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**LA THÈSE A ÉTÉ
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FEMALE SETTLING PATTERNS AND POLYGyny IN THE
YELLOW-HEADED BLACKBIRD (*Xanthocephalus xanthocephalus*)

by

JILL PATRICIA LIGHTBODY

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

Department of Biology

Carleton University
Ottawa, Ontario

May 9 1986

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submitted by
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Abstract

Existing hypotheses that have been developed to explain the factors responsible for the evolution and maintenance of polygyny were examined in a population of the yellow-headed blackbird (*Xanthocephalus xanthocephalus*). One hypothesis maintains that females within a harem are co-operative while two other hypotheses (the Verner-Willson-Orians, VWO, and sexy son versions of the polygyny threshold hypothesis) maintain that females are competitive. It was determined that females were not co-operative and were only mildly competitive. An alternate "null" hypothesis was proposed that females settled without regard to other females within suitable habitat and males competed to hold territories in order to gain access to females.

To date there have been few accurate predictions proposed for the VWO and sexy son hypotheses. In this thesis, several predictions of the VWO, sexy son, and null hypotheses were proposed regarding the settling patterns of females. These predictions were tested in order to determine which hypothesis best explained the maintenance of polygyny in this population of yellow-headed blackbirds. The VWO and sexy son hypotheses were supported for some predictions, but the null hypothesis explained the observed pattern of female settling for all predictions.

Territory features and male features (behavioural and morphological) did not affect female reproductive success (RS) or harem size thus it appeared that there was no basis upon which females could choose mates. The most aggressive males held the largest territories, which supports the null hypothesis.

The basic assumptions of the VWO and sexy son hypotheses were examined to determine why these existing hypotheses did not explain why

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the yellow-headed blackbirds were polygynous. It was concluded that there were no costs for females associated with polygyny. Polygyny occurred because it was advantageous to males and neutral to females. The results from this study indicate that the polygyny threshold hypothesis may not apply as a general model to explain the occurrence of polygyny.

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The development of scientific thought appears to be guided by two tendencies. One of these we may call empirical adequacy. This is the demand that scientific theories link up with and correspond to observable facts....The other tendency we may call integrated generality. This prompts scientific language to move toward higher, more general, more abstract, usually mathematically formulated levels of expression....These two tendencies act upon each other in such a way that in the evolution of science, theories tend to explain more and more facts, connecting with nature at more and more points, while simultaneously moving toward more abstract, more general expressions....Scientific theories tell stories about things in the universe. Old scientific theories are not so much replaced as they are taken into the more inclusive language of a more general story about the universe. These stories, like fishing tales, seem to get more and more fantastic with the passing of time.

from The Tao of Symbols, by James N. Powell

General Introduction

Finding a mate is a requirement of all species of animals and plants that reproduce sexually. The selection of a member of the opposite sex as a mate is not always passive, but often involves making a decision of who to select. Along with making decisions come a number of complicating factors. Often the needs of both sexes are not the same with respect to how many mates to have, how long the pair should remain mated, and the qualities in a mate that are deemed important.

Males are usually less discriminating in their choice of mate than are females (Darwin 1871, Bateman 1948, Fisher 1958). A possible reason is that males are not limited in the number of times they copulate because each male can produce enough sperm to fertilize an enormous number of females (Bateman 1948). On the other hand, females are limited in the number of times they can mate due to the relatively small number of eggs they produce at a time (Bateman 1948) and due to the time it takes to produce an embryo after fertilisation. Because females carry young for a period of time (in mammals and some fish), or need time to recuperate their energy stores after laying eggs, males are most often the sex that is free to desert the other sex after insemination and search for another mate. It is not surprising that polygyny is the most common mating system in mammals (Eisenberg 1966), where females are necessarily unable to remate quickly due to the gestation and lactation periods.

In contrast, in birds, monogamy is the prevalent mating system, occurring in about 91% of North American species (Lack 1968). In birds, females are not the only sex which can care for offspring since males are capable of incubating eggs and feeding nestlings. Presumably, monogamy occurs because neither sex has more ability to desert the other sex and

both parents are often required to feed nestlings. A small percentage of bird species are either promiscuous or polyandrous, and about 5% are polygynous, with one male being simultaneously mated with more than one female (Verner and Willson 1966). A species is classified as polygynous if it regularly occurs in greater than 5% of the population (Verner and Willson 1966). Because polygyny is an uncommon mating system, it has been the focus of much research.

There have been several hypotheses proposed to explain the evolution and maintenance of polygyny. The original hypothesis was the simple idea that polygyny is the result of unbalanced sex ratios (e.g. Kendeigh 1941, Mayr 1941, Williams 1952). In one recent study, Smith et al. (1982) found that by experimentally reducing the number of males in a population of normally monogamous song sparrows (*Melospiza melodia*), they could induce polygyny. Polygyny occurred naturally only seven times in five years, due to the death of males. Unbalanced sex ratios appear to be a proximate cause of polygyny in this species, but the low incidence of natural polygyny leads to the conclusion that unbalanced sex ratios do not lead to the evolution or maintenance of polygyny. Most work has shown that polygyny occurs in many natural populations where the sex ratio is close to one (e.g. Williams 1940, Fautin 1941, Carrick 1963, Verner 1964, Willson 1966, Zimmerman 1966).

Wynne-Edwards (1962) proposed that polygyny is a mechanism for limiting population numbers. He argued that, by having only a portion of the total number of males breeding, these males can then limit the number of females they mate with and thereby limit the number of females that breed if they sense that the local population is getting large. This view has been critically questioned (Maynard-Smith 1964, Williams 1966).

Orians (1969) argued that there was no evidence to date that reproductive output was regulated by polygyny. Thus, this hypothesis is not a viable explanation for why polygyny occurs.

The most widely accepted explanation for the evolution and maintenance of polygyny was first proposed by Verner (1964) and then elaborated on by Verner and Willson (1966) and Orians (1969). Verner and Willson (1966) observed that polygyny occurs most often in species that inhabit prairies and marshes where the habitat is more two-dimensional. Since all productivity is constrained in a two-dimensional space, food and nest sites become densely distributed. They argued that as a result of the density of resources, the potential variation in resources between two sites (e.g. territories) may be greater than in a three-dimensional habitat. Verner (1964) proposed that variation in territory quality was correlated to variation in female reproductive success (RS, the number of young fledged). He assumed that polygyny is costly to females but not to males because females within a harem would have to share territory resources and male assistance in feeding young. Verner suggested that some males' territories are superior to others' because of differences in the amount of food available and in how concealed the nest sites are from climatic factors and predators. He also suggested that, through competition among males, the best quality males come to hold the best quality territories. Qualities of males that are assumed to affect female fitness are the ability to help feed and defend young and the ability to sire vigorous offspring. Thus, some males on high quality territories may attract more than one female while other males remain unmated.

Verner (1964) suggested that females are likely to base their choice of mate on the quality of the territory more than on the quality of the

male. This dismissal of male quality as an important influence on female choice was based on the observation that the order of pairing in long-billed marsh wrens (*Telmatodytes palustris*) was related to territory features and not to the amount of singing by the male (Verner 1964). He also based this assumption on the observations from three studies that females returning to breed on the same study area often settled on their previous territory rather than with their previous mate, who may hold a different territory nearby (Nice 1943, Lack 1946, Mayfield 1960). However, it does not seem reasonable to dismiss the importance of male quality as an influence on female choice with such limited data. The tendency to dismiss male quality based on no empirical test or to bias interpretation of data in favour of the idea that male quality is relatively unimportant is a common error (Orlans 1969, Searcy 1979a). Another weakness of Verner's idea is that the assumption that the best males hold the best territories was not supported by data. Thus, the foundation upon which the hypothesis would later be developed was poorly laid.

Verner and Willson (1966) developed the idea that females should mate with an already mated male only when they can be compensated for the reduced RS they would suffer by being polygynous. They suggested that females are compensated through differences in territory quality such that the RS they could expect by mating polygynously with a male on a high quality territory would be at least as high as the RS they could expect by mating with a bachelor on a poorer quality territory. Verner and Willson (1966) termed the minimum difference in territory quality required to induce polygyny the 'polygyny threshold'.

Orlans (1969) developed the polygyny threshold hypothesis graphically, and outlined some assumptions and predictions of the hypothesis. Orlans

began with the assumption that the habitat in which polygynous species breed is variable and that female reproductive success is correlated with this variation. However, he presented no data to support the view that the variation in the habitat was sufficient to cause variation in female RS. Territory 'quality' was defined as being a territory which has features that enhance female reproductive success such that the best quality territories are those on which female RS is the highest. He graphically represented female reproductive success as a function of environmental (territory) quality (see figure 11). Environmental quality was presented as if the quality of territories could be ordered linearly and that the relationship between environmental quality and female RS is sigmoidal, which he stated was merely for clarity of presentation and was not essential to the argument. However, his argument does rely heavily on these assumptions (for which he presented no data).

