation of other symbols is in Fig. 3.1.

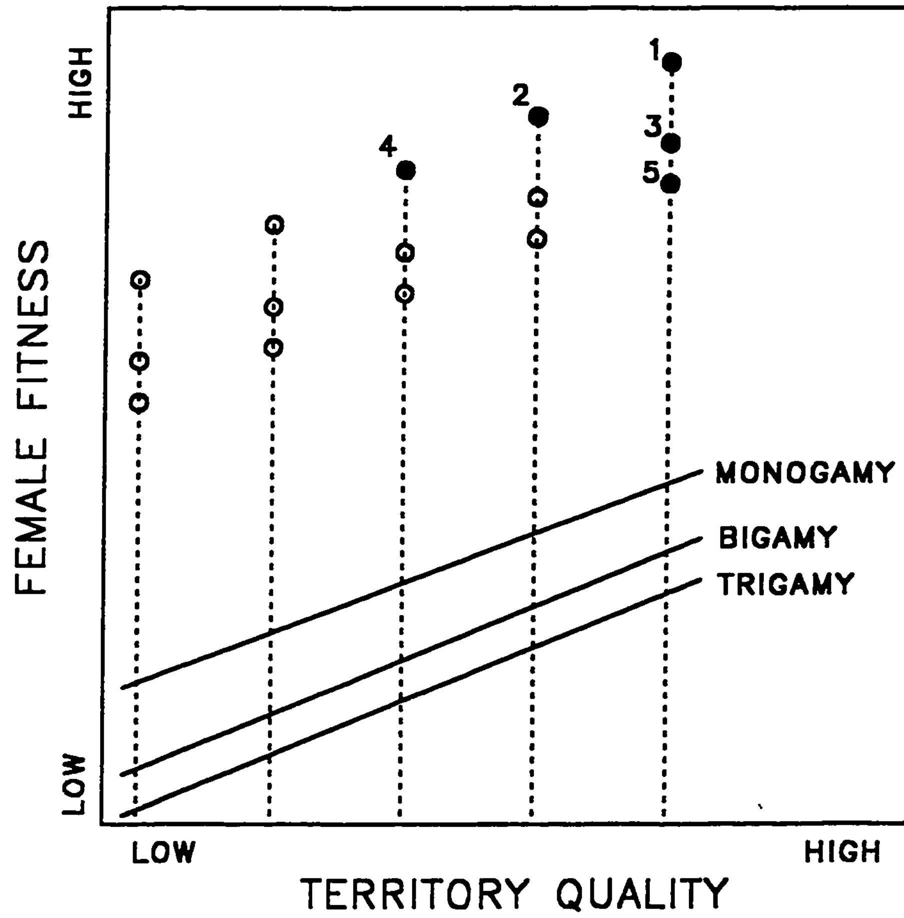


Figure 3.3: Settlement of females according to the sexy son hypothesis. Male attractiveness is an arbitrary trait that varies independently of the variation in territory quality. The fitness contribution of male attractiveness is large in comparison to the contribution of the reproductive success. Explanation of other symbols is in Fig. 3.2.

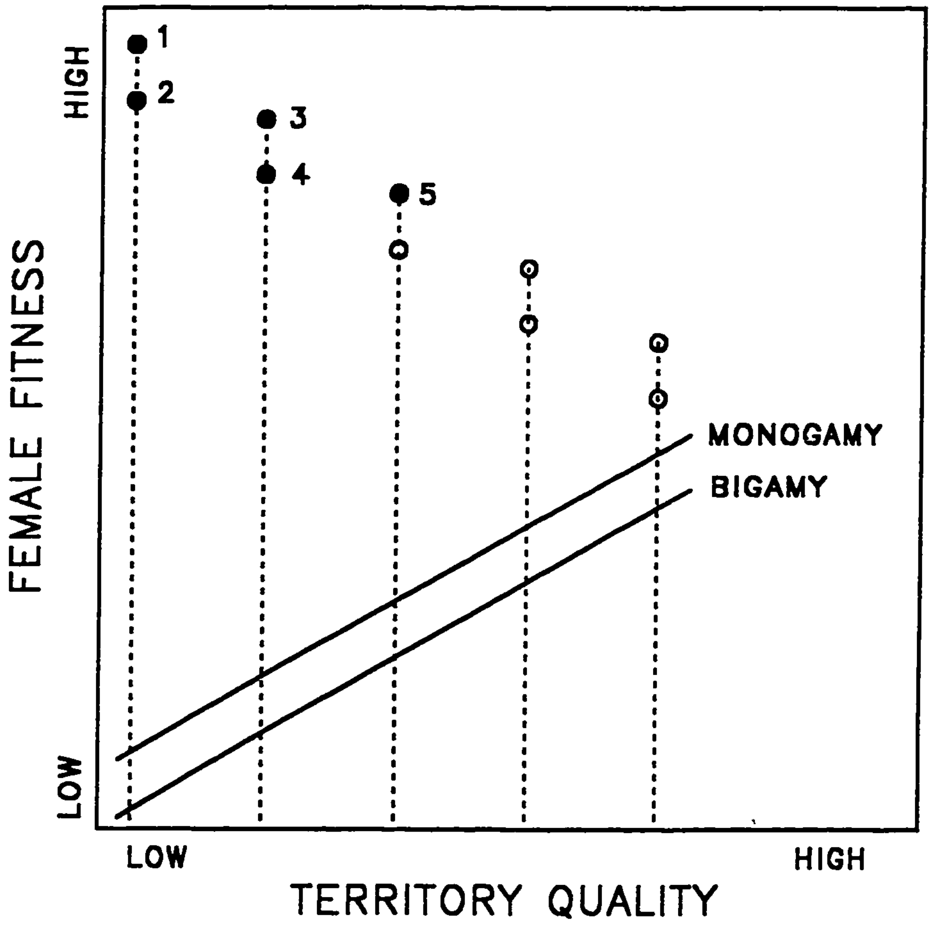


Figure 3.4: Settlement of females according to the sexy son hypothesis. Male attractiveness is an arbitrary trait that is negatively correlated with the variation in the territory quality. Explanation of other symbols as in Fig. 3.2.

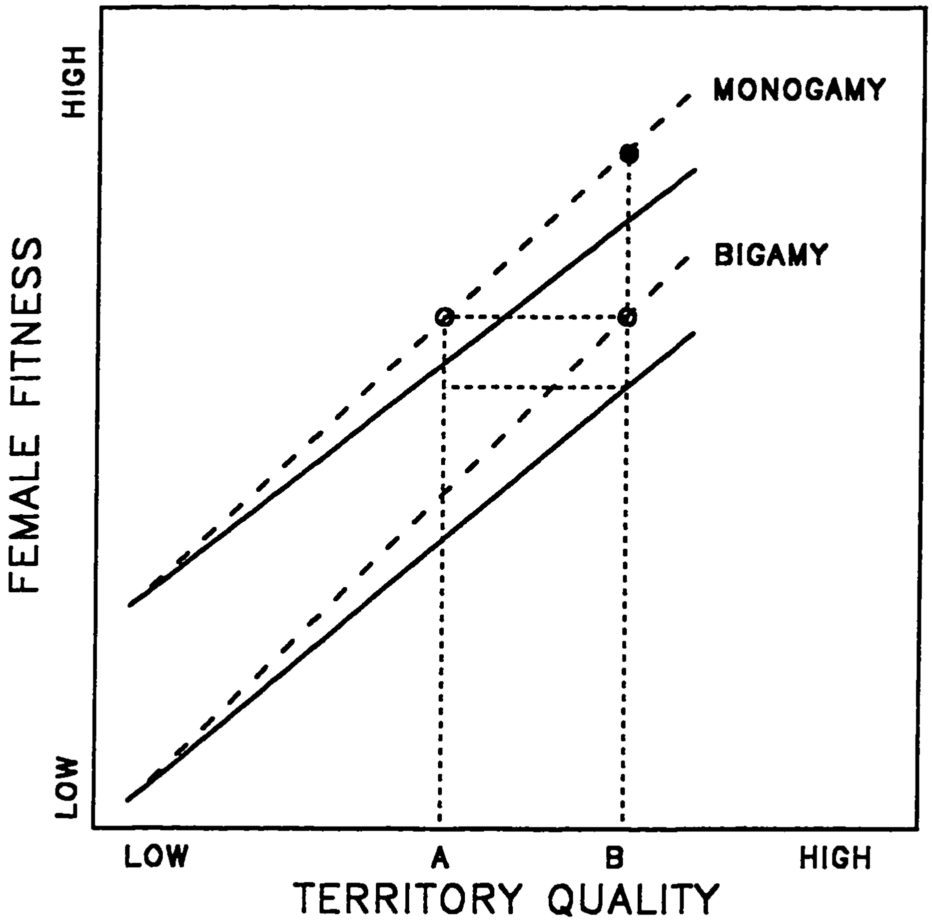


Figure 3.5: Settlement of females according to the sexy son hypothesis. Solid lines indicate how female reproductive success increases with territory quality, dashed lines how male attractiveness increases with territory quality. Male attractiveness is an arbitrary trait that is weakly positively correlated with the variation in territory quality. The fitness contribution of the reproductive success is indicated by the vertical distance below the solid lines. The fitness contribution of male attractiveness is indicated by the vertical distance between the dashed line and the solid line below. Open circles indicate options available to settling females, full circle indicates an already settled female.

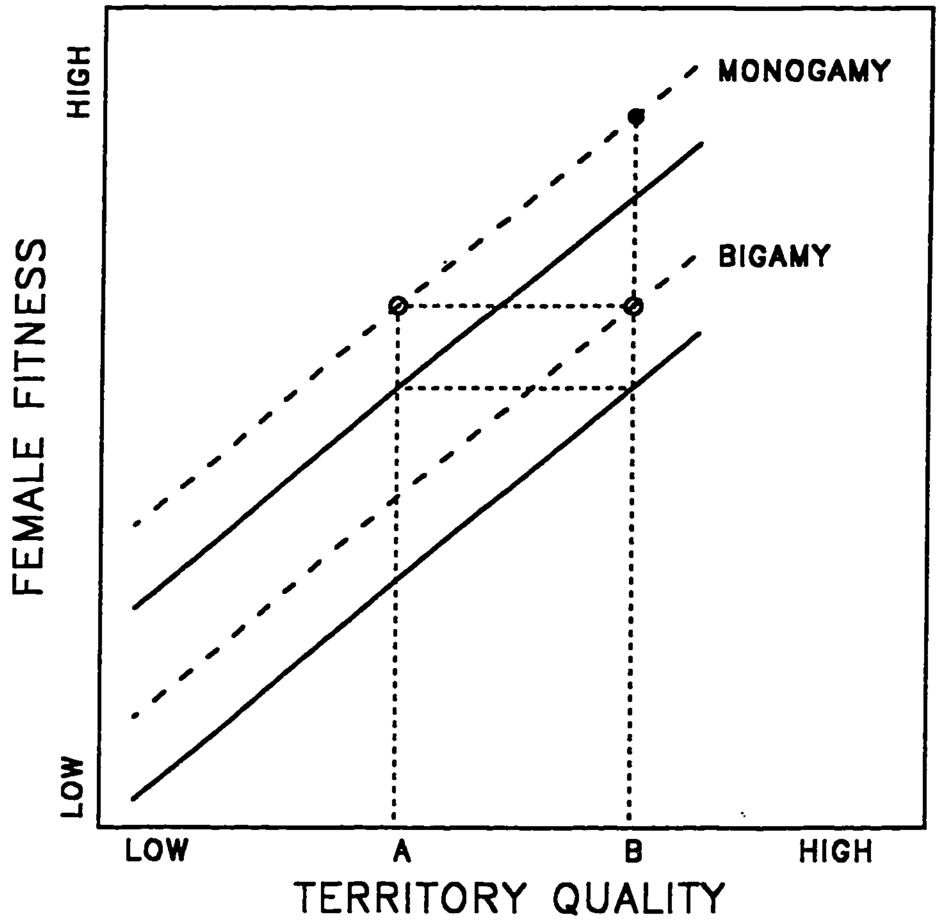


Figure 3.6: Settlement of females according to the sexy son hypothesis. Male attractiveness is an arbitrary trait that varies independently of the variation in territory quality. Explanation of other symbols as in Fig. 3.5.

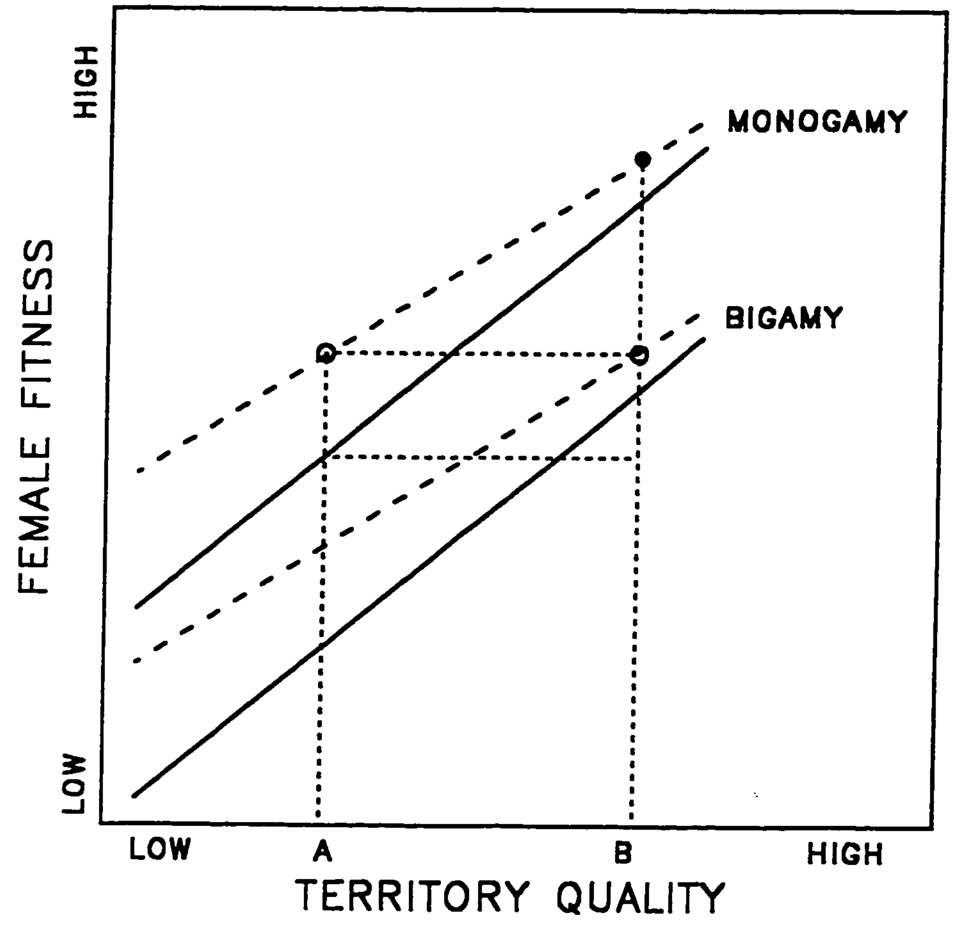
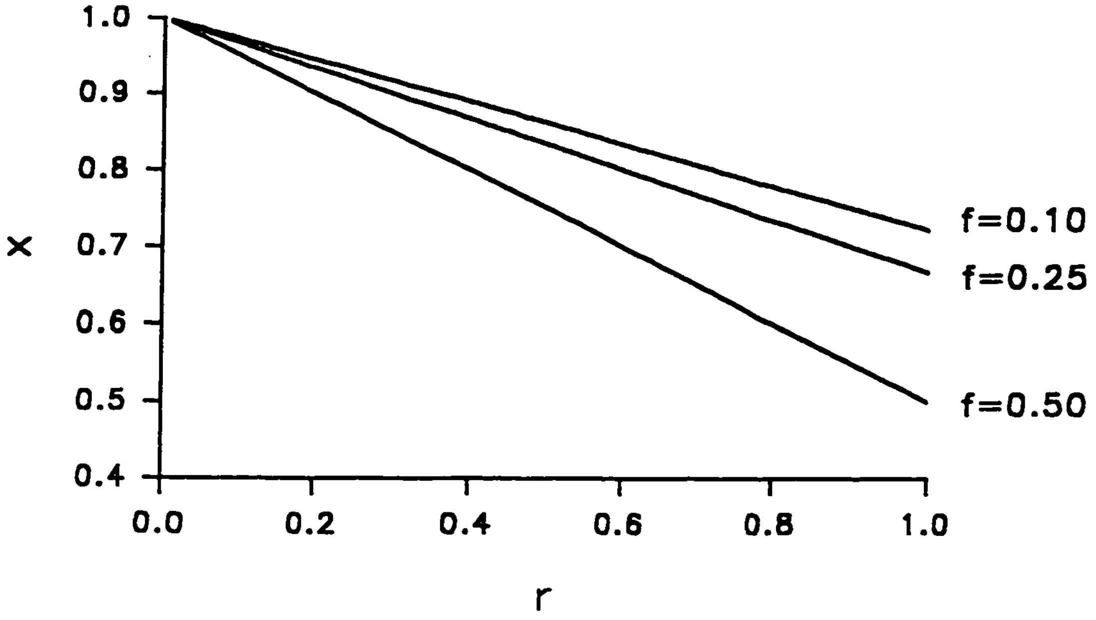


Figure 3.7: Settlement of females according to the sexy son hypothesis. Male attractiveness is an arbitrary trait that is weakly negatively correlated with the variation in territory quality. Explanation of other symbols as in Fig.3.5.



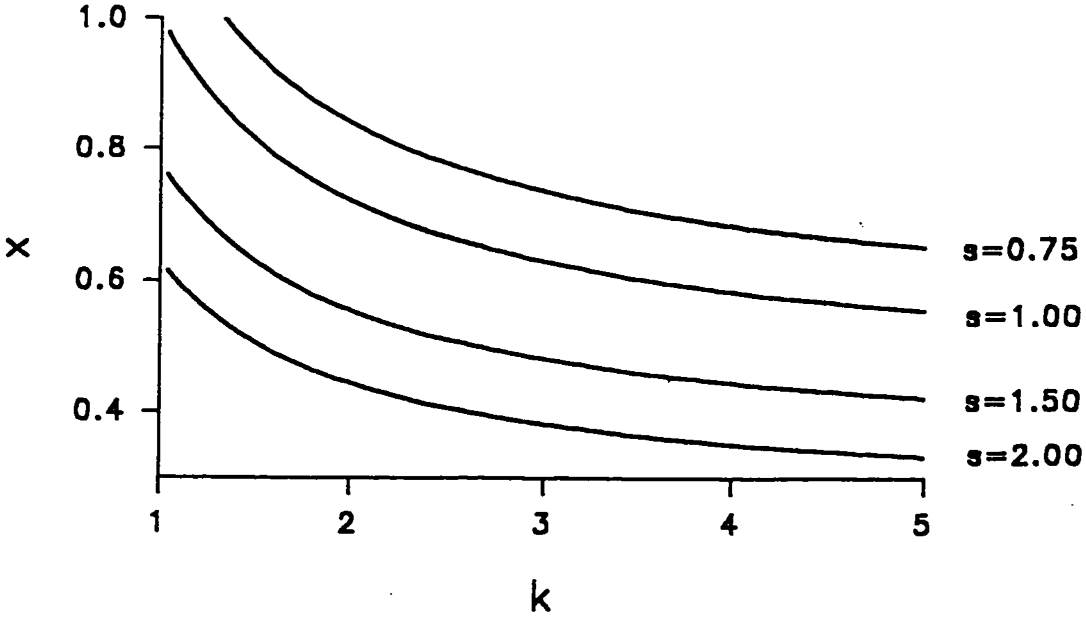


Figure 3.8: The effect of population parameters s,f and k on the size of parameter x. The parameter x is the minimum number of young that a polygynous female must fledge for every young fledged by a monogamous female. Top graph: The parameter x is plotted as a function of heritability (r) for three frequencies of polygynous males within the population (f). Values are computed using k=2.0 and s=1.0. Bottom graph: The parameter x is plotted as a function of harem size (k) for four adult sex ratios (s). Values are computed using f=0.1 and r=1.0.

CHAPTER 4: REVIEW OF HYPOTHESES THAT EXPLAIN POLYGYNY BY "RANDOM" FEMALE SETTLEMENT

INTRODUCTION

Hypotheses on the occurrence of polygyny can be divided into two broad groups. The first group includes explanations that suggest that females cannot settle monogamously because of factors beyond their control, such as by the lack of unmated males in the local population. The second group includes hypotheses that assume the presence of unmated males, but explain polygyny through other mechanisms. These hypotheses range widely in their complexity. Perhaps the most complex explanation is the sexy son hypothesis, which requires that females sample several breeding situations, evaluate each in terms of multiple variables (territory quality, male attractiveness, number of resident females) and then select one where they would achieve the highest fitness. The simplest explanation, on the other hand, is probably provided by one of the hypotheses that explain polygyny through random female settlement. Hypotheses in this category are the neutral-mate-choice hypothesis, true null model, no-cost no-benefit directed female choice model, Davies's hypothesis, and the random dispersion hypothesis (I will collectively call these the "random" hypotheses). A review of the random hypotheses, however, reveals that the hypotheses either cannot explain polygyny at all, or that they make redundant assumptions and predictions. In fact, the simplest possible hypothesis of all -- that females have no preference for monogamy or polygamy -- has not been proposed yet. Since this hypothesis explains polygamy by female indifference to the pairing status, I propose to call it the "status indifference" hypothesis.

I begin this chapter by describing the status indifference hypothesis in detail. Following that, I describe two assumptions and two predictions that "random" hypotheses frequently make, but that are not necessary for the status indifference hypothesis. Finally, I review the "random" hypotheses and contrast each with the status indifference hypothesis.

THE "STATUS INDIFFERENCE" HYPOTHESIS

The status indifference hypothesis assumes that females do not exhibit preference for being monogamous or polygamous. That is, females do not exhibit preference for the pairing status that they would achieve by settling with a particular male. The lack of a preference may arise because (1) females lack the cognitive ability to evaluate their expected pairing status, or (2) females possess the ability but do not exercise it. This may occur if there is no fitness advantage to preferring one pairing status over another.

If this assumption is fulfilled, then polygyny occurs because some females happen to settle with already mated males and thus become polygynous.

Because females do not exhibit preference for their mating status, the status indifference hypothesis predicts that experimental manipulation of a female's expected pairing status should not affect, in any systematic manner, the likelihood that the female settles monogamously or polygamously. For example, if a newly settling female is presented with two identical breeding situations (A and B) that differ only in the presence/absence of a single resident female, then an experimental transfer of the resident female between A and B should not affect the propensity of the new female to settle on A.

ASSUMPTIONS NOT MADE BY THE STATUS INDIFFERENT HYPOTHESIS

"Random" hypotheses frequently rest on two assumptions: (1) females do not choose territories and/or males by their quality (e.g., neutral-mate-choice hypothesis, true null model, several mechanisms of the random dispersion hypothesis, Davies's hypothesis); (2) female indifference to pairing status is adaptive, because female fitness does not change with harem size (e.g., neutral-mate-choice hypothesis, no-cost no-benefit directed choice hypothesis). In the following section, I will justify why neither assumption is necessary for the status indifference hypothesis.

1. Female preferences for territory/male attributes: Since a preference is trait-specific behavior, a female may choose one trait independently of another trait, or choose one trait and be indifferent to another trait. In the context of the status indifference hypothesis, this means that females, being indifferent to their pairing status, may or may not be indifferent to territory quality and male quality of potential breeding situations. In fact, it is quite possible that females actively choose breeding situations on the basis of these variables, but mate at random with respect to the number of resident females already present there. Such behavior would result in polygamy, because females would settle in the best breeding situations despite the fact that other females have already settled there.

By the same reasoning, female indifference to territory/male quality may not in itself lead to polygamy. If females exhibit preference for monogamous pairing status, then they would seek out unmated males regardless of their territory/male quality, and polygyny would never occur.

In conclusion, because females may become polygamous even if they do evaluate territory/male quality, and because female indifference for territory/male quality may not lead to polygamy, it is unnecessary to assume that females choose breeding situations on the basis of their quality.

2. Fitness consequences of behavior: Most "random" hypotheses assume that female preferences have been shaped by natural selection to optimality, i.e. females settle at random with respect to harem size because it is adaptive for them. The difficulty with this assumption is that it links a specific female behavior (i.e., lack of preference) with a specific evolutionary process (natural selection). Although it is reasonable to assume that the behavior of female birds has been shaped by natural selection and is adaptive, there may be cases when this is not true. Two examples especially pertinent to the red-winged blackbird are:

(i) Due to the rapid changes of the present-day environment, there may be an evolutionary lag between female preferences (shaped by past environments) and the current selective pressures. For example, it is believed that before the 18th century, red-winged blackbirds in eastern North America had inhabited mainly marshes (Nero 1984). However, with the widespread logging of forests during the past 200 years, vast areas of upland habitats have been opened and red-winged blackbirds have expanded their breeding range into them. The upland habitats have different composition of predator communities than marsh habitats (Picman et al. 1993, Picman and Schriml 1994) which may necessitate different spacing strategies on the part of breeding females (e.g., clumping = polygamy vs. spacing-out = monogamy).

(ii) If females in different populations have different preferences, then gene flow may cause immigrant females to exhibit preferences that are inappropriate in local conditions. In the red-winged blackbird, gene flow among populations is high (Ball et al. 1988) and females in different populations (Pensylvannia vs. Ontario) appear to exhibit different preferences (Searcy 1988, Chapter 5).

For these two reasons and possibly others, female behavior may not be optimal. Females may be indifferent with respect to their pairing status, but this indifference may not be an optimal strategy, because choosing females could achieve higher fitness than females settling at random. If the status indifference hypothesis were to assume that female behavior is optimal, then the hypothesis could be rejected on the basis of finding that monogamous females achieve higher fitness than polygamous females (or vice versa). Rejecting the hypothesis on the basis of such evidence would be, of course, wrong, because female indifference to their pairing status would still provide the correct explanation for polygamy.

The second shortcoming of this assumption is that it may not be possible to test it with empirical data. To evaluate whether females behave adaptively, one must compare the fitness of individuals exhibiting the behavior to the fitness of individuals exhibiting an alternative behavior. In the present case, the behavioral alternative to indifference is preference (either for monogamy or polygamy). However, the fitness consequences of preference are difficult to measure. One could compare fitness of females settling monogamously to that of females settling polygamously, but such comparison would be incomplete. This is because females need to have sensory and cognitive mechanisms to evaluate their pairing status and to make choices. The sensory and cognitive mechanisms entail costs of their own kind, which are difficult to measure. As a result, it is practically impossible to compare the fitness of choosing individuals (that incur the sensory and cognitive costs) to the fitness of indifferent individuals (that do not incur the costs) in the same species. Nevertheless, the sensory and cognitive costs lower female fitness Without measuring their contribution we cannot properly compare the fitness of choosing individuals to the fitness of indifferent individuals, and consequently conclude that one behavioral strategy is evolutionary better than the other.

These two reasons illustrate why linking female behavior to a specific evolutionary process may lead to erroneous conclusions.

PREDICTIONS NOT MADE BY THE STATUS INDIFFERENCE HYPOTHESIS

Several "random" hypotheses predict that: (1) the spatial dispersion of females (or their nests) follows a random pattern (e.g., Hartley and Shepherd 1995, Wootton et al. 1986); (2) the frequency distribution of harem sizes follows the Poisson distribution (e.g. Hartley and Shepherd 1995). In the following section, I will justify why neither outcome is predicted by the status indifference hypothesis.