Orians (1969) acknowledged that females may choose mates based on the capability of the male to help feed and defend nestlings (which would affect the number of young that fledge) as well as the genetic quality of the male (which would affect the viability of the offspring) and the quality of the territory. However, he assumed that territory quality would have a stronger effect than male quality on female choice.

A final assumption made by Orians (1966) was that female RS decreased with increasing harem size within a territory, that is it is costly to a female to be polygynous. Wittenberger (1978) found that the RS of the second females to settle within territories (secondary females) was lower than that of the first females to settle within territories (primary females) in bobolinks (*Dolichonyx oryzivorus*). He used these observations to support the polygyny threshold hypothesis. However,

this does not constitute support of the hypothesis because he did not consider that there may be a seasonal effect on female RS such that later nesting females would have lower RS, nor did he have sufficient data to assess whether or not later settlers had lower RS because they were younger. A correct way to test whether is it detrimental to females' RS to be polygynous would be to determine the RS of females in different-sized harems on territories of the same quality (if quality could ever be determined). Zimmerman (1966) suggested that polygyny was not detrimental to the RS of female dickcissels (*Spiza americana*) because they fed off the territory, males did not help feed young, and predation was not density-dependent. For the polygyny threshold to apply to a species, it must be demonstrated that female RS decreases with increasing harem size within a territory.

Orians suggested that the main factor affecting differences in RS between monogamous and bigamous females would be male help and the availability of food on the territory. He suggested that females could reduce the detrimental effect of polygyny by not initiating their nests simultaneously within each territory. In addition, in marshes food is rapidly renewed, which would decrease the detrimental effect of polygyny (Orians 1969). These two suggestions appear to negate Orians' last assumption, since they do not support the idea that polygyny is costly to females. If there is no disadvantage to females for mating polygynously, then polygyny could have evolved simply because it was advantageous to males and neutral to females.

An assumption that is implied in the polygyny threshold hypothesis is that females choose mates to maximize their *expected* RS and do not predict how many females will settle on the territory after them.

Therefore, any tests of the hypothesis which rely on comparing the RS of females settling at different times or in different sized harems should be based on females which are the last to settle on territories so that their expected RS equals their realized RS.

Several predictions have been made in an attempt to assess the importance of the polygyny threshold hypothesis (Verner 1964, Verner and Willson 1966, and Orrians 1969 - the VWO hypothesis). Orrians (1969) predicted that there should not be a negative correlation between female RS and harem size because females should not settle polygynously unless they can expect as high an RS as they could by settling monogamously. Several studies have examined this relationship and used the result to support this prediction of the polygyny threshold hypothesis (see Orrians 1972, Holm 1973) or to question its validity (Weatherhead and Robertson 1977a). However, this prediction is not a good test of the polygyny threshold hypothesis. Altmann et al. (1977) have shown that there is no prediction regarding the RS of females in different sized harems. They demonstrated that the magnitude of the differences in RS of females in different-sized harems and whether the differences are positive or negative is dependent upon the relative differences in quality of the territories on which those harems occur.

Due to the assumed detrimental effect of nesting polygynously, Orrians (1969) predicted that early-settling females should attempt to repel later females which attempt to settle on the same territory and later-arriving females should avoid settling on a territory on which females have already settled. That is, females should behave competitively toward one another. Aggression among females has been demonstrated in long-billed marsh wrens (Welter 1935), yellow-headed blackbirds (*Xanthocephalus*

xanthocephalus, Willson 1966), and red-winged blackbirds (*Agelaius phoeniceus*, Holm 1973, LaPrade and Graves 1982, Yasukawa and Searcy 1982, Hurly and Robertson 1984). This assumption will be examined in more detail in chapter 1.

Garson et al. (1980) examined the polygyny threshold hypothesis in detail and presented some predictions of the hypothesis. They predicted that territory quality should be positively correlated with harem size. In theory, this may be true, but in reality it is difficult to test. Since the best territories are those on which female RS is the highest, then the prediction could be stated that female RS should be positively correlated with harem size. However, an assumption of the hypothesis is that female RS decreases with increasing harem size. Weatherhead and Robertson (1977a) identified some nest site features that affected nest success for red-winged blackbirds and scored each nest site on the basis of these features to create an index of territory quality. They found that harem size was not positively correlated to territory quality. However, their method of determining territory quality is based upon the mean scores for all nest sites within a territory. This method does not take into account the number of sites available in the territory, which may affect the number of females that a territory would attract (Searcy and Yasukawa 1981a). To clearly demonstrate that territory quality is positively correlated with harem size, it is necessary to identify a territory feature that affects female RS (holding harem size constant) then manipulate the feature to see whether or not harem size is affected. Pleszczynska (1978) identified an aspect of territory quality that affected polygyny and female RS in lark buntings (*Calamospiza melanocorys*), but this has never been demonstrated in any other study.

A second prediction made by Garson et al. (1980) was that the RS of first settling females on the breeding area should be greater than later settlers. This relationship has been observed to occur in red-winged blackbirds (Dolbeer 1976) and in lark buntings (Pleszczynska and Hansell 1981). However, Altmann et al. (1977) showed that the order of settling would not be correlated with RS because a later arrival on a territory would lower the RS of the earlier settling females on the territory. This prediction can be valid only if it is restricted to the last females to settle on each territory. Thus, the evidence above is not support for the VWO hypothesis.

A third prediction made by Garson et al. (1980) and later agreed with by Wittenberger (1981a) was that a crucial test of the VWO hypothesis was that the RS of secondary females should be equal to the RS of monogamous females who select mates at the same time. This prediction has been verified for prairie warblers (*Dendroica discolor*, Nolan 1978), indigo buntings (*Passerina cyanea*, Carey and Nolan 1979), and tree swallows (*Tachycineta bicolor*, Quinney 1983). Alatalo et al. (1981) observed that the RS of secondary female pied flycatchers (*Ficedula hypoleuca*) on the better territories was less than the RS of monogamous females on poorer territories settling at the same time. They suggested that this did not support the VWO hypothesis. Their explanation was that secondary females were deceived into mating polygynously because they were not aware that the male was already mated since males held two territories that were not near each other. This is an interesting hypothesis, and may be true for this species, however it does not contradict the VWO hypothesis because the prediction is not a crucial test of this hypothesis.

Altmann et al. (1977) demonstrated that the VWO hypothesis does not

predict any relationship between harem size and RS for the following reason. If two territories are close in quality, then the RS of females in the larger harem on the better territory may be lower than that of females in the smaller harem on the poorer territory, but if the territories are far apart in quality, the RS of females in the larger harem on the better territory may be higher than that of females in the smaller harem on the poorer territory. At some intermediate difference in quality, the RS of females in both sized harems will be the same. Thus, the relative RS of females on different territories depends upon the relative differences in quality among territories. Additionally, the possibility exists that secondary females are yearlings or inexperienced breeders, which may cause lower RS (Blakley 1976, Wittenberger 1981a). Also, females may exhibit site fidelity (i.e. return to the same territory as the previous year), which may disrupt the settling pattern away from the predicted pattern. Therefore, the above prediction that the RS of monogamous and secondary females settling at the same time should be equal is not useful as a test of the VWO hypothesis.

One valid prediction of the polygyny threshold hypothesis that has been made is that the first territories settled should end up with the largest harems (Garson et al. 1980). This has been observed for indigo buntings (Carey and Nolan 1979). As will be discussed in chapter 2, this prediction is also consistent with the hypothesis that females settle randomly (the null hypothesis).

A modification of the VWO hypothesis, also based on the assumption that females are competitive, was proposed by Weatherhead and Robertson (1977a, b, 1979). They suggested that the male quality may not be strongly positively correlated to territory quality because some males

returning to the same territory as in the previous season (i.e. those exhibiting site fidelity) may be at an advantage in competing to hold that territory even though they may be of lower quality than their competitor (i.e. the returning males may exhibit site dominance). The assumption that the best males hold the best territories was refuted in a study by Eckert (1985). He demonstrated that male quality (as measured by their competitive abilities) was not correlated to territory quality by determining that the rank order of competitive abilities of territory owners and their replacements after the owners were removed were not the same. Weatherhead and Robertson (1977b, 1979) suggested that females must assess the quality of the male in addition to the quality of the territory to get the best combination. They argued that females may choose mates to maximize their fitness, as opposed to their RS (as assumed in the VWO version of the polygyny threshold hypothesis). Females would recoup the loss in RS they suffer from mating polygynously by mating with a male of high genetic quality who would sire sons that would inherit some of their father's attractive features. Thus, females would increase their fitness through the high pairing success of their sons (the sexy son hypothesis).