The most frequently tested predictions of the "random" hypotheses describe: (1) the distribution of females (or their nests) in space, and (2) the frequency distribution of harem sizes in a population. The status indifference hypothesis does not make these prediction for reasons explained below:

1. Spatial distribution of females: If females exhibit no preference for male quality or habitat quality and if suitable nesting sites are abundant, then the spatial distribution of females (e.g., as measured by the distribution of female-female distances) may follow random distribution. However, if females do choose breeding situations by their habitat quality and/or male quality, then the spatial distribution is determined by the underlying distribution of the chosen attributes. For example, if the

spatial distribution of suitable nesting sites is clumped, then the spatial distribution of nesting females should also be clumped. Similarly, if the suitable nesting sites are overdispersed, then the nesting females should also be overdispersed. Because the status indifference hypothesis does not make any assumption about female preferences for territory/male quality, it cannot make any prediction about the spatial distribution of females.

2. Frequency distribution of harem sizes: If females exhibit no preference for male quality or habitat quality and if males are equal in their competitive ability, then the frequency distribution of harem sizes should follow the Poisson distribution. Consider now that females choose territories by their quality (or by male quality) and that suitable nesting sites are abundant. Because females settle independently of other females, all females would settle in the few best territories. The best territories would contain enormous harems, while other territories would fail to attract any females at all.

Consider now that males vary in their ability to compete for territory area. For example, if the frequency distribution of male competitive abilities follows the normal distribution, then most males have territories of average size, few males have very large territories and few males have very small territories. If females have no preferences for harem size, territory quality or male quality (e.g., as postulated by neutral-mate-choice hypothesis), then most females would settle on very large territories, the average number of females would settle on the average-sized territories and the fewest females would settle on the smallest territories. The frequency distribution of male competitive abilities would therefore determine the frequency distribution of harem sizes, which would be normally distributed.

As is evident from these examples, the frequency distribution of harem sizes may significantly deviate from the Poisson distribution. Because the status indifference hypothesis does not make any predictions about female preference for territory/male quality, or about male competitive abilities, no predictions about the frequency distribution of harem sizes can be formulated for the hypothesis.

COMPARISON OF THE STATUS INDIFFERENCE HYPOTHESIS TO OTHER HYPOTHESES THAT INVOKE RANDOM FEMALE SETTLEMENT

Nine distinct explanations have been proposed to explain female polygyny through random settlement. The explanations are listed below in their chronological order. I outline the salient points of each hypothesis and then comment on how it compares and contrasts with the status indifference hypothesis.

1. The "neutral-mate-choice" hypothesis was proposed by Lightbody and Weatherhead (1988). The hypothesis states that "females settle independently of each other and independently of variation in either male quality or territory quality. This occurs when females sharing territories neither compete nor cooperate and when differences among males and territories either do not affect reproductive success or are unpredictable when females settle. Female mate choice is random, but it is an optimal behavior." (Lightbody and Weatherhead 1988).

2. The "true-null-model" was also proposed by Lightbody and Weatherhead (1988). This hypothesis states that "females settle randomly even though interactions among females and variation in male quality or territory quality affect female reproductive success and can be predicted during settling. Female mate choice is random and not optimal (i.e., not maximizing fitness)."

Comment: Both the neutral-mate-choice hypothesis and the true null model require that females settle independently of territory quality and male quality. This is unnecessary, because polygamy may arise even if females exhibit preferences for these attributes.

3. The "random-dispersion" hypothesis was proposed by Wootton et al. (1986). The hypothesis states that "some or all females settle randomly in homogeneous situations, producing a low level of polygynous pairings." The authors proposed four mechanisms by which the random settlement is achieved:

A) "Females cannot or do not choose territories or mates."

Comment: This mechanism does not specify the nature of female preference for pairing status. Since females may settle at random with respect to territory/male quality and still prefer unmated males, this mechanism alone cannot explain polygyny.

B) Females settle according to the polygyny threshold model, but some individuals make error when evaluating the quality of territories. For example, if the real quality of a territory is 6 and females can evaluate it with precision of ± 1, then the perceived quality of the territory lies between 5 and 7 (Fig. 1.1). Quality of a territory determines female fitness. An imprecise estimate of the quality translates into an imprecise estimate of the fitness. If the real quality of a monogamous option is higher than the real quality of a bigamous option, then an erring female may underestimate the quality of the monogamous option and perceive it as worse than the bigamous option (Fig. 1.1). Alternatively, the erring female may overestimate the quality of the bigamous option and perceive it as better than the monogamous option. In either case, the female would achieve lower fitness by settling bigamously than by settling monogamously.

Comment: Despite the erring, females still prefer monogamy to polygamy. This can be illustrated by considering female settlement on two territories of identical quality. If one territory contains a monogamous breeding option and the other a bigamous breeding option, then females will always prefer the monogamous option to the bigamous option.

C) Females compare characteristics of visited territories to the characteristics of their natal territories and choose those territories where the characteristics are most similar. The characteristics may include habitat quality, male quality, pairing status (i.e., monogamous vs. polygynous) and specific territory location.

Comment: Since preferences are trait-specific, consider now that females evaluate territories only on the basis of pairing status. The revised hypothesis would state that females choose territories where their pairing status would be most similar to the pairing status of their mothers. Stated in this way, it is obvious that individual females do not settle at random, but exhibit distinct preferences for pairing status.

D) Females evaluate territories on the basis of their previous breeding experience. They avoid territories similar to those in which their previous nesting attempts failed, and favor territories similar to those in which their previous nesting attempts succeeded. The hypothesis does not specify how females choose territories for their first breeding attempt. As with mechanism C, territories are evaluated on the basis of habitat quality, male quality, pairing status (i.e. monogamous vs. polygamous) and specific territory location.

Comment: Consider that females choose territories on the basis of their pairing status. Because all successful females prefer territories where their pairing status would be identical to that on their previous territories, and because all unsuccessful females prefer territories where their pairing status would be different than that on the previous territories, the females do not mate at random with respect to pairing status but rather exhibit clear preferences.

Wootton et al. (1986) labelled mechanisms C) and D) the "experience-based-choice" hypothesis.

E) "Females choose a territory during the first breeding season by following either the polygyny threshold model or the "experience-based-choice" hypothesis. After making the territory choice once, they use this experience, exhibited by high fidelity to the site within the field, to choose territories in subsequent years."

Comment: Consider female preference for male pairing status. Young, first-time breeders would exhibit distinct preferences as described in mechanisms B,C and D. Old, returning females would settle at random with respect to their pairing status. Therefore, females have specific preferences for monogamy (or polygamy) early in their life, and these preferences change into indifference late in their life.

To conclude my comments on the random-dispersion hypothesis, one mechanism (A) may not explain polygyny at all, while the other mechanisms either assume a distinct preference for monogamy or polygamy (C and D), or explain polygyny through the combination of preference and indifference (B and E). Therefore all mechanisms involve some aspect of female choice.

4. Davies's hypothesis: Davies (1992) suggested that female dunnocks (*Prunella modularis*) follow the rule "choose suitable habitat and let the outcome of male-male competition determine the mating system'. In other words, females evaluate habitat quality, but they do not evaluate male quality or a male's pairing status. As a result,

two females may become defended by a single male and thus become polygamous. Davies makes no assumptions about the effect of such behavioral rules on female fitness. Although it is obvious from the text that Davies believes that female behavior has been shaped by natural selection, the main message of his study is that "it is unwise to assume that if something is advantageous then individuals are bound to do it."

Comment: This hypothesis is very similar to the status indifference hypothesis, because it invokes female indifference to pairing status and does not make any assumptions about female fitness. The assumption that females do not evaluate male quality is, however, redundant.

5. "No-cost no-benefit directed choice" model was proposed by Searcy and Yasukawa (1989). The model states that female fitness does not change with increasing harem size, but females choose mates according to the quality of the breeding situation.

Although this hypothesis has not been elaborated, the mechanism by which polygyny occurs is presumably as follows: because polygamy has no effect on female fitness, females have no preferences for monogamous vs. polygamous breeding situations and thus settle at random with respect of their pairing status.

This hypothesis is also very similar to the status indifference hypothesis, but it does not clearly stipulate how polygyny arises (i.e. whether females settle at random with respect to harem size or not). If the lack of choice is the proximate mechanism leading to polygyny, then the hypothesis makes an unnecessary assumption that there is no fitness cost or benefit to such a indifference.

CONCLUSIONS

In this chapter, I have proposed the status indifference hypothesis. According to this hypothesis, females are indifferent to their pairing status and as a result some females settle with already mated males and thereby become polygamous. I have described assumptions and predictions made by the status indifference hypothesis, as well as assumptions and predictions not made by the hypothesis. Finally, I compared the hypothesis to nine other explanations that invoke random female settlement and pointed out their differences. Because the status indifference hypothesis makes fewer assumptions and predictions than other explanations, it provides more parsimonious explanation for polygyny.

CONCLUSIONS FROM SECTION I

In Chapter 1, I identified 9 plausible hypotheses that may explain the occurrence of polygyny in the red-winged blackbird. In Chapter 2, I reviewed one of the hypotheses (the asynchronous settlement model) and proposed a new version of the model that avoids the contradictions contained in the original version. In Chapter 3, I demonstrated by examples that one assumption and four predictions of the sexy son hypothesis do not follow from the hypothesis. As those predictions provided the only practical way of differentiating between the sexy son hypothesis and the polygyny threshold model, there are now no feasible alternatives that can be used for the same purpose. In Chapter 4, I proposed the "status indifference" hypothesis. This hypothesis resembles other hypotheses that rely on "random" female settlement, but is more parsimonious because it makes fewer assumptions. The status-indifference hypothesis thus brings the total of plausible hypotheses to 10.

CLASSIFICATION OF HYPOTHESES

There are four key aspects of female behavior that can be used to separate polygyny hypotheses: 1) female preferences with respect to harem size; 2) female preferences with respect to breeding situation quality; 3) the effect of harem size on female reproductive success; and 4) the effect of nesting asynchrony between co-wives on their reproductive success. Female preference for monogamy and the effect of harem size on female reproductive success provide analogous and complementary results: both separate the competitive models from the cooperative model and also from the neutral models. When this basic differentiation is achieved, the neutral models can be tested by examining female preferences for breeding situation quality (i.e., territory quality). If such preference is found, then the most likely explanation is provided either by the Davies's hypothesis or by the no-cost no-benefit directed female choice model. When no preference is detected, then either the neutral-mate-choice model or the true null model are likely to provide an explanation. Within the competitive models, the effect of nesting asynchrony on female reproductive success can be used to separate the asynchronous settlement model from the defence of male parental investment model. As I pointed out earlier, there is currently no feasible way of discriminating between the polygyny threshold model and the sexy son hypothesis.

This basic hierarchical classification of the models can be tested with data on the direction of female preferences and with data on female reproductive success. An in-depth review of the evidence available for red-winged blackbirds has recently been provided by Searcy and Yasukawa (1995). The main conclusions of their review are: 1) there is no cost of polygamy to females, 2) females have no preferences for harem size, and 3) females choose breeding situations by their quality. This evidence, which was mostly collected in Pennsylvania, argues in favour of the no-cost no-benefit directed female choice model (Table 4.1). However, another conclusion reached by Searcy and Yasukawa's review is that there is geographical variation in factors that affect female reproductive success, for example in the amount of male provisioning of young. Therefore, conclusions about the direction of female preferences and about the fitness costs of those preferences obtained in one population may not be readily applicable to another, geographically distant population. As there is evidence that females in eastern Ontario behave differently than females in Pennsylvania (e.g., Hurly and Robertson (1985) found that females in eastern Ontario prefer bachelor males to mated males), there is a need to test the polygyny hypotheses using data from the local population.

I will test the key assumptions described in Table 4.1 in a series of four field experiments. In the first experiment, I will examine female preferences for unmated and mated males. Results of this experiment will be described in Chapter 5. In the second experiment, I will examine whether there is any fitness cost to polygamously nesting females (results in Chapter 6). In the third experiment, I will examine the effect of nesting asynchrony on the reproductive success of bigamous females (Chapter 7) and finally in the fourth test I will examine whether females choose breeding situations by their habitat characteristics (Chapter 8). The results of these four experiments will enable me to discriminate among the alternative hypotheses and thereby establish which hypothesis, or a set of hypotheses, provides the most plausible explanation for polygyny in my study population of red-winged blackbirds.

Table 4.1: Key assumptions of the plausible hypotheses. The defence of male parental investment model (DMPIM) is presented here as a distinct hypothesis. The assumptions are stated for breeding situations (BSs) of identical quality. Bigamous females are fully synchronous, RS - reproductive success, MONO - monogamy, BI - bigamy. A dash indicates that no specific relationship is assumed.

HYPOTHESIS	ASSUMPTION			
	Do females choose BSs by their quality?	What mating status do females prefer?	RS of bigamous vs. monogamous females	Effect of increasing asynchrony on RS of secondary females
Status indifference	-	none	-	-
No-cost no-benefit directed female choice	yes	none	equal	none
Davies's	yes	none	-	-
Neutral-mate-choice	no	none	equal	none
True null	no	none	different	-
Cooperative female choice	yes	bigamy	bi>mono	negative
Random dispersion, mechanism B	yes	monogamy	mono>bi	-
Polygyny threshold	yes	monogamy	mono>bi	-
DMPIM	yes	monogamy	mono>bi	negative
Sexy son	yes	monogamy	mono>bi	-
Asynchronous settl.	no	monogamy	mono>bi	positive

SECTION II: FIELD TESTS OF PLAUSIBLE HYPOTHESES

GENERAL INTRODUCTION

In the second section of this study, I describe the results of four field experiments designed to test the key assumptions of the polygyny hypotheses. In Chapter 1, I describe an experiment in which I examined female preferences for unmated vs. mated males. The results of this experiments enable me to establish whether females prefer monogamous or polygamous mating status. In Chapter 2, I describe an experiment in which I compare the reproductive success of monogamously and polygamously nesting females. The results obtained in this experiment provide evidence about the effect of polygamy on female fitness. In chapter 3, I describe the results of en experiment that investigated whether staggering of nesting attempts affects the reproductive success of polygamous females. The findings of this experiment further illuminate the impact of polygamy on female reproductive success and also establish whether females can reduce the impact through asynchronous nesting. In Chapter 4, I describe a field study that investigated female preferences for habitat characteristics. The study will establish whether females evaluate habitat characteristics when choosing breeding situations.

The nature of female preferences, and the effect of polygamy on female reproductive success will enable me to test the principal assumptions of the polygyny hypotheses, and thus allow me to discriminate among the alternative explanations.

GENERAL METHODS

I conducted the studies in marshes near Ottawa, Ontario, Canada (45°23′ N, 75°32′ W, altitude 70 m) in the spring of 1993 and 1994. The marshes were similar in their topography: each was covered by a uniform stand of cattail (*Typha* spp.) that extended from dry land to centrally located channels of open water. The channels were 60-110 cm deep (from water surface to hard clay bottom). Each marsh was surrounded in part by willow (*Salix* sp.) shrubland and deciduous thicket, and in part by upland habitats such as fallow fields and hayfields. All four experiments were conducted in different marshes or in different sections of the same marsh.

Dominant predators on redwing nests were raccoons (*Procyon lotor*), long-tailed weasels (*Mustela frenata*) and American crows (*Corvus brachyrhynchos*) (S.Pribil unpublished data, Picman et al. 1993). There were no marsh wrens (*Cistothorus palustris*) present at the study sites described in Chapters 5,6 and 7.

I mapped male territories by observing boundary disputes between males and by recording the perches of displaying owners. I transcribed the locations of the disputes and the location of the perches onto a map, connected the outermost points using the minimum convex polygon method and calculated the size of each territory to the nearest 10 m^2.

I measured the water depth in late July of 1993 and in early July of 1994 throughout the study sites at corners of a 10 x 10 m grid. I calculated the water depth of a territory as the mean of all measurements taken within the territory.

I carried out statistical analyses using SAS statistical software (SAS Institute, Inc. 1985a,b) and standard statistical textbooks (Steel and Torrie 1980, Sokal and Rohlf 1981, Zar 1984). I calculated minimum detectable differences for $\alpha = 0.05$ and

$\beta = 0.05$ using SigmaStat statistical software (Jandel 1993). All statistical tests were two-tailed unless stated otherwise. Where Julian dates were used, 1 January was day 1.

CHAPTER 5: DO FEMALES PREFER MONOGAMY OR POLYGAMY?

INTRODUCTION

With few exceptions, the explanations for polygyny assume that unmated males are available to females when those females settle polygamously. This being the case, there are four proximate mechanisms that can lead to polygynous settlement: 1) females prefer polygamy to monogamy; 2) females have no preferences for their mating status, and as a result some females settle with males that are already mated; 3) female prefer monogamy to polygamy, but if mated males defend unusually good territories, this preference for unmated males may be surpassed by an even stronger preference for high quality territories/males; and 4) females prefer monogamy to polygamy, but sometimes make errors and settle polygamously despite their "intention" to do otherwise.

Of the 10 explanations that are plausible for red-winged blackbirds (Table 4.1), the first category of proximate mechanisms is represented by the cooperative female choice model, the second category by 5 "random" models (status indifference hypothesis, no-cost no-benefit directed choice hypothesis, Davies's hypothesis, neutral-mate-choice hypothesis and the true null model), the third category by 3 competitive models (polygyny threshold model, sexy son hypothesis, asynchronous settlement model) and finally the fourth category is represented by the random dispersion hypothesis (mechanism B).

Previously, female preferences for unmated and mated males have been examined by Hurly and Robertson (1985) and by Searcy (1988). In both studies, harem size was experimentally manipulated and female preferences deduced from the subsequent pattern of females settlement on small-harem and large-harem territories. Because harem size was randomized with respect to the variation in territory quality and male quality, it is unlikely that the pattern of settlement was influenced by any systematic differences in the quality of small-harem and large-harem territories. Hurly and Robertson (1985), who conducted their study in eastern Ontario, found that significantly more females settled in small harems than in large harems. Searcy (1988), who conducted two experiments in Pennsylvania, found that numbers of females settling in the small-harem and large-harem territories were similar. As experimental designs of all three studies were similar, the differences in results seem to indicate a geographical variation in female preferences. Because these studies found opposing results, a third study is required. I performed such a study with an improved experimental design which allowed me to control more effectively for the confounding effects of territory quality and male quality on female preferences. I performed the experiment twice during the breeding season, which enabled me to compare preferences of females settling early and late in the season.

METHODS

General methods

This study was conducted in April and May of 1993 and 1994. In 1993, the study sites were searched for nests twice a week throughout the breeding season. Harem size was scored as the maximum number of females simultaneously nesting on a territory. To avoid the potentially confounding effects of trapping and banding on the behavior of the males (Ratcliffe and Boag 1987, Metz and Weatherhead 1991) and on the choice of the females (Beletsky and Orians 1989, Burley 1981, 1986a,b, Swaddle and Cuthill 1994), no males at the study sites were banded.

Choice experiments

Two choice experiments were conducted in 1994. The first between 22 April (first removal of females) and 5 May (last removal of females), the second between 18 May (first removal) and 22 June (last removal). Their general design was to give a newly settling female a choice between two contiguous territories, one defended by an unmated male (henceforth a bachelor territory) and the other defended by a monogamously mated male (henceforth a monogamous territory). Together, those two territories constituted a choice situation (CS). In a CS, the female could settle either with the unmated male, in which case she would become monogamous, or she could settle with the monogamous male, in which case she would become bigamous. I limited the degree of female polygamy to bigamy for two reasons. First, the bigyny was the most common form of polygamy in our unmanipulated population. Second, the "cooperative female choice" hypothesis assumes that females prefer polygamy to monogamy (Altmann et al. 1977). However, the shape of the relationship between female preference and harem size is not known. It is reasonable to assume that the benefits of polygyny increase with the harem size up to a certain "optimum harem size", beyond which they decline (Altmann et al. 1977, Picman 1988). If that is the case, then females settling in harems larger than the "optimum harem size" should prefer a lower degree of polygamy to a higher degree. Although the "optimum harem size" is not known, it cannot be lower than bigamy. For this reason, I chose bigamy to represent the polygamous situation.

To create a CS, I selected two adjacent territories that 1) were of similar water depth, and 2) were both polygamous during the 1993 breeding season. Because females in the study population select territories by their water depth (Chapter 8), the first requirement was aimed at reducing inter-territory variation in the water depth. Notwithstanding a year-to-year variation in the territory quality and male quality, the second requirement was aimed at ensuring that each territory was sufficiently good to attract at least two females. As soon as both territories in a CS were settled by at least one female, one territory was randomly selected to become the bachelor territory while the other territory became the monogamous territory. All females from the bachelor territory were captured by decoy trapping (Picman 1979) and removed. All but one randomly selected female (hereafter a "resident" female) from the monogamous territory were also captured and removed. All removals in a CS were completed in one day. After the removals, each CS was monitored on a daily basis. When a new female (hereafter a "new" female) appeared, I noted her behavior and plumage (some individuals could be identified by the color of their chins or epaulets). A new female was considered settled on a territory if she was observed for three consecutive days (Muma and Weatherhead 1989). The new female and the resident female were then captured by decoy trapping and their epaulet colors, epaulet lengths, chin colors, wing lengths and aggressive behaviors were measured. These traits are related to the age and aggression of females, and it was desirable to compare resident and new females in that respect. Epaulet color was given the score of 1 (bright orange), 2 (reddish orange), 3 (reddish brown), 4 (dark orange yellow) or 5 (pale yellow). Epaulet length was measured to the nearest 1 mm as the maximum length of the epaulet on a stretched right wing. Chin color was given the score of 1 (intense orange or yellow), 2 (moderate orange) or 3 (pale orange). Wing length was measured to the nearest 1 mm on a flattened right wing from the bend of the wing to the tip of the longest primary. Aggressive behavior was scored during the decoy trapping. When the subject female was present on a territory, I placed a decoy trap (described in Picman 1979) baited with a live female in the centre of the subject's sub-territory and timed her approach within 0.5 m of the trap. The subject's behavior was scored as 1 (no approach for 20 min), 2 (approach in 10-20 min), 3 (approach in 1-10 min) or 4 (approach in less than 1 min).

Comparison of early and late season

To facilitate the comparison of female settlement in early and late season, eight randomly selected CSs used in the first experiment were also used in the second experiment. Territories in those CSs retained their bachelor and monogamous labels.

Data analysis

Nesting stage of a female was calculated as the number of days since the laying of the first egg (day = 1). Only the first female to settle in each CS was included in data analyses.

RESULTS

Female settlement in early season

The first experiment was carried out early in the breeding season, when females were dispersing from spring roosts and were settling on male territories to initiate nesting. We established 16 CSs, each containing one bachelor and one monogamous territory.

The bachelor and monogamous territories did not differ in their size, water depth and 1993 harem size (Table 1).

Before the first experiment was initiated, 18 females were present on the "bachelor-designate" territories (14x1 and 2x2 females) and 18 females on the "monogamous-designate" territories (14x1 and 2x2 females). I removed all 18 females from the bachelor-designate territories and 2 females from the monogamous-designate territories to attain the final arrangement of one female per monogamous territory and no females on the bachelor territories.

Between 23 April and 8 May, all CSs were settled by new females. In all 16 (100%) CSs, the first new female settled on the bachelor territory, whereas in no CS did the first new female settle on the monogamous territory. This difference is highly statistically significant (Binomial test, $P=0.000031$) and suggests a strong female preference for the bachelor territories. The new females had little opportunity to assess the breeding status of the resident females (on the monogamous territories) because the resident females did not start building their nests until 11 May, three days after the last new female settled.

The new females settled on average 2.6 ± 1.3 (± 1 SD) days after their respective CSs were established (Figure 5.1). The new females and the resident females did not differ in the color of their epaulets, length of their epaulets, color of their chins, length of their wings and their aggressive behaviors (Table 5.2).

Female settlement in late season.

The second experiment was carried out late in the breeding season. At the beginning of the experiment on 18 May, most females nesting in marshes adjacent to our study sites were completing their nest building. At the end of the experiment on 29 June, successful first broods were already fledged and a number of females were engaged in rearing replacement broods. Between 18 May and 22 June, I established 10 CSs, each consisting of one bachelor and one monogamous territory. Eight CSs were established by removing females from the CSs utilized during the first experiment, and two CSs were established by removing females from new territories. The bachelor and monogamous territories did not differ in their size, water depth and 1993 harem size (Table 5.1).

Before the second experiment, 13 females were present on the bachelor-designate territories (7x1 and 3x2 females) and 15 females on the monogamous-designate territories (6x1, 3x2 and 1x3 females). I removed all 13 females from the bachelor-designate territories and 5 females from the monogamous-designate territories to attain the final arrangement of one female per monogamous territory and no females on the bachelor territories.

Between 23 May and 29 June, six CSs were settled by new females. In four (67%) CSs, the first new female settled on the bachelor territory. In two (33%) CSs, the first new female settled on the monogamous territory. The number of females settling on the bachelor and monogamous territories is not statistically different (Binomial test, $P=0.68$). Of the two CSs where the new females settled on the monogamous territories, one CS was retained from the first experiment, while the other CS was newly established for the second experiment.

The new females settled on average 9.8 ± 5.0 (± 1 SD) days after their respective CSs were established (Figure 5.1), settling on the bachelor territories earlier in the season (23 and 27 May, 5 and 7 June) than on the monogamous territories (16 and 29 June). This difference is statistically significant (Julian dates compared by a two-sample t test, df=4, t=3.46, P=0.026).

To examine whether the settlement of the new females was related to the tenure of the resident females, I compared the nesting stages of the resident females in the CSs where the new females settled on monogamous territories to the nesting stages of the resident females in the CSs where the new females settled on bachelor territories. The nesting stages of the former were 14 and 16 days (since the laying of the first egg), whereas the nesting stages of the latter were 6, 7, 12 and 13 days. The nesting stages were not significantly different (one-tailed two-sample t test, df=4, 10t=2.03, P=0.055).

The new females and the resident females did not differ in the color of their chins, color of their epaulets, size of their epaulets or length of their wings (Table 5.2). I did not compare their aggressive behaviors because the resident females were already captured during the first experiment and their experience presumably biased their behavior.

Comparison of early and late season

A significantly higher proportion of new females settled on the monogamous territories late in the season than early in the season (G-test with Yates's correction for continuity, df=1, G=5.77, P=0.016). The time to settle in the CSs was shorter in the early season than in the late season (Mann-Whitney U-test, U=95.5, $n_1=6$, $n_2=16$, P<0.001; Figure 5.1). The new females that settled early and late in the season did not differ in the color of their epaulets (two-sample t test, df=20, t=-0.53, P=0.60), length of their epaulets (df=20, t=-0.50, P=0.63), color of their chins (df=20, t=1.73, P=0.11), length of their wings (df=20, t=-0.05, P=0.96) and their aggressive behaviors (df=20, t=1.08, P=0.29) (Table 5.2). Similarly, the resident females present early and late in the season did not differ in the color of their epaulets (df=20, t=-1.99, P=0.06), length of their epaulets (df=20, t=-0.19, P=0.85), color of their chins (df=20, t=0, P=1) or length of their wings (df=20, t=-0.23, P=0.82) (Table 5.2).

DISCUSSION

Female settlement in early season

I found that significantly more females settled on the territories of bachelor males than on the territories of mated males. Because the "bachelor" or "mated" status was assigned at random, quality of "bachelor" males was on average the same as quality of the "monogamous" males, and "bachelor" territories were on average as good as "monogamous" territories. The only difference between the "bachelor" and "monogamous" breeding situations was the presence or absence of a resident female. The fact that the new females settled more frequently on the bachelor territories than on the monogamous territories indicates that the females preferred a monogamous mating status to a polygamous one.

Since I assigned male mating status at random, some "monogamous" males were certainly of poor quality or defended poor territories. Despite this, new females settled with such males, which indicates that male mating status was more important in female choice than the variation in male quality or territory quality, possibly because 1) there was little variation in territory/male quality; or 2) the cost of polygyny was high. In either case, the polygyny threshold was not exceeded. The low variation in territory quality is not surprising, because I purposefully paired territories that were as similar as possible in terms of water depth (females chose territories on the basis of their water depth, Chapter 8) and harem size during the previous year (harem size was considered a measure of quality). The unanimous preference for unmated males also indicates that females are quite capable of determining male mating status. Again, this is not surprising: a female present on a territory can be quickly detected by a human observer, and there is no reason to believe that other females cannot perform this as well. In addition, resident females aggressively defend their nesting areas against intruders. Therefore, even if a prospecting female failed to detect the resident female, chances are that the resident female would detect the prospecting female and attempt to evict her.

Female settlement in late season.

I found that more females settled on the bachelor territories than on the monogamous territories. However, the difference was not statistically significant, either because the sample size was too small to detect such a difference, or because the females actually settled at random. Larger sample size would be required to distinguish between these two alternatives.

The settlement of the new females appeared related to the nesting stage of the resident females. The new females tended to avoid those territories where they would nest synchronously with the resident females yet settled on those territories where they would nest asynchronously. Their behavior is consistent with the asynchronous settlement model. According to the polygyny threshold model and the sexy son hypothesis, females choose breeding situations by their quality. If the quality is determined by the tenure of the resident females, then the females settle in relation to the degree of synchrony. Therefore, my result is also consistent with the polygyny threshold model and the sexy son hypothesis, and cannot be used to differentiate these two hypotheses from the asynchronous settlement model.

Comparison of early and late season

A significantly higher proportion of females settled polygamously late in the season than early in the season. In addition, during the late season, females that settled polygamously did so at significantly later dates than females that settled monogamously. These results suggest that there is a seasonal shift in female settling pattern: early in the season, females settle monogamously, while late in the season, females settle either at random or polygamously. I propose four hypotheses to explain this shift:

First, female preference for male mating status changes during the breeding season. Early, females prefer monogamy to polygamy. Late, they settle at random or actually prefer polygamy to monogamy. Female preference changes because the net cost (total costs minus total benefits) of polygamy declines during the breeding season. The net cost may decline for one or all of the following reasons: a) within a harem, the competition for limited resources declines because females become more asynchronous as a result of nesting failures; b) aggression of resident females declines, so that new settlers find it easier to overcome the aggression and join a harem; c) as density of nesting females declines, clumping of nests (achieved e.g. through polygamy) becomes necessary to maintain the benefits of mutual nest defence against predators (Picman et al. 1988, Westneat 1992).

Second, there are two categories of females: a) old females that settle early in the season; and b) young females that settle late in the season (this pattern was reported by Crawford 1977). Old females are experienced and prefer monogamy to polygamy. Young females are inexperienced and make errors in evaluating territory/male quality. As a result of these errors, young females settle polygamously in situations where old females would settle monogamously. Consequently, more females settle polygamously late in the season than early in the season. However, I found that early and late settling females had epaulets of similar color. Since the color is indicative of age (Payne 1969, Crawford 1977), it is unlikely that this hypothesis can explain the observed pattern.

Third, the quality of territories becomes more variable later in the breeding season. As territories become more variable, a greater number of territories exceed the polygyny threshold, and consequently more females settle polygamously. The variability may increase, for example, if the quality is determined by the abundance of emergent aquatic insects. In our study area, the first females settle on territories that are still covered with ice and snow, and hence are very similar in their insect abundance. When the last females settle, the patchy distribution of emerging insects greatly increases the quality of some territories but not of others, and thereby magnify their differences.

Fourth, by chance alone, territories selected for my second experiment were more variable in quality than territories selected for the first experiment. Consequently, more territories exceeded the polygyny threshold (and more females settled polygamously) late in the season than early in the season. This hypothesis, however, cannot explain why one female settled polygamously during the second experiment when another female settled in the same CS monogamously during the first experiment.

As seasonal changes in the female settlement pattern have important consequences for the polygyny models, these hypotheses should be tested in future studies.

Comparison to other studies

Hurly and Robertson (1985) in eastern Ontario, and Searcy (1988) in Pennsylvania examined the effect of female-female aggression on the recruitment of new females into harems. In both studies, resident females were removed from randomly selected treatment territories, while females on control territories were allowed to remain. Subsequent to the removals, Searcy found that new females settled as frequently in treatment (small-harem) as in control (large-harem) territories, while Hurly and Robertson (1985) found that significantly more females settled in the small-harem than in the large-harem territories.

I improved the experimental designs of those studies by controlling more closely for the confounding effects of territory quality and male quality. My paired-territories design offered settling females a choice of territories that were adjacent and by the virtue of proximity similar in their quality. In addition, I paired territories by their water depth and by their harem size during the previous season (harem size was used as a proxy of attractiveness to females). Because females of territorial species are restricted in their mate sampling (Slagsvold et al. 1988, Dale et al. 1990, Slagsvold and Dale 1991, Bensch and Hasselquist 1992, Dale et al. 1992, Slagsvold and Dale 1994), my paired-design maximized the probability that both territories were visited by a sampling female. Because this experimental design better controlled for the variation in territory quality and male quality, it offers a more effective way for studying female preferences.

The different results of Searcy (1988) and Hurly and Robertson (1985) can be explained by geographic variation in female preferences for small vs. large harems. The geographic variation may reflect the relative costs and benefits of polygyny as determined by local environmental conditions. For example, if key predators vary geographically, then overdispersion (i.e. monogamy) may be the best strategy to avoid predators in some areas, whereas clumping (i.e. polygamy) may be the best strategy in other areas. Our results are consistent with this explanation, because 1) my study area is in the same geographic region as that of Hurly and Robertson (1985); and 2) I obtained similar results on female preferences.

Male red-winged blackbirds in Pennsylvania react to the removal of mates by increasing their singing frequency (Searcy 1988). If males in my population behave in the same way, and if females are attracted to frequently singing males, then this may explain why widowed (unmated) males in this study attracted more females than mated males did. However, Shutler and Weatherhead (1991) found that females do not prefer males with higher song rates. Therefore, I believe that females in my study area were selecting males on the basis of their mating status.

Wittenberger and Tilson (1980) suggested that the aggression of resident females prevents new females from joining harems. Female-female aggression in the red-winged blackbird has been well documented (Nero 1956, LaPrade and Graves 1982, Yasukawa and Searcy 1982, Hurly and Robertson 1984, Langston et al. 1990), but it remains to be resolved whether new females are physically prevented from joining a harem (despite their desire and attempts to do so), or whether they choose not to join a harem because the fitness costs (risk of injury, time and effort spent) of overcoming the aggression were too high. I cannot, of course, know how the new females in the study would have settled had I not given them a choice of unmated males, but I have two reasons to believe that they would settle polygamously: 1) at the same time, females settling in other portions of the marsh were settling polygamously; 2) resident females and new females did not differ in their aggression, body size (as measured by wing length) and three plumage characteristics related to age (Table 5.2). Based on this evidence, I believe that the new females were physically capable of overcoming the aggression, but that they chose not to do so. Future studies should quantify the fitness costs of the aggression, because the aggression may constitute an important component of the cost of polygyny (Smith et al. 1993, Slagsvold and Lifjeld 1994).

I conclude that female red-winged blackbirds in the this study population prefer monogamy to bigamy. This preference is consistent with the assumptions of four hypotheses: the polygyny threshold model (and its extension, the defence of male parental investment model), the sexy son hypothesis, the asynchronous settlement model and the mechanisms B of the random dispersion hypothesis (Table 4.1). However, the fact that all females in early season chose unmated males demonstrates that the females did not make errors when evaluating quality of the breeding situations (as postulated by the mechanisms B) and hence that the random dispersion hypothesis is unlikely to explain the pattern of female settlement. Female preference for monogamy contradicts the assumptions of the cooperative female choice hypothesis, and the assumptions of the "random" models: the status indifference hypothesis, the no-cost no-benefit directed female choice hypothesis, Davies's hypothesis, the neutral-mate-choice hypothesis and the true null model. Therefore, these hypotheses are unlikely to explain the occurrence of polygyny in the study population of red-winged blackbirds.

Table 5.1: A comparison of bachelor and monogamous territories with respect to their size [m^2], water depth [cm] and 1993 harem size [females/male]. Values shown are means ± 1 SD. Probability (P) refers to results of paired-sample t-test on mean difference. The mean difference is the mean of differences between a bachelor and a monogamous territory within a choice situation (difference = bachelor - monogamous). Sample sizes: 16 bachelor and 16 monogamous territories in early season, 10 bachelor and 10 monogamous territories in late season.

	Bachelor territories	Monogamous territories	Mean difference	P
EARLY SEASON				
Territory size	1080±409	1038±524	43±145	0.78
Water depth	69±26	70±24	-1±4	0.85
Harem size	2.1±0.3	2.3±0.5	-0.2±0.1	0.19
LATE SEASON				
Territory size	777±353	900±460	-123±122	0.34
Water depth	72±19	66±25	6±5	0.23
Harem size	2.2±0.4	2.1±0.32	0.1±0.2	0.59

Table 5.2: Morphological and behavioral characteristics of resident and new females. Sample size: 16 resident and 16 new females in early season, 6 resident and 6 new females in late season (included are only those CSs where new females settled). Probability (P) refers to a two-sample t-test (t = test statistics) comparison between the resident and new females. Lengths are measured in mm.

	Resident females		New females			
Variable	mean ± S.D.	range	mean ± S.D.	range	t	P
EARLY SEASON						
epaulet color	2.4 ± 0.8	1-4	2.8 ± 1.2	1-5	1.19	0.24
epaulet length	42.3 ± 6.5	26-50	43.1 ± 7.5	21-53	0.30	0.76
chin color	2.0 ± 0.9	1-3	1.6 ± 0.7	1-3	-1.31	0.20
wing length	102.4 ± 3.8	95-109	101.4 ± 1.9	97-105	-0.94	0.35
aggression	2.8 ± 1.0	1-4	2.3 ± 1.0	1-4	-1.42	0.17
LATE SEASON						
epaulet color	1.7 ± 0.5	1-2	2.5 ± 1.2	1-4	1.54	0.16
epaulet length	41.7 ± 9.0	26-50	41.5 ± 2.9	37-44	-0.04	0.97
chin color	2.0 ± 0.9	1-3	2.2 ± 0.4	2-3	0.42	0.69
wing length	102.0 ± 2.4	99-104	101.3 ± 0.5	101-102	-0.67	0.52
aggression	-	-	2.8 ± 0.9	2-4	-	-

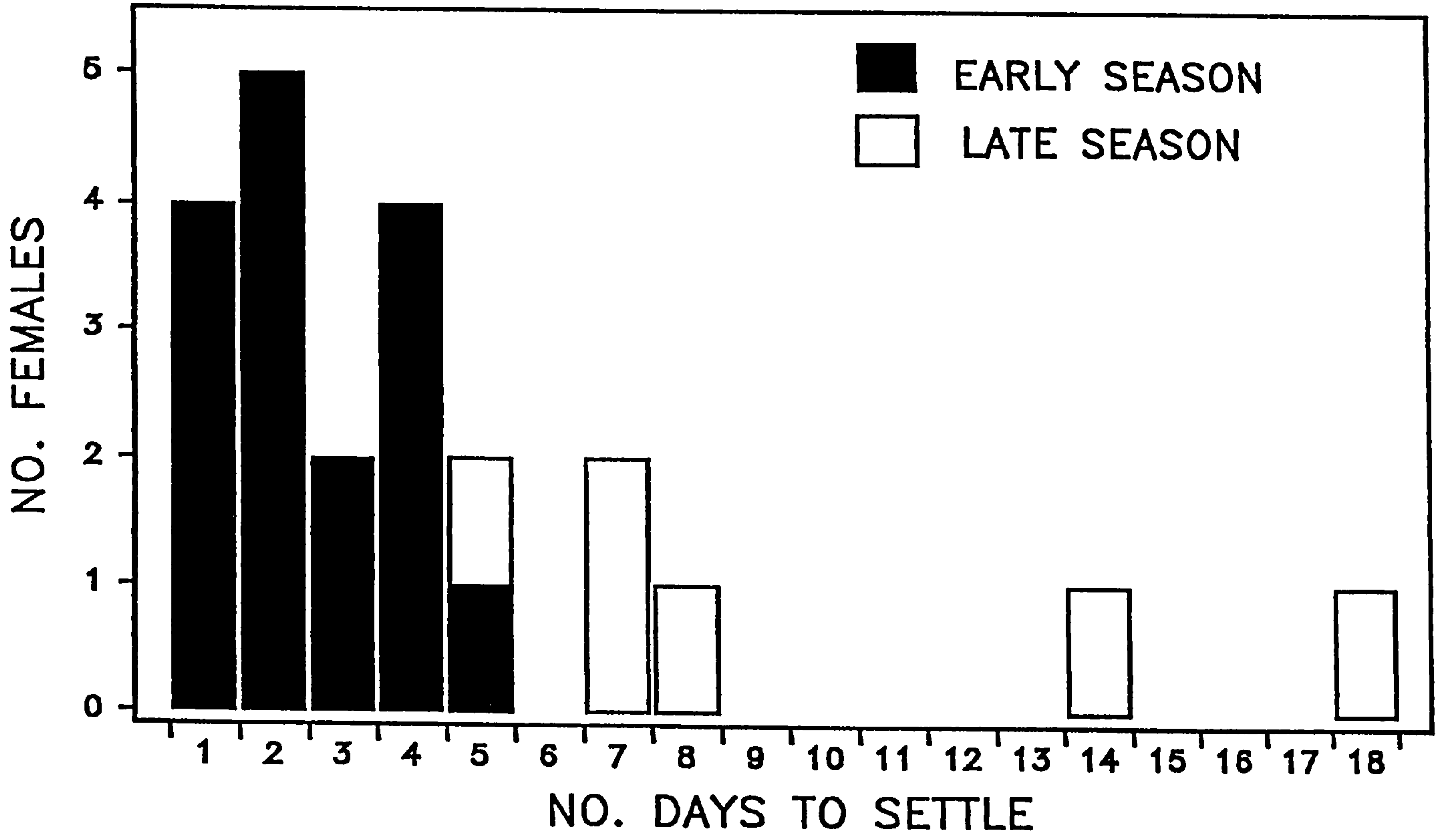


Figure 5.1 Number of days between the establishment of a choice situation and the settlement of a new female there during the early (black bars) and late (white bars) breeding season. The white bars are added on the top of the black bars.

CHAPTER 6: REPRODUCTIVE SUCCESS OF MONOGAMOUS AND BIGAMOUS FEMALES

INTRODUCTION

Many explanations of polygyny assume that female preferences have been shaped by natural selection to a near optimum. That is, the intensity of the preferences for various features of territory and male quality closely reflects the fitness gains that females achieve by selecting such features. With respect to female preferences for harem size, these models assume that when all else is equal, females select harems of sizes that provide them with the highest fitness gains.

An examination of the effect of harem size on female fitness provides a unique opportunity to test the polygyny hypotheses. First, by comparing fitness of monogamous and polygamous females, one can discriminate among the models. Second, one can use the information on fitness in conjunction with the information on the direction of female preferences to test the underlying assumption of the models, namely that there is a good correspondence between female preferences and their fitness consequences.

The hypotheses that make this assumption can be divided into three categories: (1) competitive models, which assume that females have negative impact on each other; i.e. there is a net cost of polygyny; (2) cooperative models, which assume that females have a positive impact on each other; i.e. there is a net benefit of being polygynous, and (3) neutral models, which assume neither cost nor benefit. Models that belong to the first category are the polygyny threshold model (including its extension, the defence of male parental investment model), the sexy son hypothesis, and the asynchronous settlement model. Models that belong to the second category are the two versions of the cooperative female choice model. Finally, the third category of models includes the no-cost no-benefit directed female choice model, the neutral mate choice model and the true null model.

Traditionally, the three categories of models have been tested by examining reproductive success of females breeding in harems of various sizes. For example, Holm (1973) studied a marsh-nesting population of red-winged blackbirds in Washington and found that females in large harems achieved higher reproductive success than females in small harems. Ritschel (1985), who studied a marsh-nesting population of redwings in California, found a similar relationship. The results of both studies are consistent with the cooperative models and indicate that females benefit from the presence of other females. While this may be true for Holm's and Ritschel's study populations, an alternative explanation could be that females are attracted to high-quality breeding territories, and for this reason such territories contain larger harems than poor-quality territories. Females may have neutral or even negative impact on the reproductive success of other females, but such impact could be concealed by the variation in territory quality. This variation could result in a positive correlation between harem size and female reproductive success when in fact the relationship would be neutral or even negative, if the confounding variations in territory quality, male quality and female quality were controlled for.

Subsequent authors have realised the limitations of descriptive studies and controlled for the confounding effects of male quality and territory quality by experimentally randomizing harem size with respect to those variables. Perhaps the most carefully designed experiments were conducted by Searcy (1988) in Pennsylvania. In two experiments, Searcy randomly divided territories into a treatment and a control category, and then removed females from the treatment territories while allowing females on the control territories to remain. As a result of these removals, the treatment territories had smaller harems than the control territories. Searcy found that females in treatment (small-harem) territories fledged the same number of young as females in control (large-harem) territories. These experiments indicate that harem size does not affect the number of young fledged by a female.

The effect of harem size on post-fledgling survival was indirectly assessed by Westneat (1995). Westneat examined the frequency with which males provisioned broods in harems of various sizes. Because male provisioning affects nestling growth (Muldal et al. 1986), and because the mass of fledglings is related to post-fledging survival (Magrath 1991), male parental care may have important consequences for the number of young that survive to reproduce. In a bivariate analysis, Westneat found that an index of male provisioning was significantly negatively correlated with harem size, meaning that males provisioned broods in large harems less frequently than broods in small harems. However, when the index of male provisioning was analyzed in a multivariate analysis together with other variables, the relationship was no longer significant. Although harem size appears to have no effect on male provisioning rates, there is a need to asses more directly the effect of harem size on the quality of nestlings.

In this chapter, I will examine the effect of harem size on various components of female reproductive success. I will employ the procedure of Searcy (1988) and randomize harem size with respect to territory quality and male quality. In addition, I will reduce the variation between "small-harem" and "large-harem" territories by matching territories by their quality. I will then compare females in small and large harems in terms of the number of young fledged, nesting losses, male and female provisioning rates, and the degree of nestling development. Male provisioning rates may affect the provisioning rates by females, and thereby female survival. The degree of nestling development may affect post-fledging survival of the young, and thereby the ultimate number of young that a female produces. A comparison of these components of female reproductive success between small harems and large harems will enable me to determine whether there is any effect of polygyny on female fitness, and if there is, whether the net effect is negative or positive. In addition, these results, in conjunction with the results of Chapter 5, will enable me to test the assumption that female preferences are adaptive.

METHODS

Because adjacent territories are likely to be more similar in quality than territories farther apart, I conducted the experiment using pairs of territories. To create a territory pair (TP), I selected two territories that were 1) adjacent to each other, and 2) similar in water depth. As females in the study populations appear to choose territories by their water depth (Chapter 8), the second requirement was aimed at reducing the variation in water depth between territories in each TP. Within a TP, I randomly selected one territory and designated it as "monogamous". The other territory was then designated as "bigamous". I removed all but one randomly selected female from the monogamous-designate territory using decoy trapping described in Picman (1979). If more than two females were present on the bigamous-designate territory, two females were selected at random and the remaining females were captured and removed. As a result of the removals, the monogamous-designate territory became a monogamous territory, and the bigamous-designate territory became a bigamous territory. If a new female settled on a TP after the removals, she was captured and removed in order to maintain the monogamous and bigamous status of the resident females.

I limited the degree of polygyny to bigamy for two reasons. First, bigyny was the most common form of polygyny in the study population. Second, the cooperative female choice hypothesis assumes that female reproductive success increases with harem size up to the optimum harem size, beyond which it declines (Altmann et al. 1977, Picman 1988). The optimum harem size is not known, but it cannot be lower than bigyny. For this reason I chose bigyny to represent my polygynous situations.

When resident females initiated breeding, their nests were located and checked every 3 days during incubation, every day during the presumed hatching date of young, and then every 2 days during the nestling period. During each visit, I recorded nest content and if nestlings were present, their relative size. I classified the losses of young into three categories: (1) hatching failure, if an egg did not hatch, (2) predation, if whole clutch disappeared before the presumed hatching date, and (3) other causes. This category includes: i) clutches abandoned by females, ii) clutches destroyed by inclement weather, and iii) partial egg losses due to predation (because there were no marsh wrens on the study sites, partial losses due to marsh wren attacks were likely negligible). I classified the losses of nestlings into three categories: (1) starvation, if a young considerably smaller than its siblings disappeared during subsequent visits (this category of losses may also include losses caused by diseases and parasites), (2) predation, if the whole brood disappeared before the presumed fledging date; and (3) other causes. This category includes: i) nest abandonment by the female, ii) nests destroyed by inclement weather, and iii) unexplained losses of individual nestlings.

Feeding rates

In 1994, I recorded the frequency of feeding by each parent (feeding rate) when the young were 8 and 10 days old (hatching=day 0). I observed the feeding rates between 6:00-11:00 hrs Eastern Daylight Time from a location 40 meters or more away from the focal nest. As the feeding rate may be affected by the time of day or temperature, I attempted to minimize the impact of these variables by observing the nests at approximately the same time. For most nests, this meant that 1) the time of observations on day 10 was ±10 minutes of the time on day 8, and 2) within each TP, the time of observations of bigamous nests was ±10 minutes of the time of observations of the monogamous nest.

The feeding rate was determined as follows. Observations at a nest commenced when the first parent arrived with food. As this was usually the female, I observed the nest for a minimum of 30 minutes after her first visit, plus any additional time until her subsequent visit. The feeding rate for the female was then calculated by dividing the total number of her visits (minus one) by the time (in minutes) elapsed between her first and last visit. This feeding rate per minute was then recalculated to a rate per 30 minutes. To illustrate the calculations with an example, consider that the female first fed at 8:00, with subsequent visits at 8:08, 8:16, 8:24 and 8:32. I began timing the female's feeding rate at 8:00. The female's last visit after 30 minutes was at 8:32, so the total time lapsed between her first and last visit was 32 minutes. During this time, the female visited 5 times. However, calculating the feeding rates as 5/32 = 6.25 visits/minute would inflate the rate, because the female actually visited every 8 minutes and hence her rate was 1/8 = 0.125 visits/minute. To calculate the rate correctly, I subtracted the last visit from the female's total and calculated the rate as 4 visits/32 minutes = 0.125 visits/minute. This rate was then multiplied by 30 to represent the rate of feeding per 30 minutes (i.e. 0.125*30 = 3.75 visits/30 minutes).

If the male participated in the feeding of young, then his feeding rate was measured and calculated in the same manner the female's feeding rate. If the male did not participate, then his feeding rate was zero.

Quality of young

When the young reached the age of 10 days, they were collected under a permit from the Animal Care Committee of the University of Ottawa. The young were collected between 18:00-20:00 to minimize the variation in body mass due to the time of day. Each young was weighed in the field and then euthanised with an overdose of an anaesthetic. In the laboratory, the young were sexed using the procedure described in Fiala (1979), their stomach contents removed and weighed, and the following characteristics measured: (1) the lengths of nine primaries (primary 2 to 10) on the right wing (measured to the nearest 0.5 mm); (2) the length of the longest feather in the spinal tract at approximately the level of wings (henceforth "spinal tract feather"; to the nearest 0.1 mm); (3) the length of the longest tail feather (to the nearest 0.5 mm); (4) the length of ulna (to the nearest 0.1 mm); (5) the length of tibia (to the nearest 0.1 mm). Body mass was calculated by subtracting the mass of the stomach content from the mass measured in the field. Since well developed wing feathers, wing bones and tail feathers are necessary for effective flying, I used the total length of the primaries, the length of the tail and the length of the ulna as indices of a young's ability to fly. I used the length of the tibia as an index of a young's ability to leave the nest by climbing on cattail stalks and leaves. Because older nestlings may be exposed to inclement weather, the degree of feather development on their ventral side (as characterised by the length of the longest feather) may provide an index of a young's ability to conserve energy by preventing heat loss.

Statistical analyses

Territory quality: To determine whether there were any systematic differences between monogamous and bigamous territories in terms of their quality, I compared the territories with respect to their size, water depth and initial harem size (number of resident females present at the onset of the experiment). First, I calculated the difference in quality between a monogamous and bigamous territory within each TP (difference = monogamous-bigamous), and then compared the mean of the differences to zero using a paired-sample t-test. This comparison was carried out separately for 1993 and 1994, and then for both years combined.

As the time of the season may affect female reproductive success, I examined whether there were any systematic differences between the initiation of nesting (date of first egg) of monogamous and bigamous females. As secondary females usually nest later than primary females, I carried out the analyses separately for monogamous and bigamous females of the same status. In this study, the primary/secondary status is used to reflect the relative order in which females initiated nesting, and not the order in which the females originally settled. For bigamous females, the status was determined from the first-egg dates of females remaining on the bigamous-designate territories after the removals (in the case of a tie, one female was randomly designated as primary). For monogamous females, the primary/secondary status of the remaining female was determined from the stage of nesting of that female as compared to the stage of nesting of the removed female before the removals. When there were 3 resident females on a monogamous-designate territory, and the primary and tertiary females were removed, then the status of the remaining female (which was neither first nor last to nest on that territory) was determined from the temporal proximity of her nesting to the nesting of females on the companion bigamous territory (e.g. if the monogamous female initiated nesting on the same day as the primary bigamous female, then the monogamous female was designated primary).

For each TP, I calculated the difference (in days) between the first-egg date of the primary monogamous female (if there was a primary female on the monogamous territory) and the first-egg date of the primary bigamous female. I then calculated the mean of these differences for all TPs and tested this mean against zero using a paired-sample t-test. I calculated and tested the difference between the first-egg dates of the secondary bigamous and secondary monogamous females in analogous manner.

I used two methods to analyze female nesting success. First, using a three-way repeated-measures ANOVA, I examined the number of offspring in a nest (continuous variable) during three stages of the nesting cycle (repeated-measure; the three stages were clutch completion, hatching and fledging) in relation to three categorical variables: 1) harem size (monogamy or bigamy), 2) female status (primary or secondary), and 3) year of study (1993 or 1994). To satisfy the assumptions of normality and homoscedasticity of the ANOVA, the number of offspring was transformed as follows: new number=log10(old number+1). This method has the advantage of utilizing the largest sample size available, and examining the interactions among the categorical variables. The method has, however, two disadvantages. First, despite the randomization procedure, there may be initial differences in clutch sizes of the monogamous and bigamous females, and these differences would bias the interpretation of the results. Second, the analysis disregards the fact that territories within each TP are matched by their quality. Therefore, I also used a second method of analysis that avoids these weaknesses and thus complements the results of the first method. The second method consisted of examining the losses of eggs during the incubation period (defined as time between the first egg and hatching of young), and losses of young during the nestling period (defined as time between hatching and fledging). For each TP, I calculated the difference in the number of offspring (eggs or young) lost by monogamous and bigamous females of the same status, and then tested the mean of these differences using a paired-sample t-test.

Causes of egg loss and the causes of nestling loss were classified into three categories each, and then tested in the same manner as the total losses. Where the assumption of normality of the differences was violated, I utilized the signed rank test of Lehman (1975).

Feeding rates were analyzed separately for males, females and for the combined contribution of both parents using a two-way repeated-measures ANOVA. In this analysis, feeding rate was the continuous variable, age of young (8 or 10 days) the repeated measure, and the two factors were 1) harem size (monogamy vs. bigamy), and 2) female status (primary vs. secondary). To satisfy the assumption of normality and homoscedasticity, male feeding rates were transformed as: old rates = log10(new rates + 0.01). Because very few broods survived to fledging, there was insufficient sample size to calculate differences between monogamous and bigamous females.