Even though the sexy son hypothesis has not been adequately tested, it has received some criticism (Heisler 1981, Searcy and Yasukawa 1981a, Wittenberger 1981a). The main criticism is that the hypothesis requires that there be heritability of male features which are related to pairing success, and it has been suggested that fitness is not highly heritable (Williams 1975, Maynard-Smith 1978). Whether or not the sexy son hypothesis could work, it remains a useful reminder that male quality can have an important influence on female choice of a mate and that females

may choose mates to maximize their fitness and not just their RS. The effect of male quality on female fitness may not only be through the pairing success of their sons, but may also be through the quality of their offspring (Burley and Weatherhead, MS).

There have not been many predictions made that could serve as tests of the sexy son hypothesis. The reason for this is most likely that the strongest test would be to observe the mating success of sons of "sexy" and "unsexy" males, and in most species this is virtually impossible because offspring do not return to their natal area to breed (at least not in sufficient numbers to constitute a rigorous test). One prediction that was made was that male behaviour should affect recruitment of females, independently of territory quality. Male courtship intensity has been observed to be positively correlated with recruitment of female red-winged blackbirds (Weatherhead and Robertson 1977b, Yasukawa 1979). However, this may have been due to females preferring older males, since courtship intensity has been shown to be correlated with male age (Yasukawa 1979).

In summary, most of the predictions of the VWO version of the polygyny threshold hypothesis do not constitute valid tests of the hypothesis. There have not been many crucial predictions made for the sexy son version of the hypothesis. It is unclear why the polygyny threshold hypothesis has persisted for twenty years despite much lack of support and few valid tests. Perhaps the hypothesis has intuitive appeal because it offers a reasonable explanation of how females should choose mates under the assumptions. A more general discussion of the hypothesis and its inherent assumptions is the topic of chapter 4.

The VWO and sexy son hypotheses are similar in that they both have the

assumption that female RS decreases with increasing harem size within a territory and thus females within a harem are competitive. Altmann et al. (1977) suggested that polygyny may be beneficial to females because females within a harem may co-operate in nest defense against predators or in locating food and additionally, high nest densities may deter predators. It is unlikely that females would co-operate in nest defense any less than they would under the polygyny threshold hypothesis because all females would benefit from responding toward a predator. If a predator is hovering over a neighbour's nest, all females in the vicinity should respond because they cannot predict where the predator will go next. Therefore, so-called co-operative nest defense is actually a collection of individuals behaving selfishly, not altruistically. The remaining two benefits of co-operation are probably real.

The present study was undertaken to examine the existing hypotheses of why some species of birds are polygynous using data from three years of research on the yellow-headed blackbird, a highly polygynous marsh-nesting species. In chapter 1 the question as to whether polygyny in the yellow-headed blackbird is the result of co-operation among females as opposed to hypotheses which assume females are competitive will be examined. It will be concluded that females within a harem are definitely not co-operative, and only mildly competitive. A "null" hypothesis is presented that assumes females settle without regard to other females within the habitat and that competition among males to hold territories in order to gain access to females is more important than female choice in this species. The two versions of the polygyny threshold hypothesis (the VWO and sexy son) and the null hypothesis will be examined in more detail in the remaining chapters.

In chapter 2, specific predictions will be made regarding the settling patterns of females expected under the VWO, sexy son, and null hypotheses to attempt to distinguish among the three.

Chapter 3 will examine the question regarding the relative importance of competition among males and female choice in the mating system of the yellow-headed blackbird. In addition, the relative importance of male and territory quality in influencing female choice of mate will be examined by determining the effect of features of males and territories on female RS and harem size. It will be concluded that the data from chapters 2 and 3 do not support the VWO or sexy son hypotheses, but do support the null hypothesis. Therefore, in chapter 4 the basic assumptions of the polygyny threshold hypothesis will be examined to determine why this hypothesis does not apply to this population of yellow-headed blackbirds. The discussion of chapter 4 will evaluate the assumptions and validity of the polygyny threshold hypothesis in light of the previous chapters, and will evaluate the research to date which has purported to offer valid tests of both the VWO and sexy son versions of the hypothesis. It will be concluded that the polygyny threshold hypothesis may be too restrictive to apply as a general explanation of why polygyny occurs.

General Methods

A population of yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) was studied from 1983 to 1985 on a marsh in southwestern Manitoba (49° 49' N, 100° 13' W). The study areas were two 240 x 300 metre sections (the "east end" and the "west end") of a 70 hectare marsh. This was a deep water marsh (mean depth 60 ± 10 cm in vegetated areas) vegetated mainly by cattail (*Typha* spp.) and bulrush (*Scirpus* sp.). The study areas were mapped with the aid of aerial photographs. Stakes were placed every 10 m along two edges of the marsh to facilitate mapping of males' territories. Territories were plotted on the map by observing boundary disputes between males and the extent of a male's activity over several weeks of daily observations. Territory sizes ranged from 0.02 ha to 0.2 ha. Observations were made from a car parked on the roadside along one edge of the marsh using a spotting scope, or from vantage points in the upland area surrounding the marsh.

Males were caught in mist nets and decoy traps, measured, banded with unique combinations of colour bands, and released. Females were not banded, as the few that were in 1983 did not return to the territory after being released. That females were not banded was of no consequence to the study.

Nests were located and marked with flagging tape placed in a slightly concealed spot three metres away from each nest. There were 61 nests in total in the study areas in 1983, 109 in 1984, and 101 in 1985. There were fewer nests in 1983 because the study area was slightly smaller than in 1984 and 1985. Nest locations were plotted on the map with the aid of the grid system of stakes. In this way, it could be determined to

which territory each female belonged and hence harem sizes. Harem size was defined as the number of simultaneously active nests within a territory. In 1984, nest locations were determined accurately by placing silver pie plates on the nests at the end of the breeding season and taking an aerial photograph of the marsh. Plotting nests by the grid system proved to be almost as accurate as by the aerial photographs. Nests were monitored to determine laying dates (used as a measure of nest initiation date, hence female order on a territory), clutch sizes and fledging success. Use of nest initiation dates as a measure of order of settling was appropriate in this population since the order territories were settled by females was highly positively correlated with the date of first eggs within those territories (Spearman correlation coefficient = 0.835, $P < 0.001$, $n = 66$ for all three years combined; the order territories were settled was not determined for all territories).

One measure of female reproductive success was the number of young fledged per nest (y/n), a value which includes the effects of predation of the entire brood. A successful nest is one which fledged ≥ 1 young. A second measure was the number of young fledged per successful nest (y/s), a value which reflects the effects of nestling starvation as well as predation of part of the brood. Thirdly, the percent of total nests successful ($\%s$) is a measure of predation intensity.

For all analyses, parametric statistical tests were used whenever the assumptions of the test were met, and followed Sokal and Rohlf (1969), as did non-parametric tests.

Chapter 1

Introduction

About 5% of bird species are polygynous (Verner and Willson 1966, Lack 1968). Females should mate polygynously only when the benefits outweigh the costs of group living (Horn 1968, Alexander 1974, Bertram 1978). Because males will almost always benefit by having more than one female, but females may not benefit, the female will be the sex which controls whether or not polygyny occurs by her choice of mate (Orlans 1969). Current hypotheses to explain the evolution and maintenance of polygyny fall into two categories based on the effect females have on one another. One possibility is that females within a harem are competitive, i.e. it is detrimental to a female to be polygynous and therefore females need some kind of compensation to be induced to nest polygynously. The other possibility is that females within a harem are co-operative, i.e. it is beneficial to a female to be polygynous.

Verner (1964) and Verner and Willson (1966) assumed that there is a cost to the female associated with polygyny because it means that females have to share male help in feeding nestlings, territory resources, or both. If there is a cost associated with increasing harem size, there should be competition among females which would act to stagger the initiation of nests in time and space within a male's territory and thereby decrease the detrimental effect (Verner 1964, Yasukawa and Searcy 1981). This decrease would occur since the females' peak demands on the male and territory would not be synchronous.

The notion that females within a harem may be co-operative was introduced by Altmann et al. (1977), who suggested that under some

circumstances females may benefit by mating polygynously. This could occur when males' help and resources are shareable, or non-shareable but abundant, or if males make little contribution. Females may benefit from polygyny in several ways. Females within a harem may co-operate in nest defense against predators (Alexander 1974), or high nest densities may deter predators (Picman 1980) or decrease the chance of any one nest being preyed upon. Additionally, females may share knowledge of food resources (Ward and Zahavi 1973).

Attempts to understand the evolution and maintenance of polygyny have focussed mainly on hypotheses that assume females are competitive (see Garson et al. 1981). However, few studies have tested this basic assumption. Yasukawa and Searcy (1981) and LaPrade and Graves (1982) found ambiguous results in their studies on the marsh-nesting red-winged blackbird (*Agelaius phoeniceus*). In other studies, female red-winged blackbirds have been shown to behave competitively toward intruding females (Nero and Emlen 1951, Yasukawa and Searcy 1982, Beletsky 1983, Hannon 1984, Hurly and Robertson 1984). Picman (1980) suggested that there was some co-operation among female red-winged blackbirds to deter predators. The question as to whether females within a harem in some polygynous species are co-operative or competitive has therefore not been resolved. In this study, several predictions arising from the two hypotheses are tested using data on the yellow-headed blackbird (*Xanthocephalus xanthocephalus*), a highly polygynous species.

The co-operation hypothesis predicts that females should be attracted to each other. Females should therefore settle on a territory where other females have already settled in preference to settling on a territory with no females on it. Females should initiate their nests close in time and

space to established nests within a territory, until the optimal density of females is reached. This optimal density may be the point at which the territory resources are not sufficient for all the females within it. Conversely, the competition hypothesis predicts that females should avoid settling near other females and should settle on many territories simultaneously throughout the marsh. Females within a territory should initiate their nests far apart in time and/or space; this may occur directly via aggression directed at a potential settler from a resident female, or indirectly via avoidance of existing nests by later settlers.

The co-operation hypothesis predicts that females will not be aggressive to potential settlers. Conversely, the competition hypothesis predicts that resident females should be aggressive toward potential settlers. Because females should use aggression to deter other females from nesting synchronously (Orians 1969) and because females probably have less time to be aggressive when they are incubating or feeding nestlings relative to when they are laying eggs (Orians 1969, Yasukawa and Searcy 1981), this aggression should be more pronounced at the beginning of their nesting cycle.

The competition hypothesis also predicts that if male help in feeding nestlings increases nestling survival, the primary (first on a territory) female should be the most aggressive because she stands to lose the most (Wittenberger 1979). This would occur since males tend to direct the majority of their help to the clutch that hatches first, which is typically that of the primary female (Martin 1974, Patterson et al. 1980, personal observation). The primary female should be aggressive to delay later settlers enough that her clutch hatches first.

If females are aggressive, the territorial male should attempt to

Inhibit this behaviour, as males should behave in ways which would enable them to recruit more females (Downhower and Armitage 1971, Weatherhead and Robertson 1977b, 1981).

The co-operation hypothesis predicts that females settling in large harems should have higher reproductive success (RS) than those in smaller harems on the same sized territories. This would occur because the --benefits of co-operation would increase with increasing harem size, as explained above, up to some optimal density. Because density varies with territory area as well as with harem size, this prediction is restricted to compare harems on the same sized territories. The competition hypothesis does not apply to this prediction because Altmann et al. (1977) have shown that any relationship between harem size and female RS would be consistent with the competition hypothesis.

A final prediction of the co-operation hypothesis is that female RS should increase with increasing nest density and increase as nest initiation dates approach synchrony. This would occur because females would enjoy the benefits of co-operation for the maximum length of time if nests were all initiated at the same time. Conversely, the competition hypothesis predicts that female RS should decrease with increasing nest density and as nest initiation dates approach synchrony.

Methods

The distance between nests was measured from their locations plotted on maps of the marsh which were drawn from aerial photographs (see General Methods).

Each of 14 resident females was tested for their response to an intruding female by recording their behaviour toward a taxidermic mount of a female yellow-headed blackbird in a perched position. The mount was placed 1 m from a nest for a 5 minute period once during each of 4 stages of the nesting cycle: 1) 2nd day of egg-laying, 2) 2nd day of incubation, 3) 10th day of incubation, 4) 5th day of nestling stage. Twenty four additional females were tested only once to allow a test of whether or not females habituated to the mount. It was certain that the female being observed was the nest owner, even though females were unmarked, because either she was the only female resident on the territory, had been flushed from the nest, or was attempting to return to it. An overall aggressive response score was calculated as the sum of the time performing a particular behaviour multiplied by the score for the behaviour (Table 1).

Male behaviour during the model presentations was also recorded.

Results

Data for all years were pooled because all measurements were similar each year. Independent values for each year are in the Appendices.

Nest distributions in time

A prediction of the co-operation hypothesis is that females should settle near females that have already settled within territories, until the optimal harem size is reached, in preference to settling on territories where no other female has settled. If females settled in this manner, it would be expected that the nest initiation dates of females within a harem would be the same. Thus, for a given female who settles, the next female to settle in the vicinity should settle on the same territory as opposed to on an adjacent territory (one which shares a territory boundary). Because primary females stand to lose more for nesting synchronously, they should delay the settling of secondary females more than secondary females delay tertiary females (Yasukawa and Searcy 1981). To take this into account, the spacing in time between first and second nests was analysed separately from the time between secondary and tertiary nests.

To analyse nest distributions in time, the mean time between the initiation of the first and second nests within a territory was determined. The time between the initiation of the first nest on one territory and the initiation of the consecutive nest to it on an adjacent territory was also determined for all nests, and a mean value was calculated. These two mean values were compared. The same comparison was done for the time between initiation of the second and third nests within one territory versus the time between initiation of the second nest within one territory and its consecutive nest on an adjacent territory.

The time between consecutive interterritorial nest initiations was less than the time between consecutive intraterritorial nest initiations (time between first and second nests within territories vs. time between first nest on one territory and consecutive nest on adjacent territory Mann Whitney $U = 2287$, $P \ll 0.001$; time between second and third nests within territories vs. time between second nest on one territory and consecutive nest on adjacent territory $U = 847$, $P \ll 0.001$). This indicates that the nests were not clumped in time (Figures 1, 2) contrary to the prediction of the co-operation hypothesis.

The competition hypothesis predicts that nests of females within a territory should be repulsed in time relative to a random distribution. However, the above analysis could not be used to test this prediction because it could not be determined whether the time between nest initiations on adjacent territories was greater than expected by random female settling. To do this would require that the total number of territories on the marsh and the total number of females settling on the marsh be known, and this information was not obtained. However, it is not necessary to develop an elaborate statistical method to determine if nests were repulsed in time (as did Yasukawa and Searcy 1981) because the competition hypothesis has the simple prediction that no nests within a harem should be initiated on the same day, few one day apart, with an increasing number of females settling further apart in time. From Figure 1 it is clear that many times females initiated their nests in the same territory on the same day. A further prediction of the competition hypothesis is that the primary females should delay the settling of secondary females more than secondary females delay tertiary females because primary females stand to lose more for nesting synchronously. No

differences were found ($U = 961$, $P > 0.2$) between the two groups in the average number of days between the initiation of consecutive nests (Figure 1a,b). If anything, primary and secondary females tended to settle on the same day more often than did secondary and tertiary females.

Spatial nest distributions

It was not valid to test whether nests were clumped or repulsed by comparing the distribution to a Poisson distribution. Use of the Poisson distribution requires that the habitat is homogeneous. Since the marsh had gaps of open water or fallen vegetation, it could not be considered homogeneous. To determine nest distribution in space, for each nest the distance to each of the three nearest active nests was calculated. If females were attracted to each other when settling, as predicted by the co-operation hypothesis, there should be no difference in the average distances to each of the three nearest nests for nests initiated early in the period of female settling and the distances after all nests were initiated. If females were avoiding one another when settling, as predicted by the competition hypothesis, the distance to the nearest nest should be greater for nests initiated early in the period of settling than the distance after all nests were initiated. This would occur because although early females may repel others to nest further away, the gaps between nests would get filled in as more and more females nested, because of the finite size of the marsh. The first 25% of nests initiated were arbitrarily chosen for the sample of nests initiated early. The mean distance to the nearest nest for the first 25% of nests that were initiated was compared to the mean distance to the nearest nest after all nests had been initiated. The same comparison was done for the distance to the 2 nearest nests and 3 nearest nests.

The nests in this study were neither clumped nor repulsed (Figure 3). The distance to the two nearest nests and the three nearest nests was greater for the first 25% of nests initiated than after all nests were initiated, contrary to the prediction of the co-operation hypothesis. The distance to the nearest nest was slightly, although non-significantly, further for the first 25% of nests than for all nests. Because this slight difference was in the direction predicted by the competition hypothesis, this may reflect some competition among females to spread out nests. However, this pattern would be expected even if females built nests in random positions, because later settlers would fill in the gaps between nests due to the finite size of the marsh.

Female response to intruding female

The co-operation hypothesis predicts that females should not be aggressive toward potentially settling females. If females are competitive, they should act to deter potential settlers. Females should be most aggressive toward intruding females during the early nesting stage. There were no differences in response scores for females tested in each stage versus those tested only in one stage (Table 2), which indicates that females did not habituate to the mount. The data were therefore combined for further analyses. Sample sizes do not always add up to 38 because not all females which were tested more than once were tested in each stage of the nesting cycle.

The co-operation hypothesis was not supported since females did display aggressive behaviour toward the female mount. That females were aggressive supports the competition hypothesis. However, the most aggressive behaviour observed was agitation and vocalization by a female within 5 m of the mount (score 10 in Table 1). No female was observed to

directly attack the mount. Female responses to female mounts in each of the 4 stages of the nesting cycle revealed that females were least aggressive during the laying stage, and most aggressive during the nestling stage (Figure 4), contrary to the prediction of the competition hypothesis.