To examine the effect of nesting synchrony on the feeding rates on bigamous territories, I related male, female and total (male + female) feeding rates to the degree of overlap in nesting periods of the primary and secondary female. For primary females, the overlap was calculated as the number of days when nestlings (10 days old or younger) of the primary female were present in the nest and there were also nestlings present in the nest of the secondary female. For secondary females, the overlap was calculated as the number of days when nestlings (10 days or younger) of the secondary female were present in the nest and there were also nestlings present in the nest (or fledged on territory) of the primary female.

Quality of young: Means for monogamous and bigamous broods were compared with two-sample t-tests. Where the assumption of homoscedasticity was violated, the means were compared with Wilcoxon two-sample rank test.

All statistical analyses were carried out using SAS software (SAS Institute, Inc. 1985). When monogamous and bigamous females within each TP were compared, the difference was calculated as: difference = monogamous - bigamous.

RESULTS

I established 20 territory pairs (TPs) in 1993 and 20 territory pairs in 1994. Each TP consisted of one monogamous and one bigamous territory. The monogamous territories and the bigamous territories did not differ in their size, water depth and initial harem size either in 1993, or in 1994, or when the data for both years were combined (Table 6.1). These results suggest that the randomization procedure selected monogamous and bigamous territories that were, on average, of similar quality.

Before I began the experiment in 1993, there were 46 females present on the monogamous-designate territories (16 x 2, 2 x 3 and 2 x 4 females) and 47 females on the bigamous-designate territories (14 x 2, 5 x 3 and 1 x 4 females). I removed 26 females from the monogamous-designate territories and 7 females from the bigamous-designate territories in order to achieve the final arrangement of one female per monogamous territory and two females per bigamous territory.

Before I began the experiment in 1994, 44 females were present on the monogamous-designate territories (17 x 2, 2 x 3 and 1 x 4 females) and 46 females on the bigamous-designate territories (16 x 2, 2 x 3 and 2 x 4 females). I removed 24 females from the monogamous-designate territories and 6 females from the bigamous-designate territories in order to achieve the final arrangement of one female per monogamous territory and two females per bigamous territory.

In 1993, primary females on bigamous territories initiated egg-laying at the same time as primary females on monogamous territories (Table 6.2). Likewise, secondary females on bigamous territories initiated egg-laying at the same time as secondary females on monogamous territories (Table 6.2). The same pattern was observed in 1994 and when the data for both years were combined (Table 6.2).

Nesting success of monogamous and bigamous females is summarized in Tables 6.3, 6.4 and 6.5. The number of fledlings was weakly related to harem size and female status (Table 6.6). In both years of the study, primary monogamous females fledged more offspring than primary bigamous females, and secondary monogamous females fledged more offspring than secondary bigamous females. There was no effect of year on female nesting success (Table 6.6). Because the higher nesting success of monogamous females may be partly caused by their larger clutches (Tables 6.3, 6.4, 6.5), I examined the rate of nesting losses of monogamous and bigamous females. In 1993, primary bigamous females suffered higher losses than primary monogamous females (the difference was significant using a one-tailed test), but there were no significant differences between the secondary bigamous and secondary monogamous females. In 1994, the total losses of primary bigamous and secondary bigamous females were again somewhat higher than those of primary monogamous and secondary monogamous females, but the differences were not significant (Tables 6.7, 6.8).

The most important cause of egg loss was predation, followed by hatching failure and other causes (Tables 6.10, 6.11, 6.12). The most important cause of nestling loss was starvation, followed by predation and other causes. There were, however, no significant differences in the rate in which eggs or young were lost to particular causes, neither in 1993, nor in 1994, nor when the data for both years were combined.

Females provisioned their young consistently more often than males both when the young were 8 days old and when they were 10 days old (Tables 6.13, 6.14). Male feeding rates were not related to harem size (monogamy vs. bigamy), female status (primary vs. secondary) or the age of young (8 or 10 days) (Table 6.15). Similarly, female feeding rates were not related to harem size or age of the young, but were significantly related to female status (Table 6.16): secondary females were feeding their young less frequently than primary females. Combined feeding rates by both parents ware not related to any of the factors examined (Table 6.17).

When I related parental feeding rates on bigamous territories to the degree of nesting asynchrony between the primary and secondary female, male feeding rates were significantly related to the degree of asynchrony and to the age of the young (Table 6.18): males were feeding asynchronous broods more often than synchronous broods and 8-day-old nestlings more often than 10-day-old nestlings. Female feeding rates were not related to either nestling age or the degree of asynchrony (Table 6.18), but the combined feeding rates by both parents were marginally related to the degree of asynchrony: asynchronous broods were fed more frequently than sychronous broods.

When I compared the morphological characteristics of nestlings from monogamous and bigamous territories, I found significant differences in the degree of development of female nestlings, but no comparable differences in the degree of development of male nestlings (Table 6.19). Female nestlings on monogamous territories had approximately 6% longer tibias and were approximately 7% heavier than female nestlings on bigamous territories (Table 6.19). There were no significant differences between monogamous and bigamous female nestlings in the length of their primaries, in the length of their longest spinal tract feathers, and in the length of tails or the length of their ulnas. There were no significant differences between monogamous and bigamous male nestlings in any of the morphological characteristics examined.

DISCUSSION

I established monogamous and bigamous harems by removing females from randomly selected territories. The consequence of this experimental design was that the variation in territory quality, male quality and female quality was randomized with respect to harem size, and therefore the monogamous and bigamous harems were similar in terms of their territory quality, male quality and female quality. This similarity was confirmed when monogamous and bigamous territories were compared with respect to three indices of their quality and no differences were found. In addition, the lack of any systematic difference in the quality of females nesting on the territories was confirmed when the first-egg dates of those females were compared. Therefore, if females on the monogamous and bigamous territories differ in their subsequent reproductive success, then such differences are most likely due to the different harem sizes, and not to the confounding influence of territory quality, male quality or female quality.

The main findings of this study are: (1) bigamous males provisioned asynchronous broods more often than synchronous broods, (2) 10-day-old female nestlings in monogamous broods had significantly longer tibias than female nestlings in bigamous broods, and (3) in 1993, primary monogamous females suffered lower nesting losses than primary bigamous females (difference significant in a one-tailed test). In other comparisons, the differences between monogamous and bigamous females were not significant, but they consistently pointed in the same direction: monogamous females performed better than bigamous females. Considered together, these findings indicate that polygyny is costly to females.

The relatively small cost of polygamy detected in this study is not suprising. In both years, a substantial proportion (40% in 1993, 63% in 1994) of bigamous females failed at various stages of their nesting periods. If females in this population compete mainly for male parental care, then the failure of one female represents a gain for her co-wife in the form of reduced competition. As a result of this, a large failure rate would make it difficult to detect differences in the reproductive success of monogamous females and bigamous (but effectively monogamous) females. This explanation is supported by the significant relationship between male feeding rates and the degree of asynchrony between primary and secondary females. Therefore, the small observed differences in the reproductive success of monogamous and bigamous females may not in itself mean that the cost of polygamy is small. In fact, such differences seem to suggest that the real impact of females on the reproductive success of other females is potentially quite high.

Results of this study are consistent with the findings of Searcy (1988). In agreement with my results, Searcy did not find any differences in the number of young fledged from small-harem and large-harem territories. It is possible that if Searcy were to examine other components of female reproductive success, such as feeding rates and the development of young, he would find the same small differences as I did. Alternatively, it is possible that there is a geographic variation in the cost of polygamy, and that females in Pennsylvania, where Searcy conducted his experiments, have no effect on the fitness of other females. This explanation is supported by the fact that females in Searcy's population did not exhibit any preferences for harem size, while females in this population exhibited clear preferences for monogamy (Chapter 5).

The finding that bigamous female nestlings have shorter bones (tibias) than monogamous female nestlings can be explained by the fact that the linear growth of bones is the most important factor that limits fledging time in this species. If bigamous broods receive less food than monogamous broods, then they would be affected most not in the development of tissues that are relatively easy to grow - such as feathers or body mass - but in tissues that are generally the most difficult to grow, and represent a limiting factor on the development of young. In a wide range of avian families, the most important factor that limits the fledging time of young is the degree of wing development, as determined by the growth rate of wing bones (Carrier and Auriemma 1992). Therefore, in species where young need to use wings to leave the nest, I would expect the growth of wing bones to be the limiting factor. In red-winged blackbirds, however, young usually leave nest by climbing on cattail stalks or other vegetation, and then slowly dispersing through the vegetation away from the nest. The young do not need fully developed wings in order to leave nest. I would therefore, expect that the limiting factor in the red-winged blackbird would be the growth of leg bones, rather than the growth of wing bones. The finding that bigamous female nestlings have shorter tibias in comparison with monogamous female nestlings, is consistent with this view.

In a wide variety of birds, nestling mass is positively correlated with post-fledging survival (Gustafsson and Sutherland 1988, Davies 1986, Magrath 1991, Perrins 1965, Smith et al. 1989, Tinbergen and Boerlijst 1990). Since young from polygamous broods grow at a lower rate than young from monogamous broods, one may expect that they fledge at a lower body mass, and therefore suffer higher post-fledging mortality. However, it is possible that polygamous young avoid this lower post-fleding survival by remaining longer in nests, and by fledging only when they are fully developed. This strategy may improve their post-fledging survival, but is likely to reduce their pre-fleding survival. This is because young in a nest are more vulnerable to predation than young away from the nest. A nest typically contain several young, and since feeding rates by parents are proportional to the brood size, parents visit nests more frequently than they visit solitary young. As a result of these feeding visits, the location of a nest is more conspicuous to predators than the location of a single young. As a result of these differences in predation rates, remaining longer in nest may improve the post-fledging survival of a young at the expense of reduced pre-fledging survival. Therefore, it seems that the reduced paternal feeding at polygamous nests would ultimately reduce the survival of young from those nests, and thus the total number of young that polygamous females produce.

In conclusion, the results of this study indicate that polygyny reduces female reproductive success. This finding is consistent with the competitive explanations of polygamy, such as the polygyny threshold model, the sexy son hypothesis, the asynchronous settlement model and the random dispersion hypothesis (mechanism b), while it is inconsistent with explanations that assume either neutral, or cooperative interactions (Table 4.1). These results, considered in conjunction with the results of Chapter 5, indicate that female preference for monogamy is adaptive, because it maximizes female fitness. Such finding is consistent with the underlying assumption of many hypotheses.

Table 6.1. A comparison of monogamous and bigamous territories with respect to their size (m^2), water depth (cm) and initial harem size (females/territory). Values shown are means ± 1 SD. Probability (P) refers to results of a paired-sample t-test on mean difference. The mean difference is the mean of differences between the monogamous and bigamous territory within each territory pair (difference = monogamous - bigamous). Sample sizes are in parentheses.

	Monogamous territories	Bigamous territories	Difference	t	P
1993					
Territory size	624±405 (20)	713±474 (20)	-89±246 (20)	-1.62	0.12
Water depth	41.9±25.6 (20)	43.7±25.1 (20)	-1.8±17.1 (20)	-0.47	0.64
Harem size	2.30±0.66 (20)	2.35±0.59 (20)	-0.05±0.80 (20)	-0.29	0.77
1994					
Territory size	532±297 (20)	568±325 (20)	-36.5±263 (20)	-0.62	0.54
Water depth	31.6±15.1 (20)	33.6±12.4 (20)	-2.05±13.1 (20)	-0.70	0.49
Harem size	2.20±0.52 (20)	2.30±0.66 (20)	-0.1 ±0.85 (20)	-0.52	0.61
Years combined					
Territory size	578±353 (40)	641±408 (40)	-62.8±253 (40)	-1.57	0.12
Water depth	36.7±21.4 (40)	38.7±20.2 (40)	-1.93±15.1 (40)	-0.81	0.42
Harem size	2.25±0.59 (40)	2.33±0.62 (40)	-0.08±0.80 (40)	-0.60	0.56

Table 6.2. A comparison of monogamous and bigamous females with respect to the date of their first egg. For each pair of territories, the date of the bigamous female was subtracted from the date of the monogamous female. The mean difference is the mean (± 1 S.D.) of the differences for all pairs of territories. The mean difference is compared to zero with paired-sample t-test.

	Sample size	Mean difference	t	Probability
1993				
Primary	10	0.90 ± 5.4	0.53	0.61
Secondary	10	2.20 ± 6.1	1.14	0.29
1994				
Primary	11	-1.64 ± 5.8	-0.94	0.37
Secondary	9	-0.44 ± 8.5	-0.16	0.88
Combined years				
Primary	21	-0.43 ± 5.6	-0.35	0.73
Secondary	19	0.95 ± 7.3	0.57	0.58

Table 6.3. Reproductive success of females in 1993. A comparison of monogamous and bigamous females with respect to their clutch size, number of young hatched and number of young fledged. Values are means ± 1 SD, sample sizes are in parentheses. The mean difference is the mean of differences between a monogamous and bigamous territory within each territory pair (difference = monogamous - bigamous). Probability (P) refers to results of a paired-sample t-test on mean difference.

	Monogamous females	Bigamous females	Mean difference	t	P	Minimum detectable difference
<u>Primary females</u>						
No. eggs	3.60 ± 0.52 (10)	3.60 ± 0.60 (20)	0.20 ± 0.63 (10)	1.00	0.34	0.81
No. young hatched	3.00 ± 1.25 (10)	2.70 ± 1.26 (20)	0.40 ± 2.07 (10)	0.61	0.56	2.66
No. young fledged	2.00 ± 1.05 (10)	1.25 ± 0.97 (20)	1.20 ± 1.55 (10)	2.45	0.037	2.00
<u>Secondary females</u>						
No. eggs	3.50 ± 0.85 (10)	3.15 ± 0.74 (20)	0.20 ± 0.92 (10)	0.69	0.51	1.18
No. young hatched	2.30 ± 1.49 (10)	2.20 ± 1.36 (20)	-0.40 ± 1.78 (10)	-0.71	0.49	2.29
No. young fledged	0.80 ± 0.92 (10)	0.75 ± 0.91 (20)	0.10 ± 1.29 (10)	0.25	0.81	1.66

Table 6.4. Reproductive success of females in 1994. A comparison of monogamous and bigamous females with respect to their clutch size, number of young hatched and number of young fledged. Values are means ± 1 SD. Sample sizes are in parentheses. The mean difference is the mean of differences between a monogamous and bigamous territory within each territory pair (difference = monogamous - bigamous). Probability (P) refers to results of a paired-sample t-test on the mean difference.

	Monogamous females	Bigamous females	Mean difference	t	P	Minimum detectable difference
<u>Primary females</u>						
No. eggs	3.55 ± 0.52 (11)	3.40 ± 0.82 (20)	0.27 ± 0.90 (11)	1.00	0.34	1.09
No. young hatched	2.82 ± 1.47 (11)	2.15 ± 1.57 (20)	0.82 ± 2.44 (11)	1.11	0.29	1.90
No. young fledged	1.36 ± 1.75 (11)	1.10 ± 1.41 (20)	0.18 ± 2.64 (11)	0.23	0.82	1.70
<u>Secondary females</u>						
No. eggs	3.56 ± 0.73 (9)	3.45 ± 0.60 (20)	0.33 ± 0.87 (9)	1.15	0.28	1.20
No. young hatched	2.56 ± 1.51 (9)	2.20 ± 1.74 (20)	0.11 ± 1.96 (9)	0.17	0.87	2.40
No. young fledged	1.56 ± 1.42 (9)	0.70 ± 1.13 (20)	0.22 ± 1.56 (9)	0.43	0.68	1.56

Table 6.5. Reproductive success of females for combined years 1993 and 1994. A comparison of monogamous and bigamous females with respect to their clutch size, number of young hatched and number of young fledged. Values are means ± 1 SD. Sample sizes are in parentheses. The mean difference is the mean of differences between a monogamous and bigamous territory within each experimental setup (difference = monogamous - bigamous). Probability (P) refers to results of a paired-sample t-test on mean difference.

	Monogamous females	Bigamous females	Mean difference	t	P	Minimum detectable difference
Primary females						
Eggs laid	3.57 ± 0.51 (21)	3.50 ± 0.72 (40)	0.24 ± 0.77 (21)	12.5[1]	0.27	-
Young hatched	2.90 ± 1.34 (21)	2.43 ± 1.43 (40)	0.62 ± 2.22 (21)	1.28	0.22	1.18
Young fledged	1.67 ± 1.46 (21)	1.18 ± 1.20 (40)	0.67 ± 2.20 (21)	1.39	0.18	0.99
Secondary females						
Eggs laid	3.53 ± 0.77 (19)	3.30 ± 0.69 (40)	0.26 ± 0.87 (19)	10.5[1]	0.26	-
Young hatched	2.42 ± 1.46 (19)	2.20 ± 1.54 (40)	-0.16 ± 1.83 (19)	-0.38	0.71	1.35
Young fledged	1.16 ± 1.21 (19)	0.73 ± 1.01 (40)	0.16 ± 1.38 (19)	0.50	0.63	0.88

[1] tests statistics of signed rank test

Table 6.6. Statistical analysis of female reproductive success with a three-way repeated-measures ANOVA. The dependent variable is the number of offspring per female, the repeated measure is time (3 levels of TIME: date of clutch completion, date of hatching, date of fledging), the categorical variables are HAREM (monogamy or bigamy), STATUS (primary female or secondary female), and YEAR (1993 or 1994).

Source	df	Mean square	F	P
Univariate tests of hypotheses for within subject effects:				
TIME	2	3.847	121.03	<0.0001
TIME*HAREM	2	0.036	1.15	0.32
TIME*YEAR	2	0.017	0.53	0.59
TIME*STATUS	2	0.039	1.23	0.29
TIME*HAREM*YEAR	2	0.007	0.22	0.80
TIME*HAREM*STATUS	2	0.003	0.08	0.92
TIME*YEAR*STATUS	2	1.09	1.09	0.34
TIME*HAREM*YEAR*STATUS	2	0.052	1.64	0.20
Error (TIME)	224	0.032	.	.
Tests of hypotheses for between subjects effects:				
HAREM	1	0.243	3.42	0.067
YEAR	1	0.053	0.75	0.39
STATUS	1	0.227	3.19	0.077
HAREM*YEAR	1	0.017	0.23	0.63
HAREM*STATUS	1	0	0	1.0
YEAR*STATUS	1	0.166	2.33	0.13
HAREM*YEAR*STATUS	1	0.027	0.37	0.54
Error	112	0.071	.	.

Table 6.7. Number of eggs and young lost by monogamous and bigamous females in 1993. Values are means ± 1 S.D. (sample sizes in parentheses). For each pair of territories, the loss of bigamous female was subtracted from the loss of monogamous female. The mean (± 1 S.D.) of the differences was tested against zero with a paired-sample t-test (t is test statistics, P is probability).

	Monogamous females	Bigamous females	Mean difference	t	P	Minimum detectable difference
<u>Primary females</u>						
Eggs	0.60 ± 0.97 (10)	0.90 ± 1.21 (20)	-0.20 ± 1.81 (10)	-0.35	0.74	2.33
Young	1.00 ± 1.25 (10)	1.45 ± 1.43 (20)	-0.80 ± 1.87 (10)	-1.35	0.21	2.40
Eggs and young	1.60 ± 1.17 (10)	2.35 ± 1.05 (20)	-1.00 ± 1.70 (10)	-1.86	0.096	2.18
<u>Secondary females</u>						
Eggs	1.20 ± 1.32 (10)	0.95 ± 1.23 (20)	0.60 ± 1.43 (10)	3.5[1]	0.38	-
Young	1.50 ± 1.58 (10)	1.45 ± 1.32 (20)	-0.50 ± 2.37 (10)	-0.67	0.52	3.05
Eggs and young	2.70 ± 1.25 (10)	2.40 ± 1.19 (20)	0.10 ± 1.66 (10)	0.19	0.85	2.13

[1] test statistics of signed rank test

Table 6.8. Number of eggs and young lost by monogamous and bigamous females in 1994. Values are means ± 1 S.D. (sample sizes in parentheses). For each pair of territories, the loss of bigamous female was subtracted from the loss of monogamous female. The mean (± 1 S.D.) of the differences was tested against zero with a paired-sample t-test (t is test statistics, P is probability).

	Monogamous females	Bigamous females	Mean difference	t	P	Minimum detectable difference
<u>Primary females</u>						
Eggs	0.73 ± 1.42 (11)	1.25 ± 1.48 (20)	-0.55 ± 2.07 (11)	-0.88	0.40	2.50
Young	1.45 ± 1.57 (11)	1.05 ± 1.19 (20)	0.64 ± 1.91 (11)	1.10	0.30	2.31
Eggs and young	2.18 ± 1.60 (11)	2.30 ± 1.38 (20)	0.09 ± 2.51 (11)	0.12	0.91	3.03
<u>Secondary females</u>						
Eggs	1.00 ± 1.80 (9)	1.25 ± 1.68 (20)	0.22 ± 1.56 (9)	0.43	0.68	2.15
Young	1.00 ± 1.32 (9)	1.50 ± 1.57 (20)	-0.11 ± 1.83 (9)	-0.18	0.86	2.52
Eggs and young	2.00 ± 1.66 (9)	2.75 ± 1.29 (20)	0.11 ± 1.27 (9)	0.26	0.80	1.75

Table 6.9. Number of eggs and young lost by monogamous and bigamous females in years 1993 and 1994 combined. Values are means ± 1 S.D. (sample sizes in parentheses). For each pair of territories, the loss of bigamous female was subtracted from the loss of monogamous female. The mean (± 1 S.D.) of the differences was tested against zero with a paired-sample t-test (t is test statistics, P is probability).

	Monogamous females	Bigamous females	Mean difference	t	P	Minimum detectable difference
Primary females						
Eggs	0.67 ± 1.20 (21)	1.08 ± 1.35 (40)	-0.38 ± 1.91 (21)	-0.91	0.37	1.58
Young	1.24 ± 1.41 (21)	1.25 ± 1.32 (40)	-0.05 ± 1.99 (21)	-0.11	0.91	1.65
Eggs and young	1.90 ± 1.41 (21)	2.33 ± 1.21 (40)	-0.43 ± 2.18 (21)	-0.90	0.38	1.80
Secondary females						
Eggs	1.11 ± 1.52 (19)	1.10 ± 1.46 (40)	0.42 ± 1.46 (19)	9[1]	0.24	-
Young	1.26 ± 1.45 (19)	1.48 ± 1.43 (40)	-0.32 ± 2.08 (19)	-0.66	0.52	1.82
Eggs and young	2.37 ± 1.46 (19)	2.58 ± 1.24 (40)	0.11 ± 1.45 (19)	0.32	0.76	1.27

[1] test statistics of signed rank test

Table 6.10. The causes of nesting loss of monogamous and bigamous females in 1993. Values are mean ± 1 SD number of eggs/young lost (sample sizes in parentheses). For each pair of territories, the loss of bigamous female was subtracted from the loss of monogamous female. The mean (± 1 S.D.) of the differences was tested against zero with a signed rank test (t is test statistics, P is probability).

	Monogamous females	Bigamous females	Mean difference	t	P
Primary females					
Eggs sterile	0.20±0.42 (10)	0.25±0.55 (20)	0.10±0.57 (10)	1	1.0
Eggs depredated	0.30±0.95 (10)	0.45±1.15 (20)	-0.40±1.90 (10)	-1.5	0.75
Eggs other	0.10±0.32 (10)	0±0 (20)	0.10±0.32 (10)	0.5	1.0
Young starved	1.11±1.27 (9)	1.17±0.92 (18)	0±0.82 (7)	0	1.0
Young depredated	0±0 (9)	0.61±1.20 (18)	-1.14±1.68 (7)	-3	0.25
Young other	0±0 (9)	0.06±0.24 (18)	-0.14±0.38 (7)	-0.5	1.00
Secondary females					
Eggs sterile	0.40±0.70 (10)	0.30±0.57 (20)	0±0.82 (10)	0	1.0
Eggs depredated	0.30±0.67 (10)	0.60±1.27 (20)	0.10±0.99 (10)	0.5	1.0
Eggs other	0.10±0.32 (10)	0±0 (20)	0.10±0.32 (10)	0.5	1.0
Young starved	0.89±0.93 (9)	0.88±0.96 (16)	0.25±1.39 (8)	0.51[1]	0.63
Young depredated	0.67±1.12 (9)	0.94±1.48 (16)	-0.88±2.30 (8)	-1.08[1]	0.32
Young other	0.33±1.00 (9)	0±0 (16)	0.38±1.06 (8)	0.5	1.0

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[1] test statistics of paired-sample t-test

Table 6.11. The causes of nesting loss of monogamous and bigamous females in 1994. Values are mean ± 1 SD number of eggs/young lost (sample sizes in parentheses). For each pair of territories, the loss of bigamous female was subtracted from the loss of monogamous female. The mean (± 1 S.D.) of the differences was tested against zero with a signed rank test (t is test statistics, P is probability).

	Monogamous females	Bigamous females	Mean difference	t	P
Primary females					
Eggs sterile	0.09±0.30 (11)	0.20±0.41 (20)	-0.09±0.30 (11)	-0.5	1.0
Eggs depredated	0.36±1.21 (11)	0.65±1.46 (20)	-0.18±1.89 (11)	-0.5	1.0
Eggs other	0.27±0.90 (11)	0.40±0.94 (20)	-0.27±0.90 (11)	-0.5	1.0
Young starved	0.56±0.88 (9)	0.53±0.83 (15)	0.14±1.46 (7)	0.26[1]	0.80
Young depredated	0.89±1.54 (9)	0.67±1.18 (15)	-0.29±1.25 (7)	-0.5	1.0
Young other	0±0 (9)	0.20±0.77 (15)	0±0 (7)	0	1.0
Secondary females					
Eggs sterile	0±0 (9)	0.05±0.22 (20)	0±0 (9)	0	1.0
Eggs depredated	0.56±1.67 (9)	1.20±1.70 (20)	-0.11±2.32 (9)	0	1.0
Eggs other	0.44±1.01 (9)	0.35±1.09 (20)	0±1.80 (9)	0	1.0
Young starved	0.38±0.74 (8)	0.57±0.85 (14)	-0.33±1.63 (6)	-0.5	0.64
Young depredated	0.75±1.16 (8)	0.86±1.46 (14)	0±0 (6)	0	1.0
Young other	0±0 (8)	0.21±0.80 (14)	0±0 (6)	0	1.0

[1] test statistics of paired-sample t-test

Table 6.12. The causes of nesting loss of monogamous and bigamous females for years 1993 and 1994 combined. Values are mean ± 1 S.D. number of eggs/young lost (sample sizes in parentheses). For each pair of territories, the loss of bigamous female was subtracted from the loss of monogamous female. The mean (± 1 S.D.) of the differences was tested against zero with a signed rank test (t is test statistics, P is probability).

	Monogamous females	Bigamous females	Mean difference	t	P
Primary females					
Eggs sterile	0.14±0.36 (21)	0.23±0.48 (40)	0±0.45 (21)	0	1.0
Eggs depredated	0;33±1.06 (21)	0.55±1.30 (40)	-0.29±1.85 (21)	-3	0.63
Eggs other	0.19±0.68 (21)	0.20±0.69 (40)	-0.10±0.70 (21)	-0.5	1.0
Young starved	0.83±1.10 (18)	0.88±0.93 (33)	0.07±1.14 (14)	0.23[1]	0.82
Young depredated	0.44±1.15 (18)	0.64±1.17 (33)	-0.7±1.49 (14)	-6	0.19
Young other	0±0 (18)	0.12±0.55 (33)	-0.07±0.27 (14)	-0.5	1.0
Secondary females					
Eggs sterile	0.21±0.54 (19)	0.18±0.45 (40)	0±0.58 (19)	0	1.0
Eggs depredated	0.42±1.22 (19)	0.90±1.52 (40)	0±1.70 (19)	-1	0.91
Eggs other	0.26±0.73 (19)	0.18±0.78 (40)	0.05±1.22 (19)	1	0.75
Young starved	0.65±0.86 (17)	0.73±0.91 (30)	0±1.47 (14)	0	1
Young depredated	0.71±1.10 (17)	0.90±1.45 (30)	-0.5±1.74 (14)	-4.5	0.31
Young other	0.18±0.73 (17)	0.10±0.55 (30)	0.21±0.80 (14)	0.5	1.0

[1] test statistics of paired-sample t-test

Table 6.13. Male and female feeding rates of 8-day-old young on monogamous and bigamous territories. Values are mean ± 1 S.D. number of trips/30 minutes/brood (number of broods in parentheses).