Since the primary female stands to lose the most from nesting close in time and space to other females they should be more aggressive, in the early nesting stages, than secondary or tertiary females are to potential settlers. Primary females were not more aggressive to the intruding female mount in either egg laying or early incubation (Figure 5). This result is not consistent with the competition hypothesis.

The competition hypothesis also predicts that if females can deter later settlers, the territorial male should interfere with this aggression to facilitate recruitment of females. Males were observed chasing away the resident female from the female mount, yet the degree to which males exhibited this behaviour was not related to their eventual harem sizes (Table 3).

Female reproductive success

Female RS (y/n, y/s, %s) did not increase with harem size (Kruskal-Wallis, $P > 0.2$), contrary to the prediction of the co-operation hypothesis. The combined data for all years are illustrated in Figure 6. Because the co-operation hypothesis predicts that female RS would increase with increasing harem size up to some optimal density of females, and density varies with territory area as well as with harem size, a similar analysis was done using territories of the same size. There was still no relationship between female RS and harem size (Kruskal-Wallis $P > 0.2$). The competition hypothesis does not apply to

this prediction since any outcome would be consistent with the hypothesis.

The co-operation hypothesis also predicts that females should nest densely in order to facilitate group nest defense, sharing knowledge of food resources, or to decrease the chance that any one nest will be preyed upon. If it is beneficial to nest close to others' nests, female RS should increase with increasing nest density. The competition hypothesis predicts that female RS should decrease with increasing nest density.

Female density was measured in two ways. One method was to measure territory area divided by the harem size to give values in m^2/female , and the other method was to measure the distance from a nest to the three nearest active nests. The east and west ends of the marsh were analysed separately because distances between nests were not the same at both areas. There was no relationship between female RS (measured as y/n to include the effects of predation) and either the area per female or the density of nests (Figures 7 and 8 respectively). This result is not consistent with either the co-operation or the competition hypotheses.

Co-operation should also be facilitated by females synchronizing their nesting cycles. Female RS should therefore increase as nests within a harem approach synchrony. Conversely, if females are competitive, their RS should decrease as nest initiation dates within harems approach synchrony. Since the primary females stand to lose the most from nesting synchronously, their RS should be affected more than the RS of secondary or tertiary females when nests were initiated on the same day, i.e. the RS of primary females should show a steeper relationship as nest initiation dates approach synchrony.

The distribution of nests in time was analysed by comparing the

number of days between initiation of the primary and secondary females' nests and between the secondary and tertiary females' nests. The number of days between the initiation of consecutive nests did not affect RS (y/n, y/s, %s, Figures 9 and 10). Additionally, the relationship between RS of primary females and the number of days between nest initiation dates within territories was not steeper than that of secondary or tertiary females. Thus, primary females did not suffer a relatively greater loss in RS when subsequent nests were initiated close in time. Thus, neither the co-operation nor the competition hypotheses were supported.

Discussion

The co-operation hypothesis proposed by Altmann et al. (1977) did not explain why female yellow-headed blackbirds nest polygynously. Many territories were settled simultaneously rather than one at a time and nests were not clumped in time or space as predicted by the hypothesis. Females were aggressive toward intruding female mounts, contrary to the hypothesis. Finally, female RS did not increase with increasing harem size, nest density, or as nest initiation dates approached synchrony, as predicted by the hypothesis.

The competition hypothesis was partially supported in three of the five predictions: 1) nests were slightly, but non-significantly dispersed in space within territories, 2) females were aggressive to intruder female mounts, but more so late in the nesting cycle as opposed to early as predicted by the hypothesis, and 3) males interfered with resident females' attempts to attack the intruding female mount.

None of the five predictions of the competition hypothesis was completely met: 1) nests were not dispersed in space within territories, and the time between the initiation of the primary and secondary females' nests was not greater than the time between initiation of the secondary and tertiary females' nests, as suggested by Yasukawa and Searcy (1981), 2) resident females were not more aggressive to the intruding female mount at the beginning of their nesting cycle, 3) the primary female was not the most aggressive towards intruders, 4) whether or not a male chased the resident female from the intruding female mount did not affect recruitment (eventual harem size), and 5) female RS was not lower when nests were initiated close in time or space. Primary females did not have

lower RS than secondary or tertiary females when the subsequent nest was initiated close in time.

There may be several explanations for why the data for female yellow-headed blackbirds did not support the predictions of the competition hypothesis. Alexander (1974) suggested that females may be competitive in order to defend food resources and good nest sites. This seems to be true for female dunnocks (*Prunella modularis*) (Davies 1985). Nest distribution in the present study appeared not to be influenced by competitive interactions among females. Females need only be competitive if nest distributions affect female RS. Since there was no relationship between nest distribution and female RS, then there may be no reason to expect females to be competitive. This does not necessarily mean that females settled randomly. Nest distributions were random (neither clumped nor repulsed) but this may be due to females settling non-randomly in randomly distributed resources. However, it seems unlikely that females chose where to settle based on territory resources, as females did not use the territory for food, but instead they fed mainly away from the territory (see chapters 3 and 4). In addition, no habitat variables were found to be correlated with female RS, nor were suitable nest sites in short supply (see chapters 3 and 4).

Marsh-nesting birds suffer among the highest levels of nestling mortality, chiefly from predation (Ricklefs 1969). It would be advantageous for females to build their nests far away from each other if predation was density-dependent (Alexander 1974). Weatherhead and Robertson (1977a) found that high nest density increased predation in red-winged blackbirds. However, predation was not related to nest density for dickcissels (*Spiza americana*, Zimmerman 1984) or for pied

flycatchers (*Ficedula hypoleuca*, Alatalo and Lundberg 1984). It was also found that predation was not affected by nest density in the present study (see chapter 4), so this factor may not be an important cost of polygyny.

The high level of female aggression during the nestling stage as opposed to the egg-laying stage in this study was similar to that found by LaPrade and Graves (1982) for red-winged blackbirds. It is not clear why intruding females present a threat at this stage, but the pattern is certainly not consistent with the competition hypothesis.

Aggression of resident females to potential settlers early in the nesting cycle may be due to guarding male parental investment (Alexander 1974, Yasukawa and Searcy 1982). Primary females should act to deter later females from settling more than secondary or tertiary do only if male care affects female reproductive success. Yasukawa and Searcy (1981) found that nests within a territory were initiated apart in time in an area where males helped feed nestlings in red-winged blackbirds. If male contributions are not important, then females need not be as competitive as assumed by the hypothesis. Blakley (1976) observed no interactions among females in a population of red-winged blackbirds where males did not help feed nestlings. Male presence at the nest may be more valuable in deterring predators than preventing nestling starvation (Patterson et al. 1980, Rutberg and Rohwer 1980), and this aspect of male behaviour is shareable among females within a harem. The yellow-headed blackbird females in this study exhibited only low levels of aggression to intruding female mounts during egg laying and primary females were not more aggressive than secondary or tertiary females, which may mean that male help does not affect female reproductive success (see chapter 4).

Yellow-headed blackbirds have a short breeding season with little re-nesting and 75% of nests are initiated within 1 week (personal observation). One would predict a high level of aggression among resident females in this species to delay later settlers since the pressure of settling in short time would tend to promote nesting synchrony. Female yellow-headed blackbird nests were not synchronous, yet this was not due to aggression of resident females to potential settlers during the early stages of the nesting cycle. A similar observation was made by Wittenberger (1980) who noted that female bobolinks (*Dolichonyx oryzivorus*) were not aggressive to settlers, but their nests were nonetheless asynchronous. Competition may, however, not take the form of observable aggression; females may avoid settling close in time and/or space to established nests. Most often competition between females is more subtle than that between males (Altmann et al. 1977).

Males interfered with aggression between females and this supports the idea that female aggression can potentially deter later settlers and males must act to reduce the aggression in order to recruit more females (Downhower and Armitage 1971, Weatherhead and Robertson 1977b, 1981). Male dunnocks have also been found to interfere with aggression between females (Davies 1985). However, it was found that male interference with the resident female's aggression toward an intruding female mount did not affect his eventual harem size. Males should be able to recruit more females by interfering with this aggression. In addition, only 40% of males exhibited this interference behaviour. That male interference was not widespread nor important in recruiting females supports the idea that later females were avoiding settling near resident females, or that females were settling without regard to other females.

Female yellow-headed blackbirds were not as competitive as assumed in hypotheses developed using data on other poygynous species (Verner and Willson 1966, Orians 1969, Weatherhead and Robertson 1979). The competition hypothesis implies that there are some non-shareable aspects to the territory and/or male, yet this assumption may not hold if females do not use the territory for food and if ~~male help~~ does not affect female reproductive success. There was no relationship between nest density and female RS, so there may be no reason for females to be competitive. It would be instructive to determine whether or not males or territories influence where females settle. In chapter 2 the observed order in which females settled is compared to that expected if they were influenced mainly by the quality of territory and quality of male, or if they settled randomly.