	Monogamous territories	Bigamous territories
Broods of primary females		
Male	0.70 ± 0.82 (5)	0.62 ± 0.59 (9)
Female	4.39 ± 1.95 (5)	4.64 ± 1.35 (9)
Both parents	5.09 ± 2.01 (5)	5.26 ± 1.57 (9)
Broods of secondary females		
Male	2.47 ± 2.57 (6)	0.97 ± 1.35 (6)
Female	3.71 ± 1.15 (6)	3.47 ± 1.86 (6)
Both parents	6.17 ± 2.89 (6)	4.45 ± 2.62 (6)

Table 6.14. Male and female feeding rates of 10-day-old young on monogamous and bigamous territories. Values are mean ± 1 S.D. number of trips/30 minutes/brood (number of broods in parentheses).

	Monogamous territories	Bigamous territories
Broods of primary females		
Male	1.45 ± 1.74 (5)	0.79 ± 0.37 (9)
Female	4.74 ± 1.77 (5)	4.71 ± 1.78 (9)
Both parents	6.19 ± 2.01 (5)	5.50 ± 1.64 (9)
Broods of secondary females		
Male	1.86 ± 2.12 (6)	1.64 ± 1.64 (6)
Female	3.13 ± 1.02 (6)	2.95 ± 2.50 (6)
Both parents	4.99 ± 2.30 (6)	4.60 ± 2.68 (6)

Table 6.15. Statistical analysis of male feeding rates with a two-way repeated-measures ANOVA. The dependent variable is the feeding rate, the repeated measure is time (TIME, age 8 or 10 days), the categorical variables are HAREM (monogamy or bigamy) and STATUS (primary female or secondary female).

Source	df	Mean square	F	P
Univariate tests of hypotheses for within subject effects:				
TIME	1	0.658	0.87	0.36
TIME*HAREM	1	0.520	0.68	0.42
TIME*STATUS	1	0.059	0.08	0.78
TIME*HAREM*STATUS	1	0.072	0.09	0.76
Error (TIME)	22	0.760	.	.
Tests of hypotheses for between subjects effects:				
HAREM	1	0.023	0.01	0.91
STATUS	1	0.048	0.03	0.87
HAREM*STATUS	1	0.79	0.47	0.50
Error	22	1.70	.	.

Table 6.16. Statistical analysis of female feeding rates with a two-way repeated measures ANOVA. The dependent variable is the feeding rate, the repeated measure is time (TIME, age 8 or 10 days), the categorical variables are HAREM (monogamy or bigamy) and STATUS (primary female or secondary female).

Source	df	Mean square	F	P
<u>Univariate tests of hypotheses for within subject effects</u>:				
TIME	1	0.353	0.25	0.62
TIME*HAREM	1	0.042	0.03	0.86
TIME*STATUS	1	1.78	1.29	0.27
TIME*HAREM*STATUS	1	0.091	0.07	0.80
Error (TIME)	22	1.384	.	.
<u>Tests of hypotheses for between subjects effects</u>:				
HAREM	1	0.026	0.01	0.94
STATUS	1	21.15	4.77	0.0399
HAREM*STATUS	1	0.317	0.07	0.79
Error	22	4.44	.	.

Table 6.17. Statistical analysis of the combined feeding rate by both parents with a two-way repeated-measures ANOVA. The dependent variable is the feeding rate, the repeated measure is time (TIME, age 8 or 10 days), the categorical variables are HAREM (monogamy or bigamy) and STATUS (primary female or secondary female).

Source	df	Mean square	F	P
<u>Univariate tests of hypotheses for within subject effects</u>:				
TIME	1	0.073	0.03	0.88
TIME*HAREM	1	0.169	0.06	0.81
TIME*STATUS	1	4.392	1.52	0.23
TIME*HAREM*STATUS	1	3.776	1.30	0.26
Error (TIME)	22	2.899	.	.
<u>Tests of hypotheses for between subjects effects</u>:				
HAREM	1	5.363	0.83	0.37
STATUS	1	2.65	0.41	0.53
HAREM*STATUS	1	2.00	0.31	0.58
Error	22	6.456	.	.

Table 6.18: Logistic regression analysis of the effects of nestling age (AGE) and asynchrony (ASYNCHRONY) on the feeding rates by males, females and by both parents. ASYNCHRONY is the number of days between the first-egg-date of the primary and secondary female. Sample size in each analysis is 30.

	Parameter estimate	Standard error	Wald χ^2	P
Male				
Asynchrony	-0.262	0.101	6.65	0.0099
Age	0.7389	0.368	4.03	0.045
3				
Female				
Asynchrony	-0.0509	0.073	0.49	0.49
Age	-0.167	0.32	0.28	0.60
Both parents				
Asynchrony	-0.1277	0.0756	2.86	0.091
Age	-0.0179	0.3179	0.32	0.57

Table 6.19. Morphological characteristics of nestlings from monogamous and bigamous broods. The values are means ± 1 S.D. (N is sample size). The means were compared with two-sample t-test (t is test statistics, P is probability). Primaries = total length of nine primaries, Back cover = length of the longest feather in the spinal tract, Tail = longest tail feather.

	Monogamous territories	Bigamous territories	t	P
Female nestlings				
Body mass (g)	30.2 ± 1.8	28.3 ± 2.8	2.04	0.053
Primaries (mm)	376 ± 44	363 ± 52	0.70	0.49
Back cover (mm)	21.7 ± 2.4	20.7 ± 3.0	0.97	0.34
Tail (mm)	13.1 ± 5.3	12.3 ± 6.0	0.38	0.71
Tibia (mm)	35.6 ± 0.84	33.5 ± 3.1	2.44[1]	0.0146
Ulna (mm)	28.0 ± 0.6	27.7 ± 1.5	0.20[1]	0.84
N	13	13		
Male nestlings				
Body mass (g)	39.5 ± 5.1	37.9 ± 2.18	0.53[1]	0.60
Primaries (mm)	383 ± 50	381 ± 50	0.10	0.92
Back cover (mm)	20.8 ± 2.0	21.1 ± 3.0	-0.27	0.79
Tail (mm)	10.5 ± 3.2	10.0 ± 3.4	0.36	0.72
Tibia (mm)	39.4 ± 0.9	38.8 ± 1.8	1.05	0.30
Ulna (mm)	32.1 ± 1.35	32.0 ± 1.52	0.17	0.87
N	10	13		

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[1] Z statistics of Wilcoxon two-sample rank test

CHAPTER 7: THE EFFECT OF NESTING ASYNCHRONY ON FEMALE REPRODUCTIVE SUCCESS

INTRODUCTION

Nesting asynchrony, defined here as the temporal overlap in nesting attempts of primary and secondary females, may substantially influence female reproductive success. Females in a harem may compete for limited resources, such as food, good-quality nesting sites, or male parental help. The addition of a new female into the harem increases the competition for the limited resources, and the increased competition may suppress reproductive success of the resident females. Females in a harem may also benefit from the presence of other females. The benefit may be derived from enhanced detection and avoidance of predators (Altmann 1974), from group defence of nests, sharing of information about the identity of predators (Curio 1978, Curio et al. 1978, Vieth et al. 1980, Conover 1987, McLean and Rhodes 1991) or sharing of information about the location of food sources (Pratt 1980, Bayer 1982, Evans 1982). The combined costs of all competitive interactions, and the combined benefits of all mutualistic interactions then determine whether there is a net cost or a net benefit of polygamy to females, or whether the effect is neutral. If the net effect of polygamy is negative, then females may reduce the cost of polygamy by staggering their breeding attempts in time. If the net effect is positive, then females can further increase the benefit by nesting synchronously.

The relationship between the degree of nesting asynchrony and female reproductive success can be used to discriminate between two models: the defence of male parental investment model (DMPIM), and the asynchronous settlement model

(ASM). The DMPIM is an extension of the polygyny threshold model. Whereas the polygyny threshold model does not make any specific predictions about the effect of asynchrony on female reproductive success, the DMPIM postulates that asynchrony should increase the reproductive success of primary females, but decrease the reproductive success of secondary females. This contrasts with the relationship assumed by the ASM. According to the ASM, reproductive success of primary and secondary females should increase with increasing asynchrony. The DMPIM and ASM, therefore, postulate the same relationship for primary females but differ in the relationship expected for secondary females. The nature of the relationship thus provides a way of discriminating between these two models.

In red-winged blackbirds, the effect of asynchrony on male provisioning rates (which may affect fledgling mass and thereby survival) was investigated by Yasukawa et al. (1990) and Westneat (1995). Yasukawa and his coworkers studied an upland population in Wisconsin. When male provisioning rates were related to the number of concurrently active nests on a male's territory, there appeared to be a negative relationship, indicating that males with many active nests provisioned less than males with few nests. However, when male provisioning rates were entered in a multiple regression analysis with other variables (such as brood size, nestling age), this trend ceased to be significant. Westneat (1995) examined male provisioning rates in a mixed marsh and upland population in New York. In a bivariate analysis, there was a significant negative correlation between an index of male provisioning and the number of females nesting on the territory. This relationship, however, disappeared when the index of male provisioning was examined together with other variables in a multivariate analysis. Taken together, these results indicate a need for experimental, rather than statistical, control of confounding variables, and the need to investigate the effect of asynchrony on other components of female fitness.

In this chapter, I will experimentally manipulate the degree of asynchrony between primary and secondary bigamous females. By switching eggs, I will either shorten or lengthen the incubation periods of selected females. In this way, I will create synchronous harems where both females nest approximately at the same time, and asynchronous harems where female nesting periods are staggered. By selecting the asynchronous/synchronous territories at random, I will be able to control for the confounding effects of territory quality and male quality on female reproductive success. The effect of asynchrony on secondary females will enable me to discriminate between the defence of male parental investment model and the asynchronous settlement model.

METHODS

General methods

As adjacent territories are likely to be more similar in quality than territories farther apart, I conducted the experiment using pairs of adjacent territories. To create a pair of territories (TP), I selected two territories that were (1) adjacent and (2) similar in water depth. As females in the study population appear to choose territories by their water depth (Chapter 8), matching territories by their water depth aided in reducing the variation in territory quality within each pair of territories. When several territories fulfilling these requirements were available, preference was given to territories where females were at similar stage of nesting, as that aided in the synchronizing of the females. Within a pair of territories, I randomly selected one territory and designated it as "asynchronous". The other territory was then designated as "synchronous". If more then two females were present on either territory, two females were selected at random and the remaining females were captured and removed by decoy trapping (Picman 1979). If a new female settled on a pair of territories after the removals, she was captured and removed in order to maintain the bigamous status of both territories.

Egg switches

If females on the "synchronous-designate" territories completed their clutches 0-2 days apart, their clutches were not switched between nests. Rather, I simulated the process of egg-switching by removing each clutch from the nest for 5-10 minutes and then returning it. If females on the "synchronous-designate" territories completed their clutches more than 2 days apart, I synchronized them by substituting their clutches with clutches of other females (replacement clutches) that were expected to hatch more synchronously. In most cases, enough clutches were available to enable me to select one female at random and either shorten or extend her incubation period with an equally-large replacement clutch.

On the asynchronous-designate territories, I shortened the incubation period of the primary female and extended the incubation period of the secondary females by replacing their clutches with equally-sized clutches that were expected to hatch 3-5 days earlier, or later, respectively.

After the switches, I checked the nests every 2-3 days during the incubation period, every day during the presumed hatching date of the young, and then every 2 days during the nestling period. During each visit, I recorded nest content and if nestlings were present, their relative size. Losses of eggs and losses of young were classified into categories described in Chapter 6.

Parental feeding rates and the quality of young were measured as described in Chapter 6.

Statistical analyses

To determine whether there were any systematic differences between asynchronous and synchronous territories, I compared the territories with respect to their size, water depth and initial harem size (number of resident females present at the onset of the experiment). I calculated the difference in quality between an asynchronous and a synchronous territory within each TP (difference = asynchronous - synchronous), and then compared the mean of the differences to zero using a paired-sample t-test.

As time of the season may affect female reproductive success, I examined whether there were any systematic differences between the initiation of nesting (date of first egg) of asynchronous and synchronous females. As secondary females usually nest later than primary females, I carried out the analysis separately for primary asynchronous and primary synchronous females, as well as for secondary asynchronous and secondary synchronous females. In my study, the primary/secondary status is used to reflect the relative order in which females initiate nesting (as determined from first-egg dates; in the case of a tie, one female was randomly designated as primary), and not the order in which the females originally settled. For all females, I calculated the Julian date (January 1 =day 1) of laying their first egg. For each TP, I then calculated the difference between the Julian date of the primary asynchronous female and the primary synchronous female and tested the mean of these differences against zero using a paired-sample t-test. I repeated the analysis for secondary asynchronous and secondary synchronous females.

Nesting success: I used two methods to compare nesting success of asynchronous and synchronous females. First, I calculated the difference between clutch sizes, the numbers of young hatched and the numbers of young fledged between asynchronous and synchronous females nesting in the same TP. I compared the mean of the differences to zero using a paired-sample t-test. As asynchronous and synchronous females may, despite randomization, differ in their initial clutch sizes, and as these differences may affect the analysis of their fledging success, the second method that I used compared the difference in nesting losses (number of eggs lost during incubation, number of young lost during the nestling period) between asynchronous and synchronous females within each TP. As with the previous analysis, the mean of the differences was tested using a paired-sample t-test. I classified causes of egg loss into three categories, and the causes of nestling loss into another three categories, and then examined the frequency of egg/young in each category in the same manner as the total losses. I used the signed-rank test (Lehman 1975) whenever the assumption of normality of the differences was violated.

Feeding rates: The rates were analyzed separately for 8 and 10 days old nestlings. For each parent, and also for the combined provisioning of both parents, I calculated the difference in the feeding rates between asynchronous and synchronous territories, and then tested the difference with paired-sample t-tests (or signed-rank tests where appropriate).

Quality of young: due to high nesting losses, many nests did not fledge any young or fledged young of one sex only. Consequently, there were few TPs where nestlings of the same sex could be compared between the asynchronous and synchronous territories. For this reason, I compared all the young (of the same sex) from asynchronous territories to those from synchronous territories using two-sample t-test.

The statistical analyses were carried out using SAS software (SAS Institute, Inc. 1985a,b).

RESULTS

I established 21 territory pairs (TPs), each consisting of one asynchronous and one synchronous territory. The asynchronous and synchronous territories did not differ in their size, water depth and initial harems size (Table 7.1).

Before the experiment was initiated, 44 females were present on the asynchronous-designate territories (19 x 2, 2 x 3 females) and 45 females on the synchronous-designate territories (19 x 2, 1 x 3 and 1 x 4 females). I removed 2 females from the asynchronous-designate territories and 3 females from the synchronous-designate territories in order to achieve the final arrangement of two females per each asynchronous and synchronous territory.

Primary females on the asynchronous territories initiated egg-laying on average (±1 S.D.) 0.33 ± 4.91 ($N=21$) days earlier than their primary counterparts on the synchronous territories ($t=0.31$, $P=0.76$). The secondary asynchronous females initiated their egg-laying 0.48 ± 5.05 ($N=21$) days later than their synchronous counterparts ($t=0.43$, $P=0.67$). The mean difference in the nest initiation dates of primary females did not significantly differ from the difference in the date of nest initiation of the secondary females ($t=0.53$, $P=0.60$).

Although the asynchronous/synchronous status was randomly assigned to territories, primary females on asynchronous territories laid significantly smaller clutches than primary females on synchronous territories (Table 7.2). Despite this initial difference, the primary asynchronous, as well as the secondary asynchronous females, produced a somewhat higher number of fledglings than their synchronous counterparts (Table 7.2).

Nesting losses of primary asynchronous females were significantly lower than nesting losses of primary synchronous females (Table 7.3). There were no significant differences in the nesting losses of secondary asynchronous females and secondary synchronous females (Table 7.3). The most important cause of nesting losses of primary females was starvation and predation on the young: significantly more young starved in synchronous broods than in asynchronous broods (Table 7.4), but the difference in predation on the young was not significant. In secondary females, starvation and predation on the young was also the most important cause of losses, but in neither case was the difference between asynchronous and synchronous broods significant (Table 7.4).

Males provisioned young less frequently than females (Tables 7.5 and 7.6). In primary broods, males tended to provision synchronous broods more frequently than asynchronous broods, but the difference was not significant (Tables 7.5 and 7.6). In secondary broods, males provisioned asynchronous broods more often than synchronous broods; the difference was significant for young of both ages (Table 7.6). There was no difference between asynchronous and synchronous broods in the rate of provisioning by females, either for primary females, or for secondary females (Tables 7.5 and 7.6). There was, however, a tendency for females to provision more frequently in those cases where male feeding rates were low (e.g. in secondary broods, males provisioned synchronous broods less than asynchronous broods, whereas females provisioned the synchronous broods more than asynchronous broods). This pattern can be, however, also explained by the tendency of males to provision broods where female feeding is insufficient.

As a result of the significant differences in male provisioning, the total feeding rates by both parents were significantly different between asynchronous and synchronous secondary broods, the former obtaining more food than the latter. However, despite this difference in parental feeding, 10-day-old male nestlings in asynchronous (secondary) nests were not more developed than their synchronous counterparts (Table 7.7). Female nestlings of secondary females, however, differed between asynchronous and synchronous broods in the lengths of their tibias (difference significant in a one-tailed test): the tibias of asynchronous females were approximately 4% longer than those of synchronous females (Table 7.7).

When male nestlings of primary females are compared, there was a significant difference in the body mass and the length of tibias of asynchronous and synchronous young (Table 7.8), the former having approximately 13% greater mass and 10% longer tibias than the latter. There was also a nearly significant difference in the length of ulnas between these young (Table 7.8); again, asynchronous young had approximately 10% longer ulnas than synchronous young.

There were no significant differences between asynchronous and synchronous young of either sex in the remaining characteristics, but despite the lack of statistical differences, young from asynchronous broods were generally more developed than young from synchronous broods.

DISCUSSION

Because harem size was assigned at random, the average quality of asynchronous and synchronous territories should be the same, and the average quality of males defending the territories and females nesting there should also be the same. This was confirmed by the comparison of territories with respect to their size, water depth, initial harem size, and also by the comparison of clutch-initiation dates of primary and secondary females. Taken together, these results suggest that the only systematic difference between the asynchronous and synchronous breeding situations was the different degree of nesting synchrony of the primary and secondary females.

When primary and secondary females were considered together, synchronous females suffered significantly higher losses than asynchronous females, chiefly due to the higher starvation rate of young in synchronous broods compared to asynchronous broods. There were also significant differences in the amount of male provisioning: males fed asynchronous broods more often than synchronous broods. Male and females nestlings in synchronous broods were less developed than their asynchronous counterparts, most markedly in the size of their long bones (tibias). When considered together, these results demonstrate that asynchrony between females increases several components of female reproductive success, most notably the number of young fledged and possibly their post-fledgling survival. Thus, it can be expected that fully asynchronous (i.e. monogamous) females would achieve higher fitness than fully synchronous (i.e. polygamous) females. This finding is consistent with the results of Chapter 6, and also with the results of Yasukawa et al. (1990) and Westneat (1995) as described in the Introduction.

When primary females are considered separately, the differences between asynchronous and synchronous broods point in the same direction, but are generally non-significant, compared to when primary and secondary females are considered together. Secondary asynchronous females suffered somewhat lower nesting losses than their synchronous counterparts, mainly due to starvation of the young and predation. Males provisioned synchronous broods less than asynchronous broods, and because this difference was not "compensated" by increased feeding by females, the total feeding rates at asynchronous broods were higher than at synchronous broods. This difference, however, did not translate into differential development of the young. With the exception of the length of the tibias of female nestlings, male and female nestlings in synchronous and asynchronous broods did not differ significantly in the degree of their development. Considered together, the direction of differences between synchronous and asynchronous broods points in the same direction, i.e. that there is a positive relationship between the degree of nesting asynchrony and the reproductive success of secondary females. This relationship is consistent with the asynchronous settlement model, but inconsistent with the no-cost no-benefit directed female choice hypothesis, neutral-mate-choice hypothesis, cooperative female choice hypothesis and the defence of male parental investment model (Table 4.1). However, additional evidence is required to confirm these conclusions, especially with respect to the effect of reduced male feeding rates on female provisioning and on female survival, and also on the effect of delayed development on the survival of fledglings.

Table 7.1. A comparison of asynchronous and synchronous territories with respect to their size (m^2), water depth (cm) and initial harem (females/territory). Values are means ± 1 S.D. (sample sizes are in parentheses). For each pair of territories, the value for synchronous territory was subtracted from the value for asynchronous territory. The mean of the differences was tested against zero with a paired-sample t-test (t is test statistics, P is probability).

	Asynchronous territories	Synchronous territories	Mean difference	t	P
Territory size	522±474 (21)	578±377 (21)	-56±220 (21)	-1.16	0.26
Water depth	39±40 (21)	40±22 (21)	-1±18 (21)	-0.29	0.77
Harem size	2.09±0.3 (21)	2.14±0.5 (21)	-0.05±0.6 (21)	-0.37	0.72

Table 7.2. Reproductive success of asynchronous and synchronous females. Values are means ± 1 S.D. For each pair of territories, the reproductive success of synchronous female was subtracted from the reproductive success of asynchronous female. The mean of the differences was tested against zero with a paired-sample t-test (t is test statistics, P is probability).

	Asynchronous females	Synchronous females	Mean difference	t	P
Primary females					
No. eggs	3.29 ± 0.64 (21)	3.76 ± 0.54 (21)	-0.48 ± 0.87 (21)	-2.5	0.02
No. young hatched	2.86 ± 0.96 (21)	3.05 ± 1.36 (21)	-0.19 ± 1.12 (21)	-0.78	0.45
No. young fledged	1.86 ± 1.24 (21)	1.43 ± 1.37 (21)	0.43 ± 1.75 (21)	1.12	0.27
Secondary females					
No. eggs	3.29 ± 0.46 (21)	3.14 ± 0.48 (21)	0.14 ± 0.48 (21)	1.37	0.19
No. young hatched	2.71 ± 1.10 (21)	2.10 ± 1.26 (21)	0.62 ± 1.56 (21)	1.81	0.085
No. young fledged	1.62 ± 1.20 (21)	1.14 ± 1.06 (21)	0.48 ± 1.69 (21)	1.29	0.21

Table 7.3. Number of eggs and young lost by asynchronous and synchronous females. Values are means ± 1 S.D. (sample sizes are in parentheses). For each pair of territories, the loss of synchronous female was subtracted from the loss of monogamous female. The mean of the differences was tested against zero using a paired-sample t-test (t is test statistics, P is probability).

	Asynchronous females	Synchronous females	Mean difference	t	P
Primary females					
Eggs	0.43 ± 0.75 (21)	0.71 ± 1.19 (21)	-0.29 ± 1.27 (21)	-1.03	0.32
Young	1.00 ± 1.22 (21)	1.62 ± 1.47 (21)	-0.62 ± 1.75 (21)	-1.63	0.12
Eggs and young	1.43 ± 1.21 (21)	2.33 ± 1.56 (21)	-0.90 ± 2.10 (21)	-1.98	0.06
Secondary females					
Eggs	0.57 ± 0.98 (21)	1.05 ± 1.36 (21)	-0.48 ± 1.63 (21)	-1.34	0.20
Young	1.10 ± 1.18 (21)	0.95 ± 1.16 (21)	0.14 ± 1.49 (21)	0.44	0.67
Eggs and young	1.67 ± 1.28 (21)	2.00 ± 1.26 (21)	-0.33 ± 1.68 (21)	-0.91	0.38

Table 7.4. The causes of nesting loss of asynchronous and synchronous females. Values are mean (± 1 S.D.) number of eggs/young lost per female (number of females is in parentheses). For each pair of territories, the loss of synchronous female was subtracted from the loss of monogamous female. The mean of the differences was tested against zero with a signed rank test (SR is test statistics, P is probability).

	Asynchronous females	Synchronous females	Mean difference	SR	P
Primary females					
Eggs sterile	0.29 ± 0.46 (21)	0.33 ± 0.91 (21)	-0.05 ± 0.80 (21)	0	1.0
Eggs depredated	0 ± 0 (21)	0.14 ± 0.65 (21)	-0.14 ± 0.65 (21)	-0.5	1.0
Eggs other	0.14 ± 0.65 (21)	0.14 ± 0.65 (21)	0 ± 0.95 (21)	0	1.0
Young starved	0.38 ± 0.67 (21)	1.33 ± 1.08 (21)	-0.89 ± 1.37 (18)	-2.76[1]	0.013
Young depredated	0.62 ± 1.24 (21)	0.44 ± 1.15 (21)	0.17 ± 0.86 (18)	2.5	0.75
Young other	0 ± 0 (21)	0.06 ± 0.23 (21)	-0.06 ± 0.24 (18)	-0.5	1.0
Secondary females					
Eggs sterile	0.19 ± 0.40 (21)	0.24 ± 0.54 (21)	-0.05 ± 0.74 (21)	-2	1.0
Eggs depredated	0.29 ± 0.90 (21)	0.62 ± 1.32 (21)	-0.33 ± 1.71 (21)	-4.5	0.53
Eggs other	0.10 ± 0.30 (21)	0.19 ± 0.68 (21)	-0.10 ± 0.77 (21)	-1	1.0
Young starved	0.42 ± 0.69 (18)	0.69 ± 0.87 (18)	-0.21 ± 1.19 (14)	-2.5	0.69
Young depredated	0.63 ± 1.26 (18)	0.56 ± 1.21 (18)	-0.0 ± 2.03 (14)	0	1.0
Young other	0.16 ± 0.50 (18)	0.0 ± 0.0 (18)	0.21 ± 0.58 (14)	1.5	0.5

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[1] test statistics of paired-sample t-test

Table 7.5. Male and female feeding rates of 8-day-old young on asynchronous and synchronous territories. Values are mean (± 1 S.D.) number of feeding trips/30/minutes/brood (sample sizes are in parentheses). For each pair of territories, the feeding rate on synchronous territory was subtracted from the feeding rate on asynchronous territory. The mean difference was tested against zero with a paired-sample t-test (t is test statistics, P is probability).

	Asynchronous territories	Synchronous territories	Mean difference	t	P
<u>Broods of primary females</u>					
Male	0.80±0.81 (17)	1.30±2.23 (11)	-0.19±1.95 (10)	-0.31	0.77
Female	3.62±0.75 (17)	3.13±1.84 (11)	0.33±1.55 (10)	0.68	0.52
Both	4.42±0.93 (17)	4.43±2.38 (11)	0.14±2.56 (10)	0.18	0.86
<u>Broods of secondary females</u>					
Male	2.13±3.52 (16)	0.14±0.47 (12)	1.91±3.56 (8)	10.5[1]	0.031
Female	2.94±1.99 (16)	3.64±1.30 (12)	-0.21±3.03 (8)	-0.20	0.85
Both	5.07±3.54 (16)	3.78±1.44 (12)	1.70±2.24 (8)	2.14	0.069

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[1] test statistics of signed rank test

Table 7.6. Male and female feeding rates of 10-day-old young on asynchronous and synchronous territories. Values are mean (± 1 S.D.) number of feeding trips/30/minutes/brood (sample sizes are in parentheses). For each pair of territories, the feeding rate on synchronous territory was subtracted from the feeding rate on asynchronous territory. The mean difference was tested against zero with a paired-sample t-test (t is test statistics, P is probability).

	Asynchronous territories	Synchronous territories	Mean difference	t	P
<u>Broods of primary females</u>					
Male	0.80±0.72 (17)	1.39±2.26 (11)	-0.30±2.05 (10)	-1.5[1]	0.88
Female	3.55±0.86 (17)	2.78±2.41 (11)	0.66±1.98 (10)	1.06	0.32
Both	4.35±0.99 (17)	4.18±2.95 (11)	0.37±3.08 (10)	0.38	0.72
<u>Broods of secondary females</u>					
Male	1.99±2.73 (16)	0.89±1.42 (12)	2.94±3.32 (8)	18[1]	0.0078
Female	3.12±2.76 (16)	3.89±1.40 (12)	-1.10±2.85 (8)	-1.09	0.31
Both	5.10±2.56 (16)	4.78±2.23 (12)	1.84±1.77 (8)	2.96	0.021

1 test statistics of signed rank test

Table 7.7. Morphological characteristics of female nestlings from asynchronous and synchronous broods. Values are means ± 1 S.D. (N is sample size). The means were compared with two-sample t-test (t is test statistics, P is probability). Primaries = total length of nine primaries, Back cover = length of the longest feather in the spinal tract, Tail = longest tail feather.

	Asynchronous nests	Synchronous nests	t	P
<u>Young of primary females</u>				
Mass (g)	27.5 ± 3.3	26.9 ± 2.4	0.43	0.68
Primaries (mm)	341 ± 43	316 ± 53	1.05	0.31
Back cover (mm)	19.5 ± 2.7	18.8 ± 3.3	0.50	0.62
Tail (mm)	11.3 ± 5.3	6.4 ± 5.3	1.85	0.086
Tibia (mm)	35.0 ± 1.4	34.5 ± 1.3	0.65	0.53
Ulna (mm)	27.5 ± 1.1	27.0 ± 1.4	0.87	0.40
N	9	7		
<u>Young of secondary females</u>				
Mass (g)	28.5 ± 4.1	27.3 ± 5.1	0.61	0.55
Primaries (mm)	360 ± 48	331 ± 55	1.36	0.19
Back cover (mm)	21.0 ± 3.1	19.7 ± 3.9	0.87	0.39
Tail (mm)	12.6 ± 5.9	9.6 ± 5.0	1.37	0.18
Tibia (mm)	35.3 ± 1.5	33.9 ± 2.0	1.97	0.061
Ulna (mm)	27.8 ± 1.4	26.9 ± 2.3	1.25	0.22
N	13	11		

Table 7.8. Morphological characteristics of male nestlings from asynchronous and synchronous broods. Values are means ± 1 S.D. (N is sample size). The means were compared with two-sample t-test (t is test statistics, P is probability). Primaries = total length of nine primaries, Back cover = length of the longest feather in the spinal tract, Tail = longest tail feather.

	Asynchronous nests	Synchronous nests	t	P
Young of primary females				
mass (g)	37.3 ± 2.7	33.0 ± 5.6	2.15	0.046
primaries (mm)	361 ± 32	341 ± 37	1.24	0.23
back cover (mm)	20.1 ± 3.1	19.3 ± 2.7	0.59	0.56
tail (mm)	9.5 ± 3.2	8.3 ± 4.6	0.67	0.51
tibia (mm)	38.7 ± 1.6	35.3 ± 4.2	2.39	0.029
ulna (mm)	31.4 ± 1.2	28.8 ± 4.0	1.97	0.065
N	10	9		
Young of secondary females				
mass (g)	38.8 ± 2.6	38.0 ± 5.3	0.37	0.72
primaries (mm)	366 ± 44	351 ± 38.1	0.69	0.50
back cover (mm)	21.1 ± 3.0	20.0 ± 2.3	0.80	0.47
tail (mm)	8.6 ± 5.5	7.1 ± 2.0	0.71	0.49
tibia (mm)	39.1 ± 1.2	38.2 ± 1.6	1.15	0.27
ulna (mm)	32.0 ± 1.2	31.5 ± 1.6	0.62	0.54
N	7	8		

CHAPTER 8: THE IMPORTANCE OF USING PROPER METHODS AND SPATIAL SCALE IN THE STUDY OF NEST SITE SELECTION BY FEMALE RED-WINGED BLACKBIRDS

INTRODUCTION

The knowledge about female preferences for the attributes of territory quality and male quality can provide two important insights into the mechanism by which polygyny arises. First, the presence of absence of such preferences can be used to discriminate between two categories of models - those that assume that females choose breeding situations by their quality, and those that assume that female settlement is random with respect to breeding situation quality (Table 4.1). Second, several models postulate that females evaluate both the breeding situation quality and their expected mating status, and then settle on those breeding situations where their fitness would be the highest. Models in this category include the polygyny threshold model, which is considered by many researchers to be the most plausible explanation for polygyny. A decisive test of the polygyny threshold model, as well as of other models that belong in this category, would require the experimental manipulation of those territory and male attributes that affect female choice. However, before such test can be conducted, attributes that affect female choice of breeding situations must be identified. To reliably identify such attributes, one must (1) select the proper methodology for studying female preferences, and (2) conduct the study at appropriate spatial scales (Orians & Wittenberger 1991).

Proper Methodology

The traditional method of studying female preferences has been to correlate female reproductive success with the variation in territory and male quality. When a significant correlation was found, it was inferred that females exhibit the corresponding preference for a given quality. However, this approach is potentially unreliable for at least three reasons:

First, it may fail to detect preferences. If females choose habitat by its quality, then all females should preferentially settle in the best habitat. If the best habitat is abundant, then there would be virtually no variation in the characteristics of the nest sites. Consequently, correlating this constant value with the success of the nests would yield a zero correlation coefficient, and one would falsely conclude that females lack preferences for that habitat characteristic.

Second, reproductive success may be correlated with variables that females cannot assess prior to their settlement (Searcy 1979). Consequently a significant correlation between these variables would erroneously imply a female preference for a given habitat characteristic.

Third, this traditional approach assumes that female preferences reflect current selective forces. However, due to evolutionary lag the current preferences may reflect the original rather than the current selective pressures (Futuyma 1986). For example, many North American bird species have recently expanded their ranges of distribution into novel geographic areas (or habitats) where they have become exposed to new predator communities and new predation patterns. Although the new predation patterns may significantly affect the reproductive success of those species, there may not have been enough time for natural selection to adjust habitat preferences of individuals.

The above three problems summarize the major shortcomings of inferring female preferences from their reproductive success. An alternative method that avoids these problems is to compare the pattern of female settlement to the distribution of habitat characteristics available to females at the time of their settlement. If females prefer a given characteristic, then their observed pattern of settlement should statistically deviate from the pattern expected under random settlement.

Proper Spatial Scale

Female habitat selection is a hierarchical process in which females first select the general area in which to live. Within this area they select among the available patches, and finally they choose a nest site within the selected patch. However, with few exceptions (e.g., Orians & Wittenberger 1991), previous studies have examined female habitat selection on a single spatial scale. Using a single spatial scale approach would fail to identify habitat characteristics that females select at other spatial scales. Therefore, to obtain a complete information on the habitat preferences, it is essential to perform the analyses at more than one spatial scale.

The goal of this study is to identify habitat characteristics that determine the quality of male territories and that can be experimentally manipulated. To achieve this goal, I concentrate on two spatial scales that reflect the heterogeneity among and within territories. As this study was conducted in a marsh, I examine: 1) the choice of a nesting area within the marsh, and 2) the choice of a nest site within the nesting area.

METHODS

This study was conducted in the spring and summer of 1993 and 1994 in the Ramsayville marsh and in the Beaver Lodge marsh. The Ramsayville marsh was approximately 30 ha large and was covered by a homogeneous stand of cattail (Typha sp.). The study area was located in the north-eastern corner of this marsh (Fig. 8.1), was rectangular in shape, approximately 200 m x 400 m in size, and was surrounded by a wet meadow to the north and by extensive cattail stands to the west and to the south. To the west, it was separated by a paved road from a willow (*Salix* sp.) scrubland. The Beaver Lodge marsh consisted of approximately 5 ha of cattail encircling a beaver pond. In that marsh, the study area was located on the northern shore. Along this shore, the cattail strip was approximately 200 m long and 20-30 m wide, and was bordered on one side by a deciduous thicket and on the opposite side by open water. Male territories were linearly organized along this strip and water depth in each territory varied from 0 - 70 cm.

Both study areas were divided into a grid of squares 20 m x 20 m marked in corners by 2.4 m high wooden stakes. Male territories were mapped throughout early spring, and the study areas were searched for nests weekly in May and June. Nest locations were plotted on maps of the study areas.

Nest-site characteristics

Between June 15 and 30, 1993, the following six variables were measured for all nests in the Ramsayville study area:

1) Water depth: measured to the nearest 5 cm as the vertical distance from water surface to the hard clay bottom.

2) Distance to the nearest shore: locations of all nests and the contour of the shoreline were drawn on the map of the study area. The distance of each nest to the nearest shore was measured on the map to the nearest 1 m.

3) Width of water channels within 1 m of the nest: estimated to the nearest 10 cm if the channels were narrow (< 2 m), or to the nearest 1 m if the channels were wide (> 2 m).

4) Clumping of vegetation: categorized as coarse, fine, or uniform. The cattail vegetation was coarsely clumped when large (> 1 m in diameter), well defined clumps of cattail were separated by >50 cm wide channels of open water. The vegetation was finely clumped when small (< 1 m in diameter) clumps were separated by 20-50 cm wide channels of open water. The vegetation was categorized as uniform when no clumps were apparent and there were no channels of open water.

5) Density of vegetation within 5 m of the nest: categorized as dense, medium, or sparse. In general, the vegetation was classified as dense when the observer, standing at the nest, could not see the water surface 5 m away from the nest through the surrounding cattail stalks. The vegetation was classified as sparse when the observer could readily see the water surface in all directions, and it was classified as medium when the view was partly obstructed and partly clear.

6) Density of cattail shoots: estimated for old shoots (i.e. those that had grown prior to the current growing season). I did not analyze density of new cattail shoots because those could not be directly assessed by females (they started to grow after the majority of females settled). To estimate the density, I used a 2 m long stake that was divided into 10 cm intervals. The stake was placed at the water surface and centred under the nest, and the number of cattail shoots growing within 10 cm of one

side of the stake were counted for each 10 cm interval. The stake was then placed perpendicularly to its original position and the shoots were counted as above. The individual counts in 10 cm x 10 cm quadrats thus measured the density of cattail shoots at various distances from the nest.

In addition to nests, I measured the above six characteristics for 231 sampling points. The points were uniformly distributed throughout the Ramsayville study area and their distribution paralleled that of the grid stakes (Fig. 5.1). The sampling points were systematically placed 1.5 m north-west of the grid stakes.

Water depth and location of nests in the Beaver Lodge study area were determined in the same way as in the Ramsayville marsh.

Statistical Analyses

I analyzed female preferences on two spatial scales. First, I examined female choice of a nesting area (defined as a circle of 1-5 m in diameter, depending on the particular characteristic) within a marsh. Second, I examined female choice of a nest site (defined as a circle 20 cm in diameter) within a nesting area.

Female preferences within the marsh

The preferences were analyzed for six habitat characteristics: water depth, distance to the nearest shore, width of water channels, vegetation clumping, vegetation density, and the density of cattail shoots. The density of cattail shoots was calculated by dividing their total number (within 10 cm of both transects) by the total area of the transects (excluding areas covered by water channels). Using vegetation clumping as an example, I will demonstrate how the female preferences were established. First, I established the observed distribution by counting the number of nests located in sparse vegetation, medium vegetation and dense vegetation. Second, I established the expected distribution as follows: I counted the number of sampling points located in sparse, medium and dense vegetation, and then calculated the total area for each vegetation density by multiplying the total number of counts by 400 m^2 (the area of a 20 m x 20 m quadrat). However, as some quadrats extended into open water areas, I adjusted their size to reflect the actual area of the cattail cover by subtracting the area of open water (estimated to the nearest 100 m^2) from the quadrat area. Third, I compared the observed and expected distributions using a chi-square goodness-of-fit (Zar 1984). If the two distributions deviated significantly, I concluded that female settlement was non-random, and examined the pattern of the deviations to establish the direction of preference.

This procedure analysed female preferences with respect to individual habitat characteristics. However, the univariate analyses cannot establish which of the characteristics are actually chosen by females and which ones appear to be chosen due to their covariation with the actually selected characteristics. To examine the relationships among the characteristics, I used the Spearman rank correlation (Zar 1984). Finally, to establish the relative importance of individual characteristics in female preferences, I examined the effect of all six habitat characteristics on nest density (No. nests/20 m x 20 m quadrat centred on a grid stake) using logistic regression. The nest density was used as an index of female preference for the given area. In the logistic regression, nest density was treated as the dependent variable and the habitat characteristics as the independent variables. The analysis was carried out using PROC LOGISTIC in Statistical Analysis Systems (SAS Institute, Inc. 1985).

Since the logistic regression indicated that water depth was the most important predictor of nest density, I examined the shape of the relationship between the two variables by fitting the logistic regression of the form

$$\text{DENSITY} = a/(1 + b*\underline{e}\hat{}(c*\text{DEPTH}))$$

to the data using PROC NLIN in SAS (op. cit.). In the equation, $\underline{e}$ was the base of natural logarithmus ($\underline{e}=2.718$), a,b,c were the parameters, DEPTH was the water depth and DENSITY was the mean density for all quadrats located in a given water depth interval. To increase the accuracy of this analysis, I combined data on the nest density for four years (1989, 1990, 1993 and 1994).

To establish whether females chose deep water areas within individual male territories, I examined the distribution of nests in the Beaver Lodge study area in 1993 and 1994. I chose this study area because water depth within all territories varied from 0 - 70 cm, as compared to the Ramsayville study area, where the variation within territories was small. I mapped the boundaries of all male territories and then measured their water depth (as described above) at 5 m intervals along transects spaced 5 m apart. These measurements were plotted on a map and isoclines of water depth (at 10 cm increments) were established. For each water depth increment, I measured the area of all territories from the map and counted the number of nests present there. The frequency of nests in the water depth increments was the observed distribution. To obtain the expected distribution, I partitioned the total number of nests among the water depth increments according to the area of territories located within the increments. The two distributions were compared by chi-square goodness of fit (Zar 1984). To satisfy assumptions of this analysis with regard to the expected values, I combined the water depth increments into four categories: 0-19 cm, 20-39 cm, 40-59 cm, and 60-70 cm.

Female preferences within a nesting area

The preferences were examined for the density of cattail shoots at the Ramsayville marsh in 1993. I did not analyse the other five characteristics at this spatial scale because there was little biologically meaningful variation (e.g. within a nesting area, water depth varied by less than 1 cm). In contrast to previous analyses, the density of cattail shoots was expressed as the number of shoots in a 10 cm x 10 cm quadrat. The quadrats were located at various distances (0-10, 10-20, ... 90-100 cm) from either the nest or the sampling point. Since I obtained the densities in four directions from the nest/sampling point, the final value for each distance category was calculated as the mean of the four measurements.

My goal was to address the following questions: 1) Are nests constructed in vegetation that is sparser or denser than would be expected for randomly selected nest sites?; and 2) are nests surrounded by vegetation that is sparser or denser than would be expected for randomly selected sites? To answer the first question, I conducted two analyses. In the first analysis, the mean density of cattail stalks for all nests was calculated for quadrats 0-10, 10-20, ... 90-100 cm, and the means were compared by the Analysis of Variance (PROC GLM in SAS). The differences between means were then tested by Tukey's range test. In the second analysis, I repeated the above calculations for sampling points. For each distance category, I then compared the mean for the sampling points to the corresponding mean for the nests with a t-test.

To answer the second question, I used results of the previous analyses. In those analyses I found that females built their nests in clumps that are denser than would be expected for randomly selected sites. The dense clumps extended 20 cm from the centre of the nest, and the modal number was 11 cattail shoots per 400 cm^2 (four 10 cm x 10 cm quadrats centered on nest). I used this information to locate clumps of the same size and shoot density within the sampling points. As each sampling point consisted of two 2-m-long transects, I searched each transect for four adjacent 10 cm x 10 cm quadrats that contained a total of 11 shoots. When such a set of quadrats was found, I examined density of the shoots in both directions along the transect in relation to their distance from the set. When two or more sets were found along a single transect, I selected the one nearest to the centre of the transect. When the selected set was located off the centre, I examined the shoot density along the entire short side of the transect, but only within 80 cm of the set along the long side of the transect. I then calculated the density of cattail shoots as a function of their distance from the set. Where counts were available for a given distance for both sides of the transect, I averaged the two values. Where only one count was available, I used that count directly.

This calculation was performed for all transects, and the mean shoot count for each distance was calculated. The means for the sampling transects were then compared to their corresponding means obtained for the nests (as described above) by *t*-test.

All tests are two-tailed unless mentioned otherwise.

RESULTS

I] Selection of a Nesting Area Within a Marsh

I measured six habitat characteristics (water depth, distance to shore, width of water channels, vegetation clumping, vegetation density, density of cattail shoots) for 88 nests and 231 sampling points. The sampling points represented 8.638 ha of the marsh. In the first part of my analyses, I established female preferences for the individual habitat characteristics; in the second part, I established if the characteristics are inter-correlated; and in the third part, I evaluated their relative importance.

1. Do females settle at random with respect to habitat characteristics ?

Water depth: The majority (86.4 %) of all redwing nests were located in areas with water depth greater than 60 cm, 13.6 % of the nests in water 30-60 cm deep, and no nests were located in shallow (< 30 cm) water (Fig. 8.2). This distribution of nests along the water depth gradient contrasted with the availability of potential nesting areas: 39.8% of the marsh had water depth greater than 60 cm, 46.9% had water 30-60 cm deep and 13.3% had shallow (<30 cm) water (Fig. 8.2). The distribution of nesting areas along the water depth gradient significantly differed from the distribution of available sites (chi square=88.7, df=9, P<0.0001). This result demonstrates that females do not settle at random with respect to water depth, but that they strongly prefer deep water areas of the marsh to shallow water areas (Fig. 8.2).

Distance to the nearest shore: Relative to the availability of nesting areas, fewer nests were located within 80 m and farther than 120 m from the shore. However, a disproportionately large number of nests were located 80-120 m from the shore (Fig. 8.3). The distribution of nests and the distribution of the potential nesting sites were significantly different (chi square=61.2, df=10, P<0.0001). This indicates that female redwings prefer sites at the intermediate distance from the shore (Fig. 8.3).

Width of water channels: Most nests (58.3 %) were constructed near channels wider than 100 cm, whereas only 2.8 % nests were constructed in cattail stands without open water (Fig. 8.4). In contrast, sampling points near wide water channels were far less common than sampling sites without channels (Fig. 8.4). This indicates strong female preference for areas near open-water channels (chi square = 77.4, df = 4, $P<0.00001$).

Index of vegetation clumping: Although approximately equal areas of the marsh were covered by coarsely clumped, finely clumped, and uniform cattail, the majority (85.2 %) of nests were located in the coarsely clumped vegetation (Fig. 8.5). This female preference for the coarsely clumped vegetation is statistically highly significant (chi square = 91.8, df = 2, $P<0.0001$).

Vegetation density: Despite the fact that similar areas of the marsh were covered with sparse, medium, and dense cattail (Fig. 8.6), 81.8 % of nests were located in sparse vegetation (Fig. 6). The female preference for nest sites in sparse vegetation was highly significant (chi square = 94.1, df = 2, $P<0.0001$).

Density of cattail shoots: The frequency of occurrence of redwing nests at sites with different shoot counts did not significantly differ from the availability of such areas (Fig. 8.7; chi square = 14.3, df = 8, $P = 0.075$). Thus, the density of shoots in the nesting area was not associated with redwing nest site selection.

In conclusion, the analyses show that female redwings settled non-randomly with respect to five of the six habitat characteristics that I examined. This would seem to suggest that female choice of nesting areas is based on each of the five characteristics. However, if these characteristics were intercorrelated, the actual choice could be based on fewer than five or perhaps even on a single characteristic.

2. Are the habitat characteristics intercorrelated?

I correlated each habitat characteristic with the other five characteristics. Four of these characteristics were mutually intercorrelated. There was a highly significant positive correlation between water depth and distance to shore, clumping of vegetation, and width of water channels, and a negative correlation between water depth and vegetation density (Table 8.1). Thus, as distance from the shore increased, water became deeper, vegetation more dense and clumped, and water channels became wider. The density of cattail shoots was significantly correlated with some characteristics but not with others (Table 8.1). The strong intercorrelations between most variables make it to difficult to establish which of the characteristics females actually select.

3. Which characteristics do females prefer?

To determine which characteristics are actually selected by females, I related nest density to all six habitat characteristics using a logistic regression. In the regression, water depth was the only characteristic significantly related to the nest density (Table 8.2); as water depth increased, the density of redwing nests also increased. Other characteristics did not enter the regression, indicating that water depth was the only important predictor of nest density. Hence, I conclude that the apparent non-random distribution of nests with respect to five characteristics (distance to shore, width of water channels, clumping and density of vegetation) was likely caused by their covariation with water depth (Table 8.1, 8.2).

To examine whether females exhibit the same preference for the deep water areas in different years, I computed nesting densities in the same set of quadrats for four years and then correlated the densities between years. The densities were significantly correlated for all six combinations of the four years (Table III). Thus, some quadrats always had high density of nests while others had always low density of nests. These correlations demonstrated that the female preference for deep water was consistent among years.

Using the combined data for the four years, I plotted the relationship between nest density and water depth (Fig. 8.8). In general, the density was very low in the shallow (0-50 cm) water areas, sharply increased between 55-65 cm, and remained generally high throughout the deep water (65-100 cm) areas (Fig. 8.8). The equation that relates the nest density to water depth was:

$$\text{DENSITY} = 0.685/(1 + 4521609*\underline{e}\hat{}(-0.263*\text{DEPTH}))$$

The inflection point of the equation is 58 cm. The inflection point suggests that the threshold water depth that separates the deep water areas (preferred by females) from the shallow water areas is approximately 60 cm.

I also related nest density to the habitat characteristics separately for the shallow (less than 60 cm) water and deep (more than 60 cm) water areas. None of the habitat characteristics, including the water depth, were significantly related to the nest density in either the shallow or the deep water areas (Table II). This strengthens my earlier conclusion that, within the whole marsh, female redwings exhibit preference only between the shallow (<60 cm) and deep (>60 cm) areas.

Female selection of nesting areas in the whole marsh could be affected not only by the habitat characteristics of the available sites, but also by the quality of males defending those areas (i.e. males defending territories in deep water areas could be of higher quality than those defending territories in shallow water). To establish whether females continue selecting nesting areas in deep water when the quality of males is controlled, I examined the distribution of nests within 11 male territories at the Beaver Lodge marsh. In this marsh, all territories extended from the dry land to water 70 cm deep. Within the territories, disproportionally more redwing nests were located in the deep water sections, while fewer nests than expected were located in the shallow water sections (Fig. 9; chi square=36.4, df=3, P<0.001). Therefore, I conclude that female preference for deep water areas remains strong when the possible effects of male quality are controlled.

II] Selection of a Nest Site Within a Nesting Area

At this spatial level, I examined whether females consider the density of cattail shoots when selecting the location for their nests within a nesting area. I asked the following questions: 1) Do females locate their nests in denser or sparser clumps of cattail than would be expected if they settled at random?; and

2) Is vegetation surrounding nests denser or sparser than would be expected for vegetation surrounding randomly selected nest sites?

1. Density of cattail shoots at nests

The density of cattail shoots significantly varied with their distance from a redwing nest (one-way ANOVA, F=108.1, df=9;869, P<0.0001). The density was the highest under the nest, declined throughout the first 40 cm and then remained low thereafter (Fig. 8.10). This result suggests that redwing nests are constructed in dense clumps of cattail. However, an alternative explanation is that the nests are located in clumps of average density which are surrounded by unusually sparse vegetation. To test these explanations, I compared the density of shoots at various distances from redwing nests to the densities at corresponding distances from randomly selected sampling points. The densities at 0-20 cm were significantly greater at nests than at sampling points (for each distance, the densities were compared with a two-sample t-test; both tests df=87;230 and $P<0.005$; Fig.8.10). In contrast, the densities at 30-100 cm distances were significantly lower at nests than at the sampling points (all df=87;230; all $P<0.005$; Fig.8.10). These results confirm my initial finding that redwings construct their nests in unusually dense clumps of cattail.

2. <u>Density of cattail shoots around nests</u>

In the previous analysis, we found that vegetation at 30-100 cm from redwing nests is less dense than is the average for the marsh. This suggests that female redwings choose nest sites that are surrounded by vegetation that is sparser than usual. However, an alternative explanation is that dense clumps of cattail are always surrounded by sparse vegetation. Females do not actively choose the sparse vegetation, but rather the sparse vegetation is a consequence of their preference for dense clumps. To test these two explanations, I first located clumps of similar density in the marsh, measured the density of the surrounding vegetation, and then compared those measurements to the corresponding measurements obtained for the redwing nests. I found that the density of cattail shoots was significantly lower at the nests than at the sampling points for the 20-30 cm distance (t-test, df=18;87; t=-3.24; P=0.0016), for the 30-40 cm distance (df=17;83; t=-2.17; P=0.02), and for the

40-50 cm distance (df=17;80; t=-3.81; P=0.0002; Fig. 8.11). For the remaining distances, the density at nests was lower than the density at sampling points, but the differences were not significant (Fig. 8.11; for the 50-60 cm distance df=13;82; t=-1.58 and P=0.12; for the 60-70 cm distance df=10;83; t=-0.76 and P=0.45; for the 70-80 cm distance df=13;82; t=-1.57 and P=0.12; for the 80-90 cm distance df=15;81; t=-0.73 and P=0.47; for the 90-100 cm distance df=18;75; t=-1.63 and P=0.11). This implies that female redwings do select cattail clumps that are surrounded in their immediate vicinity by unusually sparse vegetation.

DISCUSSION

I analyzed female preferences on two spatial scales. First, I examined female selection of nesting areas within a marsh. Second, I examined female selection of nest sites within the nesting areas. Within the marsh, females based their choice of nesting areas on water depth, but not on the distance to the nearest shore or on the physical features of the cattail cover. However, the intensity of female preference (as measured by the density of their nests) did not increase proportionally with water depth. Rather, the density was higher in the deep water (> 60 cm) section of the marsh than in the shallow water section. Within those sections, the density of nests was independent of water depth. This indicates that the intensity of female preference has a "threshold" shape: females prefer deep water areas to shallow water areas, and their preference within those areas is independent of water depth. However, females should exhibit this "threshold" response only in marshes (such as mine) where a large proportion of the marsh exceeds the threshold water depth. In shallow marshes, the shape of the preference function should follow a different pattern. In such marshes, females should always prefer to nest in the deepest portion of the marsh, regardless of its actual depth. However, this preference may not always be obvious because the actual pattern of female settlement in marshes is determined not only by their preference for water depth, but also by various other factors, such as the availability of the most preferred areas, the role of female-female interactions in population dynamics, and by female preferences for other habitat and male characteristics.