Introduction

In most bird species, females choose mates from available males and therefore are the sex which controls whether or not polygyny occurs (Orlans 1969). Polygyny has been assumed to be reproductively costly to a female because females within a harem may compete for resources, or they may each receive a reduced amount of male parental care, or predators may be more attracted to the territory due to the high density of nests. If females have evolved mate selection mechanisms which would enable them to maximize their fitness, then a female should only settle with an already mated male if the fitness she could expect would be at least equal to that she could expect to achieve by mating monogamously (Orlans 1969).

Female reproductive success (RS, the number of young fledged) is assumed to increase with increasing territory quality (Figure 11a) because the territory provides food and nest sites. Verner (1964), Verner and Willson (1966) and Orlans (1969) suggested that, through competition among males, the best males come to hold the best territories. Orlans (1969) suggested that female RS should be affected by both the territory and male, a combination Wittenberger (1976) termed the 'breeding situation'. However, in Orlans' (1969) graphical model, he assumed that the quality of the territory affected female RS to a greater degree than male quality. Male quality may influence female RS because some males may be better at defending the nest from predators or feeding nestlings. While territory quality only influences a female's immediate RS, the quality of male may also influence a female's long-term RS because her

offspring would inherit his superior genes. Wittenberger (1976) assumed that male and territory quality are highly correlated, as in the VWO hypothesis. If territory quality is highly correlated with male quality, then a female need only base her choice of mate on the quality of his territory to maximize her expected RS (Verner and Willson 1966). Since the addition of females to a territory lowers the expected RS of all the females on the territory, a female should only settle polygynously when the quality of the territory is high enough that she would achieve at least the same RS as if she chose monogamy on a poorer territory (Figure 11a). The minimum difference in territory quality required to induce a female to nest polygynously has been termed the 'polygyny threshold' (Orlans 1969)(Figure 11a). The hypothesis that females choose mates by the quality of their territories so as to maximize their RS will be referred to as the VWO hypothesis in this paper.

A modification of the VWO hypothesis was presented by Weatherhead and Robertson (1977b, 1979). They suggested that under some circumstances, such as site dominance and site fidelity (i.e. returning to the same territory as in previous years) by males, male quality and territory quality may become only weakly correlated. Recently, Eckert (1985) has demonstrated that the quality (as measured by competitive abilities) of male red-winged blackbirds (*Agelaius phoeniceus*) was not strongly correlated with territory quality. In this case, a female must base her decision of where to settle on both territory quality and male quality to get the best breeding situation. Weatherhead and Robertson (1977b, 1979) suggested that females may choose breeding situations so as to maximize their fitness (the proportion that an individual's genes comprise of the total gene pool, over future generations) rather than their

RS (as in the VWO hypothesis). According to Weatherhead and Robertson, females may choose polygyny sooner than they would if they settled so as to maximize their RS (Figure 11b). Females that suffer a loss in RS by mating with a high quality male are assumed to recoup that loss through their sons who inherit some of their father's ability to acquire large harems (the sexy son hypothesis). Females would therefore maximize the number of grandoffspring they have, which is a function of their fitness. In this hypothesis, as in the VWO, territory quality is assumed to have a greater effect on female RS than male quality, such that the combination of the poorest quality male on the best territory still offers females (in the same sized harem) higher RS than the combination of the best male on the poorer quality territory.

A basic assumption of both hypotheses is that females are capable of assessing the options of where to settle and can choose the best situation available at the time they settle. However, under some circumstances, it may not be possible or economical for a female to assess the male or territory (Wittenberger 1981b, Oring 1982, Mock 1983). For instance, when the female is settling the quality of the territory may be very different from what it would be when the nestlings are being reared. This time lag may create some unpredictability (Wittenberger 1981b) so that a female is unable to make an accurate assessment of the future territory quality. Additionally, it may not be economical for a female to spend time choosing a mate if there is little variability in quality among territories or males.

The VWO and sexy son hypotheses also assume that females within a harem have a negative effect on each other and therefore it is detrimental to be polygynous. It is possible that females within a harem have a

positive effect on each other by co-operating in nest defense or locating food and that it is beneficial to be polygynous (Altmann et al. 1977). However, in chapter 1 it was shown that the reason female yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) were polygynous was not because they benefitted from associating with each other.

An alternate hypothesis proposed in this paper is that females settle within suitable habitat without regard to territory boundaries, other females, or male features (the null hypothesis). This 'random' settling may be the most economical when territory or male quality are unpredictable or not very variable.

Several predictions can be made from the three hypotheses stated above regarding the order in which females should choose mates and how this should affect their RS. No study to date has tested the VWO, sexy son and null hypotheses in this manner. The purpose of the present study was to test predictions of the VWO, sexy son, and null hypotheses of mate choice in polygynous species with data from the yellow-headed blackbird.

To illustrate how the predictions of the three models differ, consider the following hypothetical situation. A marsh contains three males with territories of different qualities on which eight females settle (Figure 12). A female that settles first on the breeding area will have all options available to her, and she should be able to make the best choice of mate and territory. The order in which females should settle on these three territories when territory quality is highly correlated with male quality and territory quality has a greater effect on female RS than does male quality, as assumed by the VWO hypothesis, is shown in Figure 12a. A hypothetical order in which females may settle on the three territories when territory quality is not strongly correlated with male quality, as

assumed in the sexy son hypothesis, is shown in Figure 12b. For both hypotheses, it can be seen that a female's expected RS is reduced by later females settling on the same territory such that the RS of all females within a harem is equal to that of the last female to settle (the trigamous curve). An exception to this could occur if males only helped feed nestlings of the first female to settle and this assistance affected female RS. If this occurred, later settling females would reduce the RS of the first female, but not quite to the level illustrated by the trigamous curve. Because a female cannot predict how many later females will settle in the same harem, any predictions which examine settling patterns of females and their expected RS should be restricted either to the last females to settle in a harem or to females that end up in the same sized harems. In this way, either the expected RS of a female will not be affected by later settlers, or the effect will be the same.

One prediction of the VW0 hypothesis is that among the last females to settle on a territory, female RS should be negatively correlated with the order in which they settle. In Figure 12a, the RS of female 4" should be higher than that of female 7'. Conversely, the sexy son hypothesis predicts that the RS of last females to settle on territories should not be strongly correlated with the order in which they settle because they are not choosing mates based only on their expected RS in the present breeding season. For example, in figure 12b, female 8 will have higher RS than females 5 or 7. The null hypothesis predicts that the RS of last females to settle on territories should not be correlated with the order in which they settle (as in the sexy son hypothesis) because they are settling without regard to territory boundaries or other females within habitat that is uniformly suitable and are not deciding where to settle based on their

expected RS. Thus, from these predictions it is possible to distinguish between the VWO and the other two hypotheses.

A second prediction of the VWO hypothesis stems from the assumption that the first polygynous female to settle should settle on a territory which offers her the highest expected RS. Therefore, for females in harems of equal size, the reproductive success of all females should be negatively correlated with the order in which the harems achieved their final size (i.e. the order in which last females in those harems settled). This prediction is a corollary of the one above. It follows because, according to the graphical model, the success of all females in a harem is equal to that of the last female to settle in the harem. For example, in figure 12a, a female settling second on a territory (eg. female 2') should have higher or equal RS than a later female settling second on a territory (female 4'). Female 2' should also have higher or equal RS than a later female settling first on a territory (female 4 if she ended up in a harem of three). The sexy son hypothesis predicts that among females in harems of equal size, RS will not be correlated with the order in which those harems achieved their final size because females are not choosing mates so as to maximize their immediate RS. From figure 12b, female 3 has lower RS than a later settling female that is also second on a territory (female 5') and female 7 has lower RS than female 8 (if female 7 ended up in a harem of three). However, female 5' does have higher RS than female 7. The null hypothesis also predicts that there would be no correlation between the RS of females in the same sized harems and the order the harems received their last female because they are not choosing mates based on their expected RS. From these predictions, the VWO hypothesis can be distinguished from the sexy son and null hypotheses.

A third prediction of the VWO hypothesis is that the order of territories chosen by the first females to settle will be highly positively correlated with the order that they are chosen by the second females to settle within the same territories (Altmann et al. 1977). From figure 12a, territory A should be chosen before territories B or C. The sexy son and null hypotheses both predict that there would not necessarily be a strong positive correlation between the order that territories are chosen by first and second settlers. These predictions can distinguish the VWO from the sexy son and null hypotheses.

A fourth prediction that has been proposed for the VWO hypothesis is that for females settling at the same time there should be no relationship between female RS and harem size (Garson et al. 1980). However, this prediction is not valid because later settlers reduce the RS of earlier settlers on the same territory and therefore the expected RS of females settling at the same time may be different from their realized RS. Therefore the prediction is that there would be no relationship between female RS and harem size for the last females to settle on each territory. The sexy son hypothesis predicts that females settling in larger harems should have lower RS than females settling at the same time in smaller harems, for the last females to settle on a territory. This would occur because, by definition, males which can attract many females do so due to their genetic quality which would not increase female RS in the present breeding season. In figure 12b, female 5 is in a harem of three and has lower RS than female 5' which settles at the same time (if she ended up in a harem of two). The null hypothesis predicts that there would be no relationship between the RS of females settling at the same time and harem size, as in the VWO hypothesis. From the above prediction, it is

only possible to support or not support the sexy son hypothesis:

The VWO and null hypotheses predict that the first territories settled will end up with the largest harems (Orlans 1969), but for different reasons. In the VWO hypothesis, the best quality territory would be settled first and would be the one with high enough quality to compensate females for mating polygynously. For the null hypothesis, since females are assumed to settle in an unpredictable manner, the first territories settled would end up with the most females, for territories of equal size. This would occur since each territory would have equal probability of having females settle on it every day of the settling period. The sexy son hypothesis predicts that later territories settled may get the largest harems because females are being induced to nest polygynously by the quality of the male in addition to the quality of the territory. These predictions can be used to distinguish between the sexy son and the other two hypotheses.

The null hypothesis predicts that if females settle without being influenced by other females or by territory or male quality, the largest territory should get the most females, provided that the total area of large territories is no less than the total area of small territories. The VWO and sexy son hypotheses do not predict any relationship between territory size and harem size, unless territory size is related to territory quality. However, several studies have found no relationship between territory size and territory quality (Willson 1966 for yellow-headed blackbirds, Bédard and LaPointe 1984 for savannah sparrows *Passerculus sandwichensis*, this study - see Chapter 3). Additionally, in chapter 1 it was shown that the density of females on a territory did not affect their RS, thus it appears that territory size is not synonymous with territory

quality. These predictions can be used to distinguish the null hypothesis from the VWO and sexy son hypotheses.

The VWO and sexy son hypotheses assume that females are competitive, therefore they predict a repulsion of nests in both time and space. The null hypothesis predicts that there would be no pattern to the distribution of nests, neither clumped nor repulsed. These predictions can differentiate the null from the VWO and sexy son hypotheses. All of the above sets of predictions can, in combination, be used to unambiguously distinguish among the three hypotheses.

Methods

See General Methods.

Results

The data from all years were pooled. Individual values are presented in the Appendices.

The first egg layed in the study areas in 1983 was on May 20, on May 15 in 1984 and on May 14 in 1985. To determine female RS relative to the order in which they initiated their nests, the order of dates the first eggs were laid in each nest were ranked and these values were used rather than using the actual dates because the dates that first eggs were laid differed for each year. Since the VWO and sexy son hypotheses assume that later settling females on a territory reduce the RS of females that have already settled, only the RS of the last females to settle on territories were compared. In all three years, RS (the number of young fledged per nest, y/n , the number of young fledged per successful nest, y/s , and the percent of nests successful, $\%s$) was not related to the order in which they settled on the marsh (Figure 13). This result does not support the prediction of the VWO hypothesis, but is consistent with both the sexy son and null hypotheses.

The VWO hypothesis also predicts that for females in the same sized harems later settling females will not have higher RS than earlier settling females. Conversely, the sexy son and null hypotheses predict that later settlers may have higher RS than earlier settlers in harems of the same eventual size. In all years, later settlers had higher RS than earlier settlers more often than vice versa, contrary to the VWO hypothesis. The combined data for all years are shown in Table 4.

The VWO hypothesis also predicts that the order that territories are

chosen by the second females to settle should be highly correlated to the order that territories are chosen by the first females to settle on the same territories. Both the sexy son and null hypotheses predict that there would not be a strong correlation between the order of territories chosen by the second females or first females to settle within the same territories. A Spearman rank correlation revealed that there was no significant relationship between the order that territories were chosen by the first females to settle and the order the same territories were chosen by the second females to settle (Figure 14, $P > 0.05$, correlation coefficient = 0.269), which is not consistent with the VWO hypothesis, but is consistent with the sexy son and null hypotheses.

The sexy son hypothesis predicts that for females settling at the same time, the one in the largest harem will have the lower RS, for the last females to settle on a territory. The VWO and null hypotheses predict that there would be no relationship between the RS of females settling at the same time and harem size. The RS of females settling last in large harems was higher than that of females in small harems 16 times, equal 16 times and lower only 12 times. Thus females settling in large harems did not have lower RS than those settling in small harems, contrary to the prediction of the sexy son hypothesis and consistent with the VWO and null hypotheses.

The sexy son hypothesis predicts that there will be no relationship between the order in which territories are settled and their eventual harem size. Both the VWO and null hypotheses predict that the first territories settled will end up with the largest harems. For all years, the first territories settled ended up with the largest harems (Figure 15, Spearman correlation = -0.504, $P \ll 0.001$). However, this result, used as

support for the null hypothesis, was confounded by differences in territory size. The null hypothesis also predicts that the largest territory should have the most females (see below) since a larger territory has a higher probability of having a female land on it each day that females settle. The above correlation between the order territories were settled and harem size may therefore be due to the larger territories being settled first and ending up with the most females. It is therefore necessary to control for the effect of territory size to examine the relationship between the order that territories were settled and harem size. For the few territories of the same size that had different sized harems, the first territory settled had the most females in the end (Figure 15). This result does not support the sexy son hypothesis but is consistent with both the VWO and null hypotheses.

A final prediction can distinguish the null hypothesis from the VWO and sexy son. If females settle in no particular pattern, the largest territory should end up with the most females. The VWO and sexy son hypotheses predict no relationship between territory size and harem size. This is true for the VWO hypothesis only if territory area is not an index to territory quality. From chapter 1 it was clear that the density of females did not affect female RS, thus territory size is not an aspect of territory quality. There was a significant positive correlation (Spearman correlation coefficient = 0.774, $P < 0.01$) between territory area and harem size (Figure 16), which is consistent with the null hypothesis.

Discussion

The data from this study on settling patterns of female yellow-headed blackbirds do not support predictions from the VWO hypothesis (Verner 1964, Verner and Willson 1966, Orians 1969). Only two predictions of six were met. First, the first territories to receive females ended up with the largest harems. The same result was found by Carey and Nolan (1979) for indigo buntings (*Passerina cyanea*) and used as support for the VWO hypothesis. However, this is the same pattern expected if females settled in no particular pattern, without regard to other females or territory boundaries, as in the null hypothesis. Secondly, the RS of females settling at the same time was no different for females in different sized harems. This result is also consistent with the null hypothesis.

The data supported the sexy son hypothesis (Weatherhead and Robertson (1979), in which male quality is assumed to influence female choice of mates in addition to territory quality, in 3 of the 7 predictions. First, a substantial number of later settling females had higher RS than earlier females, comparing the last females to settle on each territory. This indicates that females were not choosing mates to maximize their RS. A different result was found by Carey and Nolan (1979) who observed that the average number of young for earlier settling female indigo buntings was almost twice that for later settling females, although the difference was not significant, which would support the VWO hypothesis. However, they did not rule out the possibility that there were seasonal effects on RS, as has been shown to occur in pied flycatchers (*Ficedula hypoleuca*, Alatalo et al. 1981). Additionally, Carey and Nolan did not consider that some later settling females may have been yearlings, which have been

found to have lower RS in some species (Martin 1974, Crawford 1977). Yearling female yellow-headed blackbirds can be distinguished from adults by plumage (Willson 1966, Crawford 1977), and yearlings have been observed to nest later than adults (Willson 1966). However, female age was not a confounding factor in the present study since there was no trend for yearling females to settle later (personal observation).

Secondly, some later settlers had higher RS than earlier females in the same eventual harem sizes.

Thirdly, there was no correlation between the order territories were settled by the second females and the order the same territories were chosen by the first females. This result and the previous two results indicate that some early females made the wrong choice of mate if they were choosing to maximize their RS, as assumed in the VWO hypothesis. This supports the idea that later females settled polygynously with superior males with which they could increase their fitness. However, the results from these three predictions are also consistent with the null hypothesis.

The null hypothesis was supported in all 7 of the predictions. Five of the predictions were discussed above. A sixth prediction was that larger territories should have more females on them if females settle in no particular pattern, and this was found to be true. Verner and Engelson (1970) also found a positive correlation between territory area and harem size in long-billed marsh wrens (*Telmatodytes palustris*), and Fincke (1984) found a positive correlation for dickcissels (*Spiza americana*). In other studies Willson (1966) found a negative correlation between territory area and harem size for yellow-headed blackbirds, and Bédard and LaPointe (1984) found no correlation for savannah sparrows. It

appears that the relationship between territory area and harem size is complex.

A final prediction of the null hypothesis is that females should not initiate their nests in a repulsed manner or in a clumped manner in time or in space. The sexy son and VWO hypotheses assume that females within a harem are competitive and that they should initiate their nests apart in time and space from other nests within the territory. In chapter 1 it was concluded that females initiated their nests neither clumped nor repulsed in time or space, which supports the null hypothesis.