I propose that female preference for deep water areas reflects the pattern of predation within the marsh. In the study area, Picman et al. (1993) found that predation was significantly higher in the shallow water areas (82% of experimental nests depredated) than that in the deep water areas (65% nests depredated). Based on this evidence, I propose that female redwings preferred the deep water areas because they were safer for nesting. I propose that the threshold pattern of nest density is related to the composition of the local predator community. In the shallow water areas, 88% of the predation was caused by raccoons (*Procyon lotor*) and long-tailed weasels (*Mustela frenata*) (Picman et al. 1993). I believe that those predators can effectively search the entire shallow water areas up to the threshold water depth of 60 cm, and, as a result, female redwings avoid those areas. In the deep water areas, 95% of predation was caused by marsh wrens (Picman et al. 1993). As marsh wrens in the marsh occur throughout the deep water area, female redwings cannot avoid them by spatially segregating along the water depth gradient. Hence, within the deep water, the density of redwing nests is independent of water depth.

Although I delimited the shallow water area by the 60 cm water depth, I measured the water depth to the hard clay bottom. The range of water depths within which the terrestrial predator can operate is presumably determined not by the depth of the hard clay bottom, but by the depth of the cattail root system and by the width of water channels that separate neighbouring cattail islands. In my case, the 60 cm distance from the water surface to the hard clay bottom actually corresponded to approximately 30 cm of water column above the cattail roots, which may, therefore, represent the maximum water depth within which these terrestrial predators can operate.

I also examined female preferences of nest sites within nesting areas. Within the nesting areas, females preferentially built nests in dense clumps of cattail shoots that were surrounded by unusually sparse vegetation. I propose that females chose the dense clumps to attain adequate support for their nests and to conceal their nests from predators, and that they selected the sparse surrounding vegetation to facilitate their detection of predators approaching the nest.

This study is the only study on red-winged blackbirds that examines female selection of habitat characteristics (cattail vegetation) by comparing the characteristics of available nesting sites to those actually selected by females. Several other studies inferred female preferences from the correlations of female reproductive success with the variation in selected habitat characteristics. The main findings of those studies with respect to the characteristics that we examined are summarized in Table 8.4. Generally, female nesting success (i.e. the proportion of nests fledging at least one young) was related to two variables: the number of stems supporting the nest, and the cattail density on the territory (Table 8.4). One characteristic (the distance to shore) did not have any effect on the nesting success, and the effect of the remaining three characteristics varied between study areas or between years (Table 8.4). With the exception of Lenington (1980), these studies examined only one component of fitness, the nesting success. Lenington (1980) also related habitat characteristics to fledging success (the number of young fledged from successful nests). Her analyses indicated that three characteristics that were correlated with nesting success (water depth, the number of stems supporting nest, cattail density on territory; Table 8.4) were not correlated with fledging success. In contrast, one characteristic that was correlated with fledging success (amount of cattail edge) was not correlated with nesting success. Lenington's study demonstrates that the examination of different fitness components may yield different conclusions about the nature of female preferences.

The Importance of Using Proper Methodology

The traditional approach of inferring female preferences from correlations between reproductive success and habitat characteristics has three shortcomings. First, it may fail to detect preferences due to the limited variation in selected habitat characteristics. Second, it may detect false preferences when females cannot predict variation in habitat characteristics at the time of their settlement. Third, due to evolutionary lag, females may not have had enough time to evolve preferences that would reflect the current selective pressures.

The first problem can be illustrated by comparing the results of my study to those of Milks and Picman (1994). Milks and Picman examined the effect of water depth on female nesting success in the Ramsayville marsh several years prior to my study. They found that water depth was not related to nesting success in either of the three years of the study. This was true when water depth was related to the nesting success in both the univariate and multivariate analyses. One possible explanation for the difference in Milks and Picman (1994) and my results is that the two studies were conducted in different years. However, the lack of a relationship between water depth and nesting success reported by Milks and Picman (1994) was consistent for all three years of their study. Similarly, the results of the present study were consistent for the four years under consideration. This suggests that the differences between the two studies are not due to different conditions between years. The most likely explanation is that the differences are due to different approaches in studying female preferences. In my study, female redwings strongly preferred deep water areas for their nesting, and, consequently, the majority of them constructed their nests there. As a result, the nests were not distributed throughout the entire range of the water depth gradient, but were concentrated only at one end of the range. This narrow range of water depth reduced the chances that Milks and Picman (1994) would detect a significant correlation between the water depth and the nesting success. In contrast, in my study, I considered the entire range of the water depth gradient, and this could explain why I detected female preference for water depth.

The Importance of Using Proper Spatial Scale

One habitat characteristic, the density of cattail shoots, illustrates the importance of using a proper spatial scale. The examination of this characteristic at the broad scale (choice of nesting areas within a marsh) failed to detect female preference for this characteristic. In contrast, the examination at the narrow scale detected strong female preference. Females chose sites located in dense patches that were surrounded by sparse vegetation. The inconsistency between the results of the two analyses are evidently caused by the fact that the variation in female preference at the narrow scale was averaged out when examined at the broad scale. Specifically, at the broad scale, dense vegetation at the nest was combined with the sparse vegetation around the nest, thereby yielding vegetation of average density that was not different from the average density in the marsh. Therefore, if I were to conduct the study at the broad scale only, I would have failed to recognize the importance of cattail density in female nest site selection.

Several other studies have correlated female nesting success with cattail density ("Nest visibility" in Table 8.4). In those studies, the density was estimated as the visibility through the cattail vegetation standing between the nest and the observer positioned 1-2 m away. Three of these studies found no correlation between the nest visibility and nesting success, implying that females exhibit no preferences for cattail density. An alternative explanation for those findings is that the role of vegetation density was examined at an inappropriate scale. Since those studies measured the cattail density by combining the dense vegetation at nests with the sparse vegetation around the nests, they may have failed to detect the preferences for the same reason as I did at the broad scale.

The results of this study have several implications for explaining the occurrence of polygyny in the marsh-nesting red-winged blackbirds. First, my finding that females settle non-randomly with respect to water depth contradicts all hypotheses that assume random female settlement with respect to habitat characteristics (Table 4.1), particularly the neutral-mate-choice hypothesis, the true null model and the asynchronous settlement model. Second, my study identified habitat characteristics that can be experimentally manipulated and hence used to test the polygyny threshold model and the sexy son hypothesis. According to those hypotheses, polygyny occurs when the quality of breeding situations exceeds the polygyny threshold, i.e. females could achieve higher reproductive success when polygamously mated on good quality territories than they could when monogamously mated on poor quality territories (Orians 1969). Therefore, if territory quality is increased above the polygyny threshold, such territories should attract two or more females. This prediction can be tested by offering females a choice between two adjacent territories, one where the territory quality is experimentally increased, and one where the quality is experimentally reduced. In my study, I identified two habitat characteristics that affect territory quality, namely water depth and cattail density. Cattail density could be effectively manipulated on territories that are centred on small patches of cattail. Water depth could be most effectively controlled in territories that are arranged along a linear stretch of cattail growing around a small stream. By damming the stream at selected locations, one could create territories with deep water (=high quality) and shallow water (=low quality). The pattern of female settlement, and the resulting level of polygyny, on the low quality and high quality territories would then present a powerful test of the two hypotheses.

Table 8.1. Spearman rank correlations between seven habitat characteristics. The correlation coefficient is above the probability level. N=231 sampling sites.

	Width of water channels	Density of cattail shoots	Vegetation density	Vegetation clumping	Distance to nearest shore
Water depth	0.686 <0.0001	-0.098 0.14	-0.511 <0.0001	0.660 <0.0001	0.737 <0.0001
Distance to nearest shore	0.620 <0.0001	-0.051 0.44	-0.519 <0.0001	0.658 <0.0001	
Vegetation clumping	0.728 <0.0001	-0.142 0.031	-0.642 <0.0001		
Vegetation density	-0.686 <0.0001	0.343 <0.0001			
Density of cattail shoots	-0.177 0.007				

Table 8.2. The relationship between nest density and various characteristics of the marsh. Nest density was entered into a logistic regression as the dependent variable, characteristics of the marsh as the independent variables. P = probability. Sample sizes: N = 231 for all water depths; N = 141 for depths 0-59 cm; N = 89 for depths 60-99 cm.

	Water depth [cm]					
	0-99		0-59		60-9	
Variable	Parameter estimate	P	Parameter estimate	P	Parameter estimate	P
Water depth	0.059	<0.0001	0.06	0.11	0.02	0.24
Distance to shore	-0.005	0.19	0.01	0.51	-0.008	0.06
Width of channels	-0.0015	0.03	0.001	0.84	-0.001	0.08
Vegetation clumping	0.32	0.28	-0.18	0.74	0.38	0.36
Vegetation density	-0.17	0.55	0.03	0.96	-0.06	0.88
Density of shoots	0.03	0.02	0.04	0.12	0.02	0.14

Table 8.3. Between-year correlations of nest density across the water depth gradient. The water depth gradient was divided into twenty increments, each 5 cm wide. The nest density in the increments observed in one year was correlated with Spearman rank correlation to the density observed in another year. Sample size was 20 for all correlations. All coefficients were statistically highly significant (P<0.0001).

	Year		
Year	1994	1993	1990
1989	0.889	0.825	0.884
1990	0.917	0.888	-
1993	0.901	-	-

Table 8.4. The number of studies (references in brackets) that have reported positive, negative, and no relationship between nesting success and habitat characteristics examined in the present study.

Characteristic	Positive relationship		Negative relationship		No relationship	
Water depth	3	(1,2,6)	-		1	(3)
Distance to shore	-		-		2	(2,3)
Number of stems supporting nest	1	(2)	-		-	
Nest visibility	3	(4*,5,6)	-		3	(2,3,4*)
Vegetation density within 5 m	-		1	(4**)	1	(4**)
Cattail density on territory	1	(2)	-		-	

1 Goddard & Board (1967); 2 Lenington (1980); 3 Milks & Picman (1994); 4 Picman (1980a,b); 5 Ritschel (1985); 6 Weatherhead & Robertson (1977).

* Positive relationship in 1 year of study, no relationship in 2 years

** Negative relationship in 1 year, no relationship in 1 year

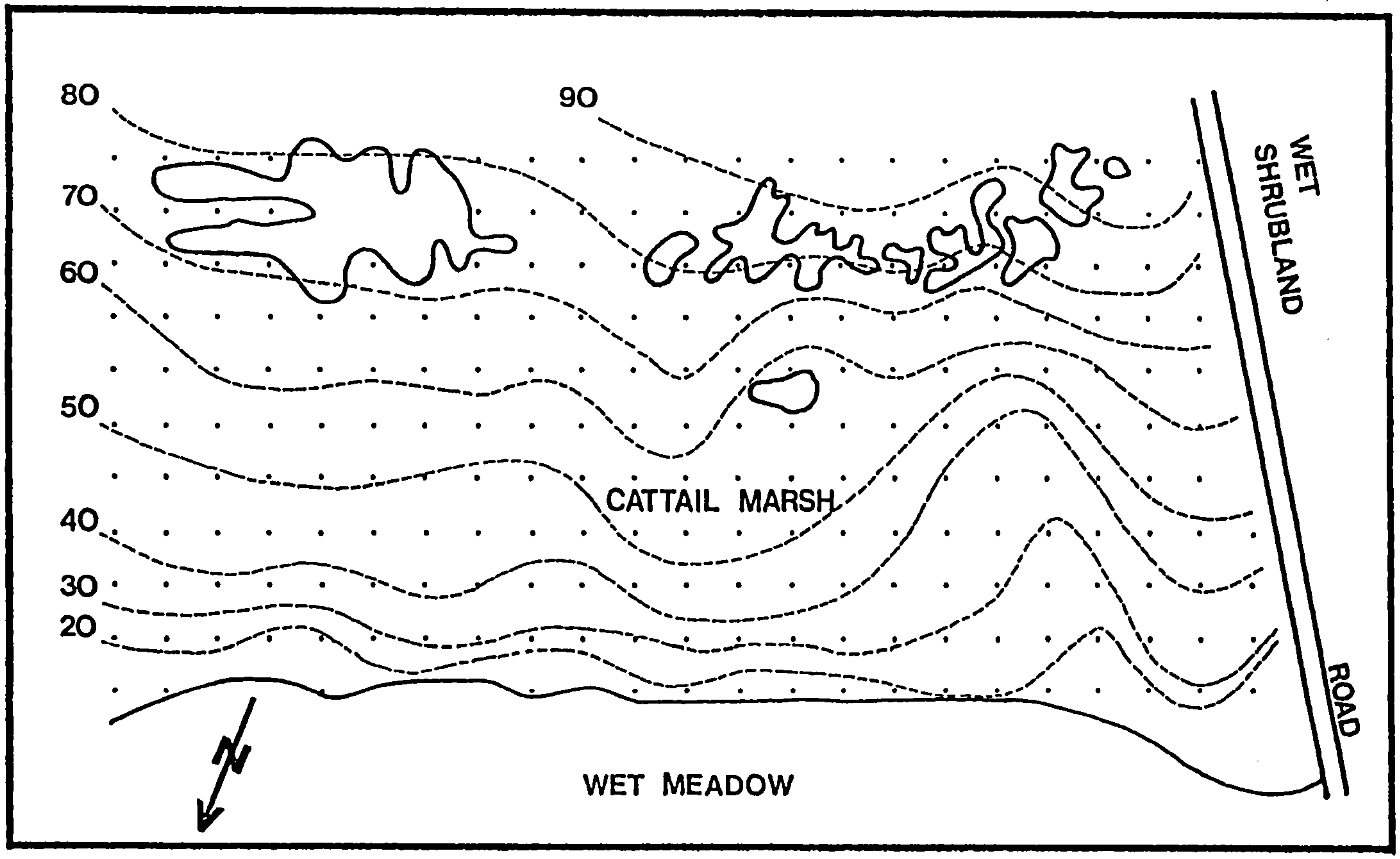

Figure 8.1. Map of the study area at the Ramsayville marsh. Water depth [cm] isoclines are indicated by dashed lines. Edge of the cattail vegetation and the areas of open water are shown by solid lines. The uniformly distributed dots are 20 m apart and indicate location of the sampling points.

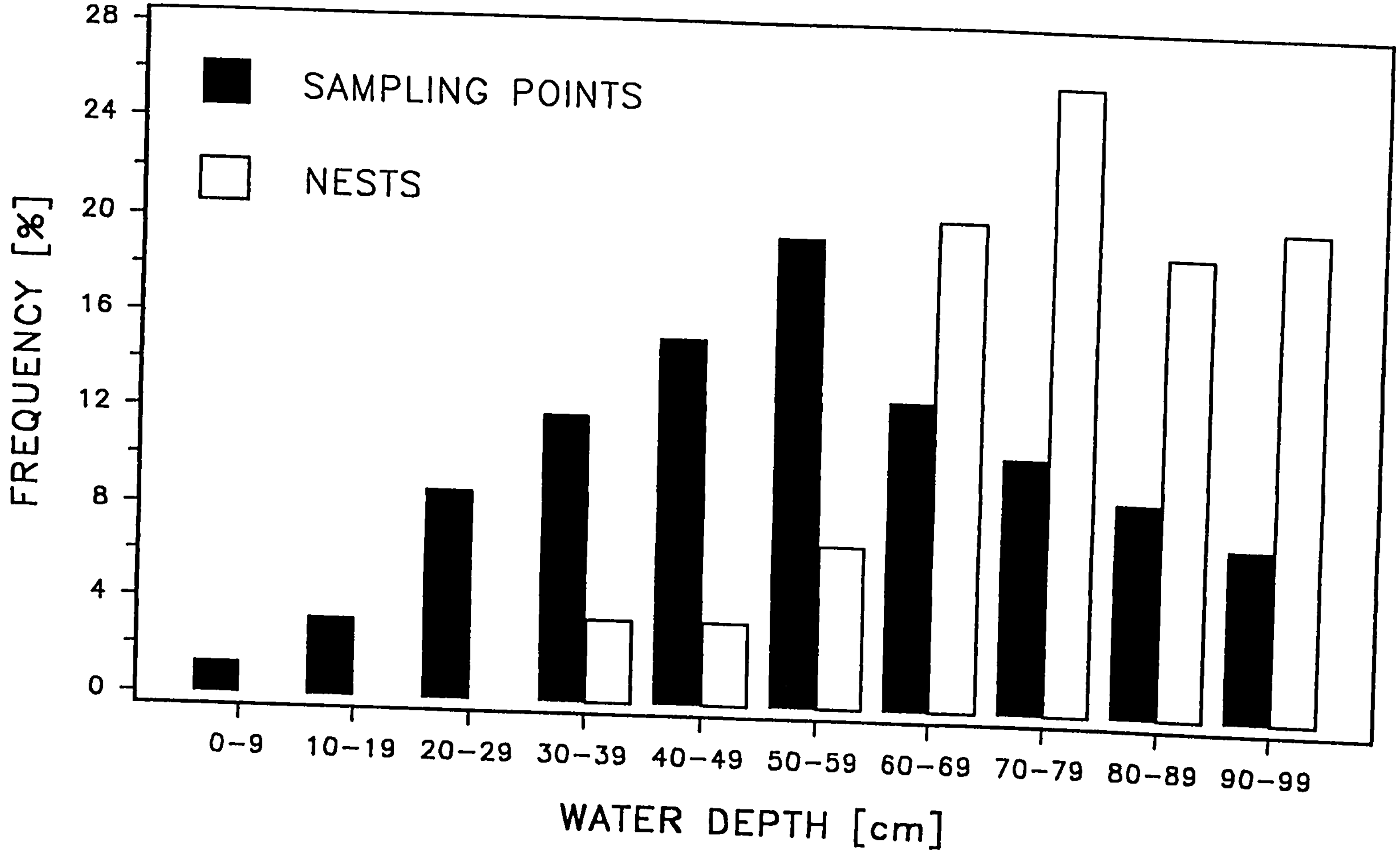

Figure 8.2. Frequency distributions of redwing nests and sampling points with respect to water depth.

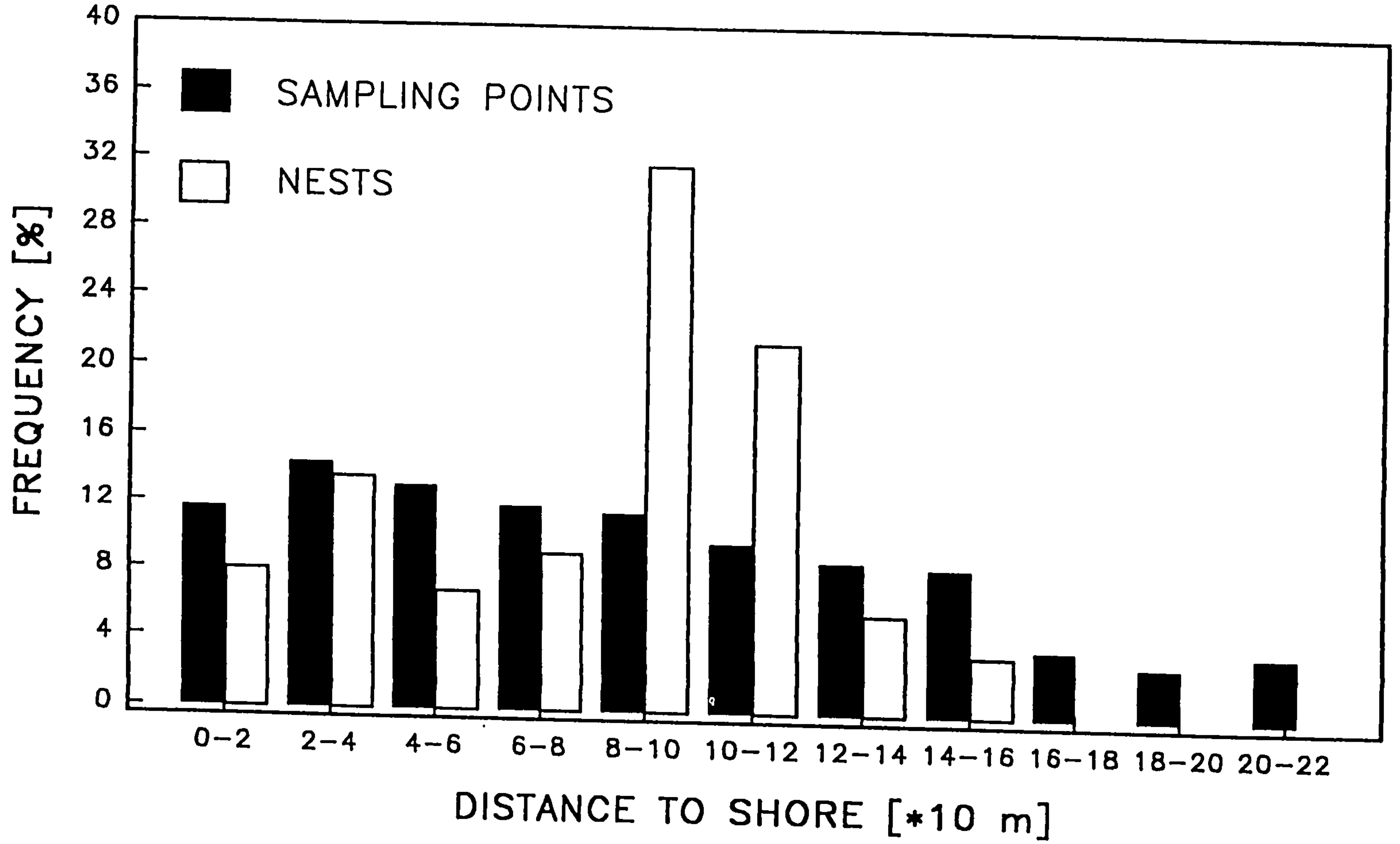

Figure 8.3. Frequency distributions of redwing nests and sampling points with respect to their distance to the nearest shore.

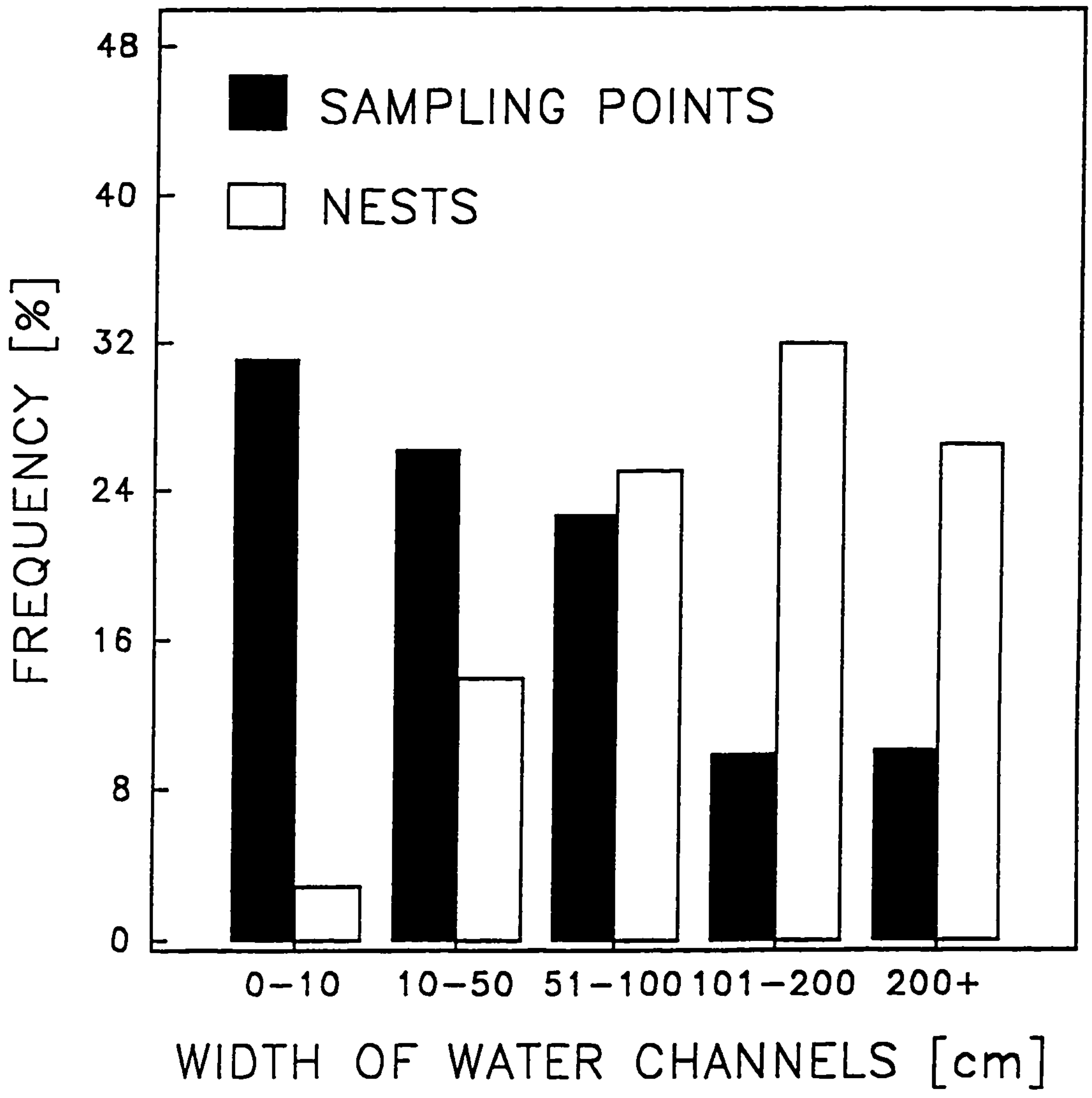

Figure 8.4. Frequency distributions of redwing nests and sampling points with respect to the width of water channels.

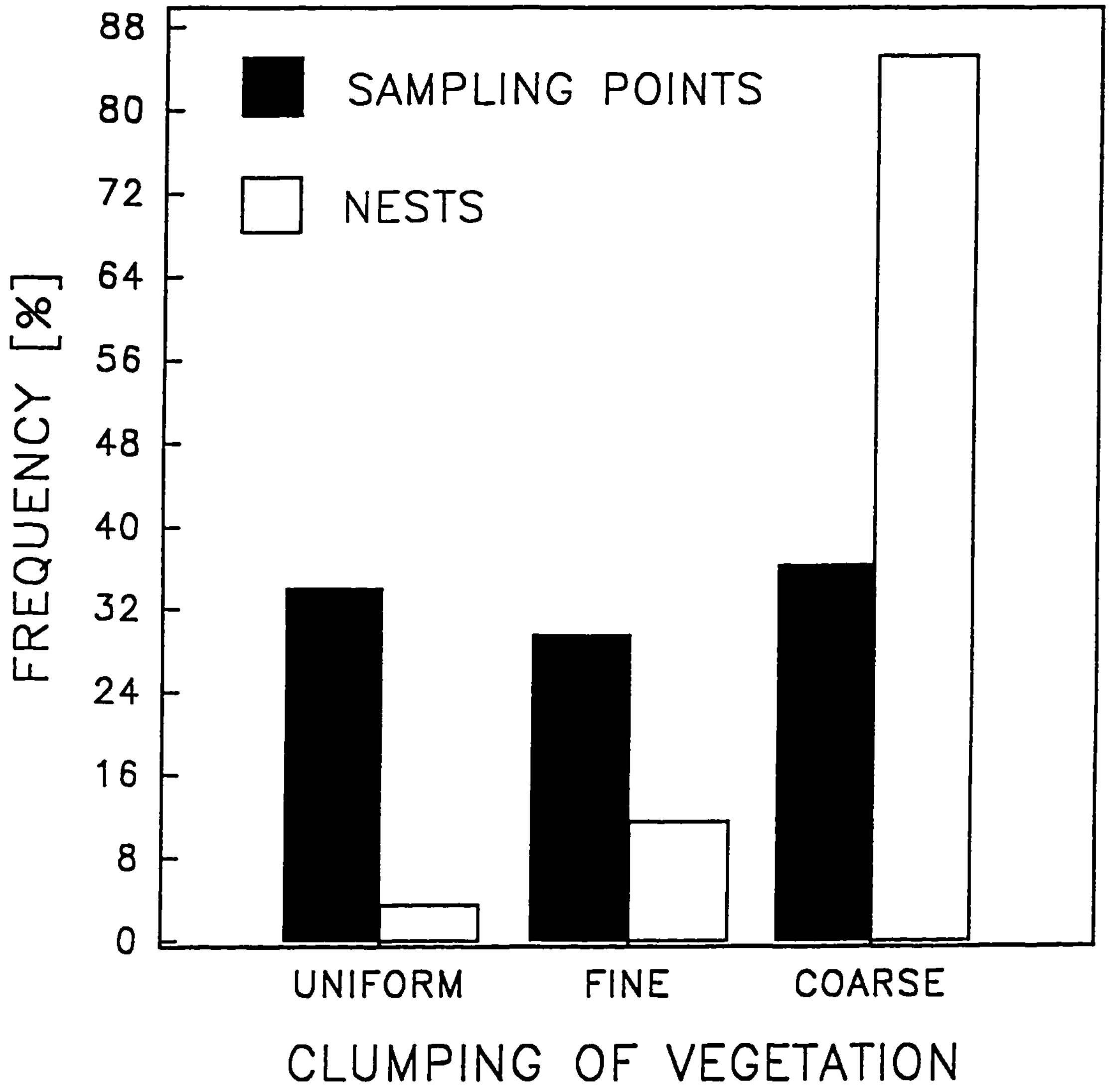

Figure 8.5. Frequency distributions of redwing nests and sampling points with respect to the degree of clumping of cattail vegetation.

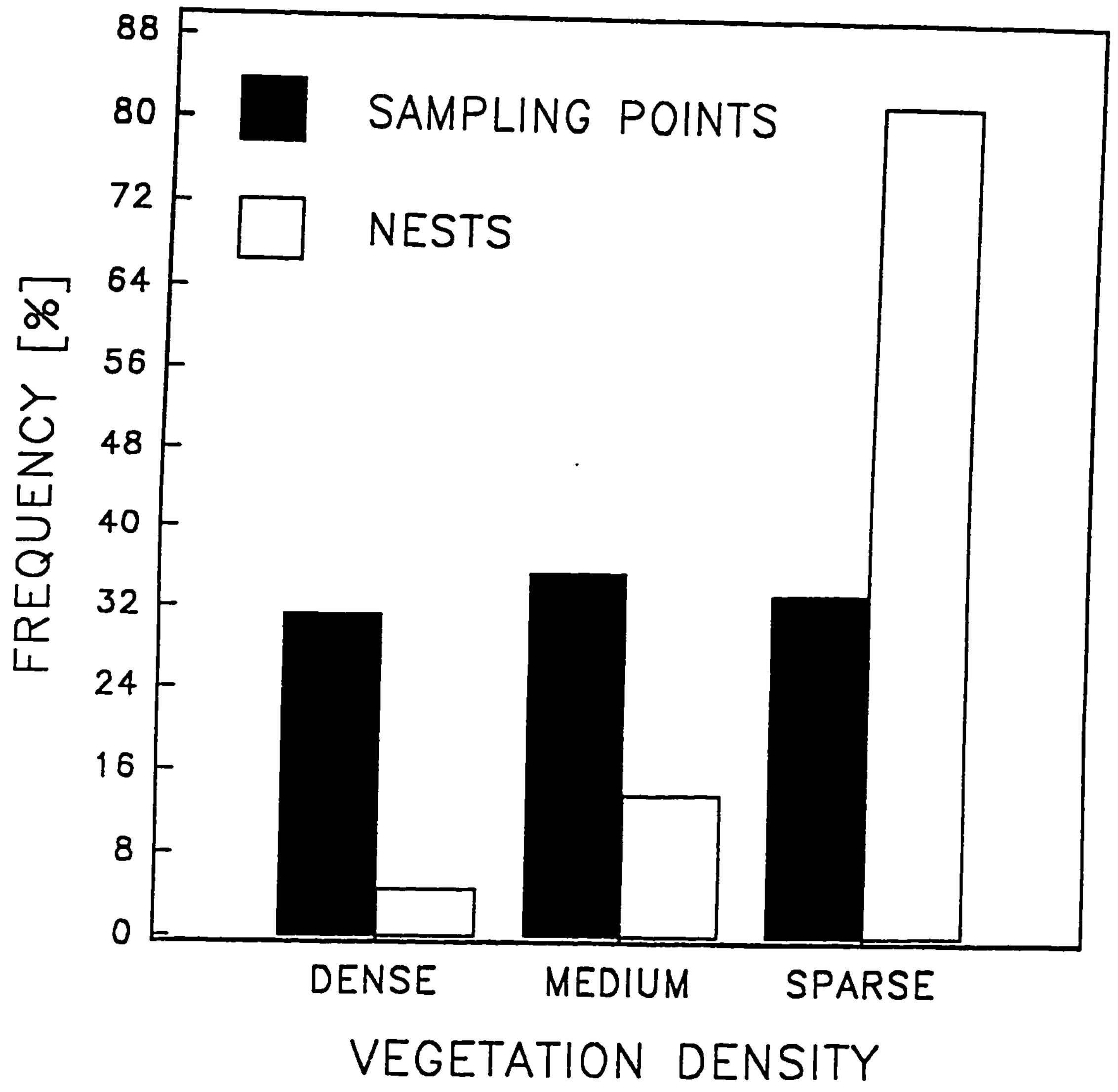

Figure 8.6. Frequency distributions of redwing nests and sampling points with respect to the density of cattail vegetation.

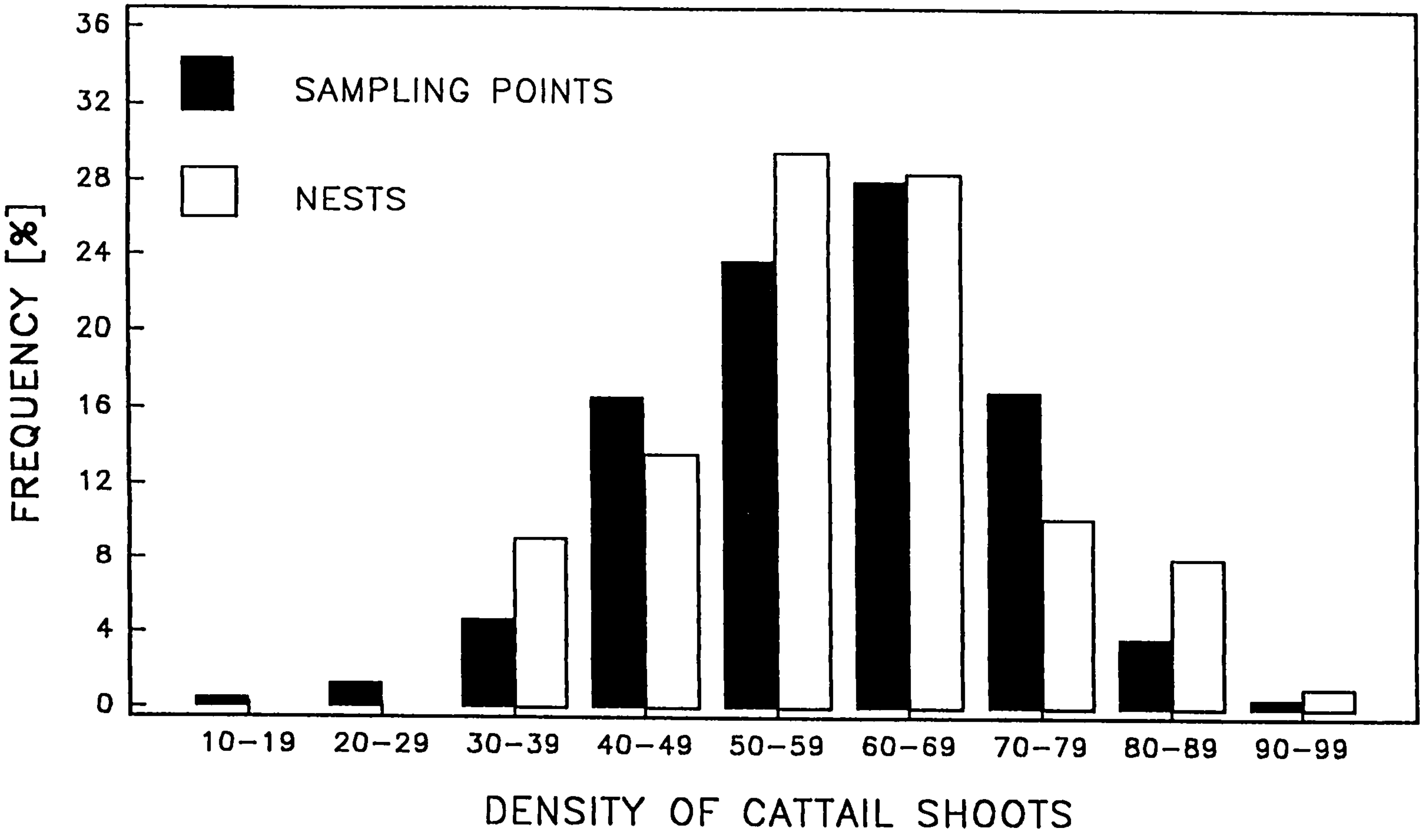

Figure 8.7. Frequency distributions of redwing nests and sampling points with respect to the density of cattail shoots.

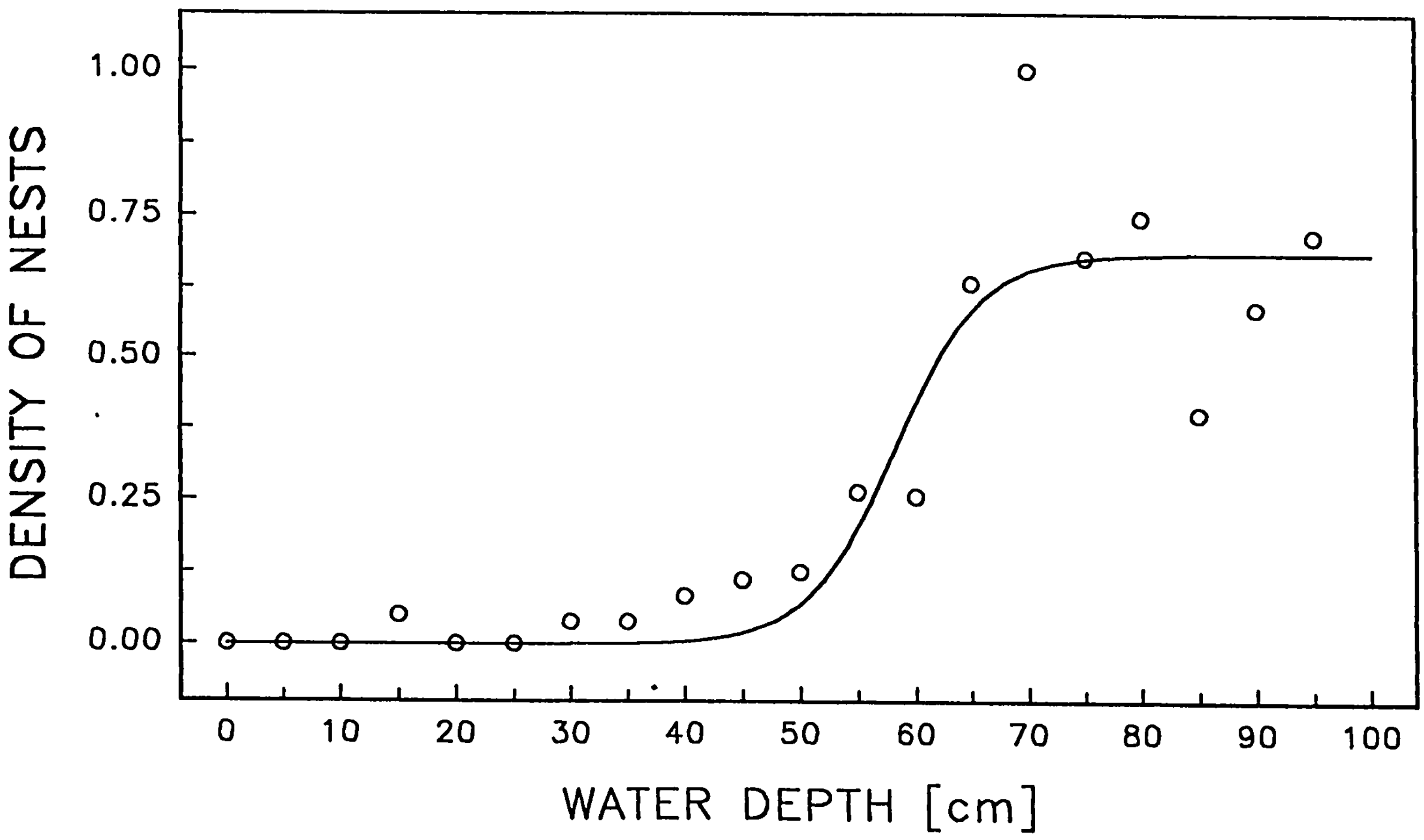

Figure 8.8. The relationship between the density of redwing nests and water depth in the Ramsayville marsh. The open circles represent the mean density of nests for 4 years. The equation describes logistic curve (shown by solid line) fitted to the means.

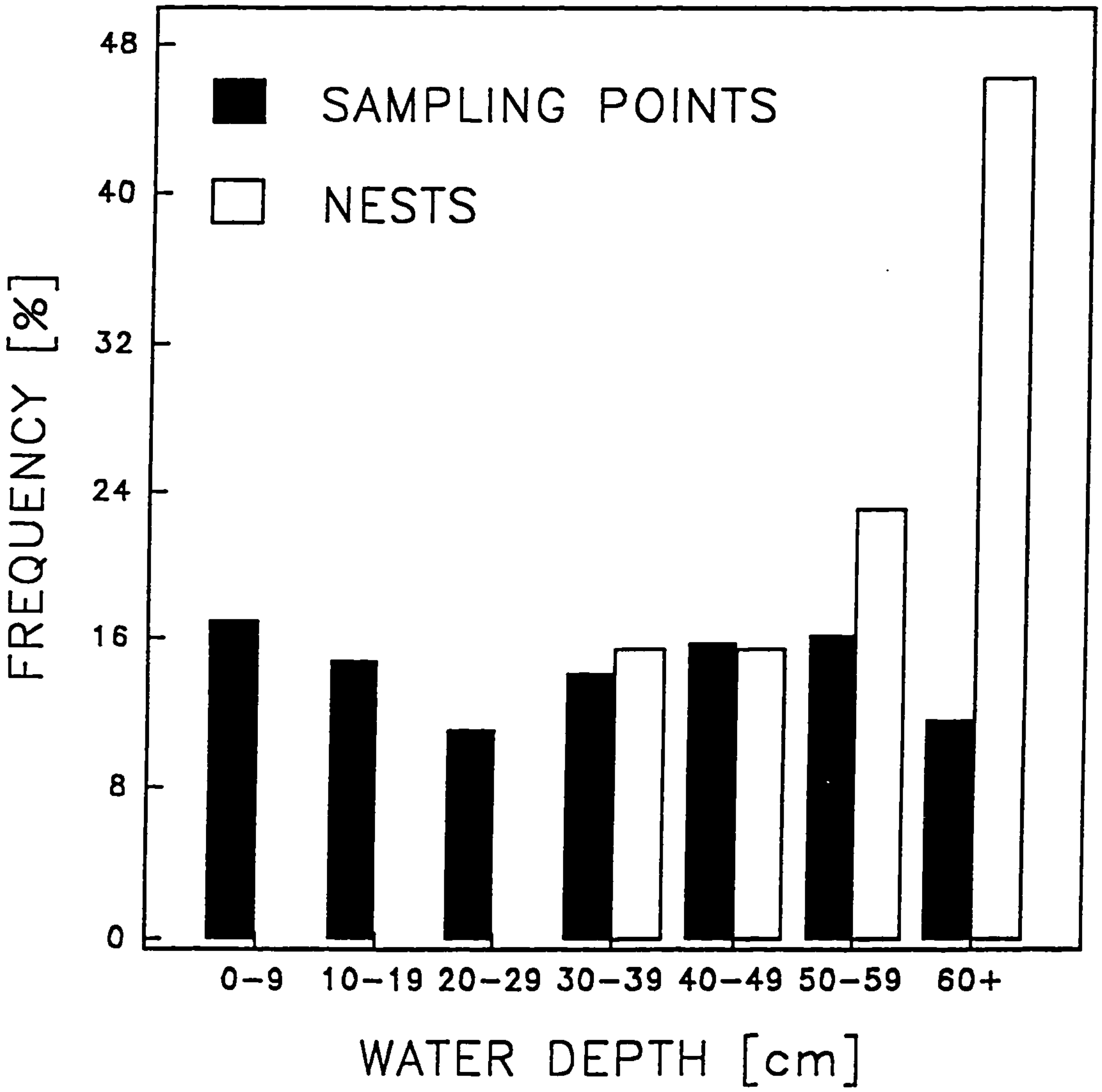

Figure 8.9. Frequency distributions of redwing nests and sampling points with respect to water depth within male territories in the Beaver Lodge marsh.

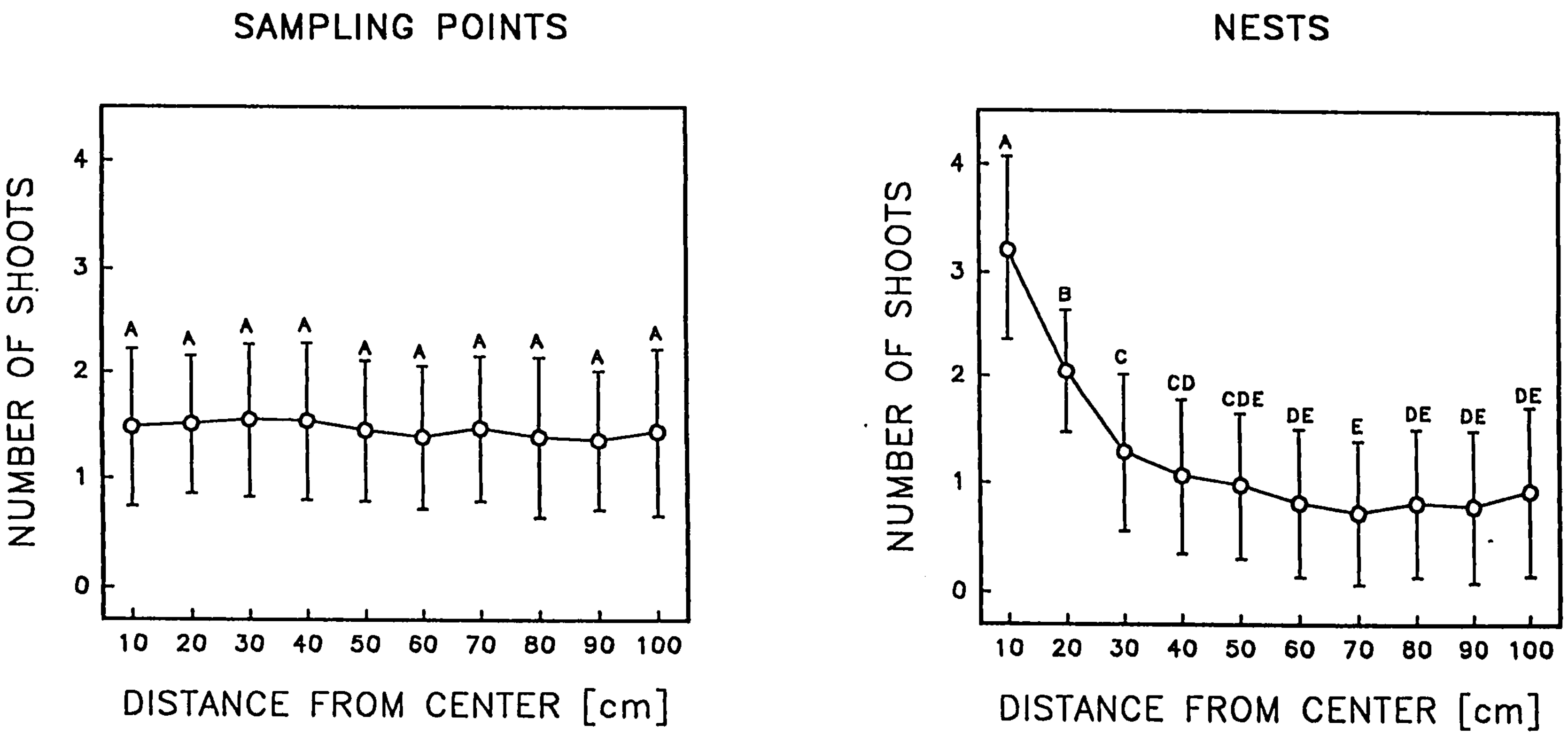

Figure 8.10. The mean density (± S.D.) of cattail shoots at various distances from the centre of nests and from the centre of sampling points. The density is expressed as the number of shoots per 0.01 m^2. Different letters indicate statistically different means.

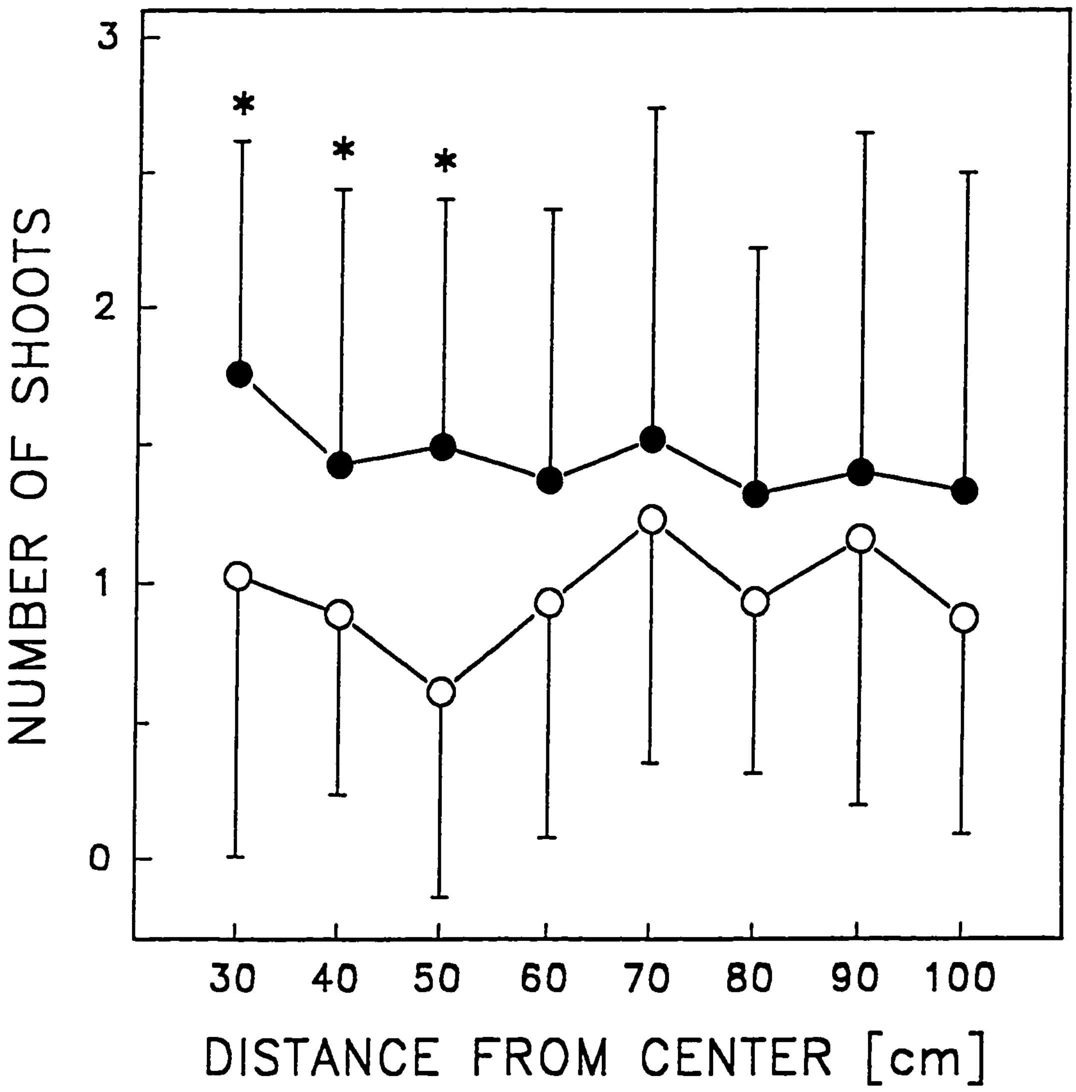

Figure 8.11. The mean (± 1 S.D.) density of cattail shoots as a function of the distance from the center of a redwing nest (open circles) and from the center of a sampling point (filled circles). An asterisk indicates open circles that are significantly different from filled circles.

CONCLUSIONS FROM SECTION II

The second section of this study tested several key assumptions of the polygyny models. The results of Chapter 5 demonstrate that females strongly prefer monogamy to polygamy: early in the season, 100% of females preferred bachelors to mated males. The results of Chapter 6 suggest that there are small, but systematic, differences in the reproductive success of monogamous and bigamous females: monogamous females achieve somewhat higher reproductive success than bigamous females. In Chapter 7, I found that asynchrony improves reproductive success of primary and secondary females. For primary females, the effect was most pronounced in their nesting losses (higher losses on synchronous than asynchronous territories) and in the development of their male nestlings (heavier young with longer bones on asynchronous than synchronous territories). For secondary females, the greatest difference was in male provisioning rates (males fed asynchronous broods more frequently than synchronous broods) and partly in the degree of development of female nestlings (asynchronous young had longer tibias than synchronous young). In Chapter 8, I found that females choose habitat characteristics on at least two spatial scales: they prefer nesting areas located in deep water, and within those, they prefer nest sites in dense clumps of vegetation.

The findings that 1) females prefer monogamy to polygamy, and that 2) polygamy reduces female reproductive success, are consistent with the competitive models, but inconsistent with the cooperative female choice model and the five models that assume neutral interactions (Table 8.4). The strong preference for unmated males indicates that females do not make any error when choosing breeding situations, and provides evidence against the mechanism B of the random dispersion hypothesis.

The finding that nesting asynchrony improves the reproductive success of secondary females runs contrary to the relationship postulated by the defence of male parental investment model. The finding that females evaluate habitat quality when choosing nesting areas contradicts the assumption of the asynchronous settlement model. The results of the experiments are, therefore, inconsistent with all but two explanations: the polygyny threshold model and the sexy son hypothesis (Table 8.4). As I indicated in Chapter 3, there are no feasible tests currently available that could separate these two models. Therefore, I conclude that the most plausible explanation for the occurrence of polygamy in my population of red-winged blackbirds is either the polygyny threshold model or the sexy son hypothesis.

Table 8.5: Implications of the experiments for the validity of the hypotheses. Experimental support for a given assumption is indicated by YES, the lack of support by NO. A dash indicates that no specific relationship was assumed. BS = breeding situation, RS = reproductive success.

HYPOTHESIS	ASSUMPTION			
	Do females choose BSs by their quality?	What mating status do females prefer?	RS of bigamous vs. monogamous females	Effect of increasing asynchrony on RS of secondary females
Status indifference	-	NO	-	-
No-cost no-benefit directed female choice	YES	NO	NO	NO
Davies's	YES	NO	-	-
Neutral-mate-choice	NO	NO	NO	NO
True null	NO	NO	YES	-
Cooperative female choice	YES	NO	NO	NO
Random dispersion, mechanism B	YES	YES	YES	-
Polygyny threshold	YES	YES	YES	-
DMPIM	YES	YES	YES	NO
Sexy son	YES	YES	YES	-
Asynchronous settl.	NO	YES	YES	YES

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