In the past it has generally been assumed that the female is the sex which chooses with whom to mate (Orlans 1969, Garson et al. 1980), yet this has rarely been critically challenged. Natural selection should favour females choosing males if males care for the young, or have access to resources, or if they have genotypes which enhance the viability of offspring (Heisler 1981). However, females may not be able to assess territories or males if no accurate cues to their quality are available. For instance, there may be no reliable cues from the male during female settling regarding the quality of paternal care or genetic quality (Searcy 1979a). Likewise, territory quality at the time of female settling may not be a reliable indicator of the quality of the territory when nestlings are being reared (Wittenberger 1981b). Females could wait to settle until they have more reliable information on territory quality, but this would mean that they would be raising their young past the optimal date (Wittenberger 1981b). The pressures of time constraints can have substantial effects on female choice. For instance, Alatalo et al. (1981) suggested that female pied flycatchers were deceived into mating polygynously because they could not afford the time to adequately assess

the mated status of males.

Not only may females be unable to assess mates, but it may not be necessary for them to do so if there is little variability among territories or males. Under these circumstances a female could expect the same RS wherever she settles and therefore settling 'randomly' would be the fastest way to find a mate. Considering that the breeding season of yellow-headed blackbirds is short, with little re-nesting (personal observation), it seems likely that females should settle in the shortest possible time.

If females settle on the marsh in no pattern rather than choose mates based on the quality of their territories or on male quality, then competition among males for territories to gain access to females may be more important than female choice in maintaining polygyny. Males may vary in quality, but this variation may be in characteristics that do not affect female RS. Instead, males may vary in their aggression toward other males, as has been found for red-winged blackbirds (Yasukawa 1979b, Eckert 1985). Aggressive interactions among male yellow-headed blackbirds may be important in competitions for territories to gain access to females. Since females settle in no particular pattern, the most aggressive males would be able to defend the largest territories and would have the largest harems (see chapter 3).

Given that all the predictions of the null hypothesis were supported in the present study, it appears that, based on female settling patterns, females were not influenced to choose mates by the quality of their territories or by the attractiveness of males. To fully understand the question of whether or not there is a basis for female choice it is necessary to determine whether territory and/or male characteristics are

variable, predictable, and affect female RS. This question is examined in chapter 3.

Introduction

Many species of birds are sexually dimorphic with males being larger and more brightly coloured than females. Males often have elaborate courtship displays associated with these morphological traits. This dimorphism is thought to have evolved through the action of sexual selection. Sexual selection is a mechanism which leads to the evolution of traits related to mate acquisition, and variation in these traits is both a cause and a result of differential reproductive success of the sex with the trait (Darwin 1871, Huxley 1938, Fisher 1958).

There are two ways sexual selection can act; by differential female choice of mates, or by competition among males for females (Darwin 1871, Selander 1972). Sexual selection leading to the evolution of brilliant colours and elaborate courtship displays by males may arise because females prefer males with these traits (Darwin 1871, Selander 1972, also see Andersson 1982). The large size of males in dimorphic species is thought to have evolved mainly through competition among males to gain access to females, with larger males being the more successful competitors (Darwin 1871, Selander 1972). Although large males may gain an advantage in competitions with other males, there will be an upper limit on size determined by energy constraints (Searcy 1979d). Males gain access to females usually by competing for territories which contain resources necessary for females to nest. Both variation within traits of males (behavioural or morphological) and variation in their ability to hold territories is most pronounced in polygynous species because sexual selection is stronger in these species (Darwin 1871). The

presence of sexual dimorphism can be used to predict polygyny in species for which the mating system is unknown (Orlans 1969, Carey and Nolan 1979).

In polygynous, territorial species, female reproductive success (RS, number of young fledged) is assumed to increase with increasing quality of the territory (Verner 1964, Verner and Willson 1966) because territories provide food and nest sites. Female RS is also assumed to increase if the male demonstrates superior abilities at feeding offspring, defending the nest from predators, or other beneficial qualities (Verner 1964). However, neither of these assumptions were supported by empirical data. Male quality may also affect female fitness because some males may be genetically superior to others and therefore their offspring would be more viable than those of a poor quality male (Orlans 1969, Wittenberger 1976). Wittenberger (1976) termed the combination of male and territory quality the quality of the 'breeding situation'. In general, polygyny is usually beneficial to males but not to females because it means that females would have to share male help in caring for offspring, or share territory resources, or high nest densities may attract predators (Verner 1964). Females should choose mates so as to maximize their RS, thus females should not mate with an already mated male unless their expected fitness is at least equal to that they could expect by mating with a bachelor (Verner 1964, Verner and Willson 1966). Over the last twenty years, much work has been devoted to assessing the relative importance of male quality and territory quality in inducing a female to mate polygynously (e.g. Verner 1964, Verner and Willson 1966, Orlans 1969, Holm 1973, Martin 1974, Wittenberger 1976, Weatherhead and Robertson 1977a, 1979, Searcy 1979a,b, Lenington 1980, Yasukawa 1981, Alatalo et al. 1981).

Verner (1964) and Verner and Willson (1966) proposed that, through competition among males, the best males come to hold the best territories. They suggested that features of the territory affect female RS more than features of the male and therefore territory quality is the main factor females assess when choosing mates. Females should settle polygynously only when they would achieve the same RS by mating polygynously on the better territory as they could by mating monogamously on a poorer quality territory, that is, the difference in quality of the territories must exceed the 'polygyny threshold' (Verner and Willson 1966). Orians (1969) elaborated on this idea and produced a graphic model illustrating the RS of females on different quality territories mated monogamously or polygynously. This hypothesis that male quality is correlated with territory quality and differences in territory quality compensate a female for mating polygynously will be referred to as the VWO hypothesis in this paper.

Weatherhead and Robertson (1977a, 1979) suggested that male and territory quality may not be highly correlated and that male quality influences female choice of mates in addition to territory quality. Some males attract many females due to their attractiveness and instead of choosing breeding situations to maximize their RS, females choose to maximize their fitness by mating with an attractive male which will sire attractive sons (the sexy son hypothesis).

The two hypotheses outlined above assume that female choice is the most important aspect of sexual selection. It is possible that competition among males to gain access to females is a more important force in the evolution and maintenance of sexual dimorphism and polygyny. A third "null hypothesis" is that females settle without regard to other females or

territory boundaries within suitable habitat and that males superimpose their territorial system on the habitat where females nest. Males may defend resources that are critical to females (e.g. a place to build a nest) as in resource-defense polygyny (Emlen and Oring 1977), however females may not be choosing with whom to mate if all options are equally suitable (see chapter 4). From chapters 1 and 2 it appears that female yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) are not influenced where to settle by other females and do not choose mates based on the quality of male or territory. It was suggested that males compete for territories on the marsh in which females nest. In this chapter, features of males and territories which could affect female RS and which may affect recruitment of females are examined for the yellow-headed blackbird. The data will be used to distinguish among the VWO, sexy son and null hypotheses. The approach taken to examine these three hypotheses is outlined below.

If female choice is important as a mechanism for the maintenance of polygyny in yellow-headed blackbirds, then it should be determined whether females choose mates primarily based on territory features to maximize their RS (VWO hypothesis), or based on male quality in addition to territory quality to maximize their fitness (sexy son hypothesis). If territory quality affects female RS, then it would be expected that some features of the territory would be correlated with female RS and harem size. Several studies have failed to demonstrate such a relationship for other polygynous species (Verner and Engelson 1970, Garson 1978, Bédard and LaPointe 1984), while others have found some positive correlations between territory features and RS (Willson 1966, Zimmerman 1971, Martin 1974, Searcy 1979a, Weatherhead and Robertson 1977a, Lenington 1980,

Catchpole et al. 1985). To examine the importance of territory quality in female choice of mates in the present study on yellow-headed blackbirds, correlations will be sought between territory features and female RS and harem size.

Additionally, if territory quality is important to females then female RS on randomly selected portions of the habitat and the attractiveness of these portions (number of females settling, the order in which they settle relative to other portions) should be correlated year to year. This prediction relies on the assumption that the relative quality of the portions does not change year to year. These random portions of the habitat, the edges of which do not correspond to real territory boundaries, will be referred to as 'arbitrary territories' in this paper. Searcy (1979a) concluded that territory quality was more important than male quality by examining the number of female red-winged blackbirds (*Agelaius phoeniceus*) nesting on arbitrary territories year to year. In the same species, Yasukawa (1981) found that the number of females on arbitrary territories was correlated with the proportion of males returning to those territories, and concluded that male quality was more important than territory quality. Examining attractiveness of arbitrary territories to determine whether territory quality affects female choice of where to settle should be less ambiguous in the yellow-headed blackbird because the males did not exhibit site fidelity (personal observation), contrary to the red-winged blackbird (Nero 1956, Case and Hewitt 1963). In this paper, the attractiveness of arbitrary territories and the RS of females on these territories over a three year period will be examined.

A basic assumption of the VWO hypothesis is that male quality (parental care, competitive abilities, and genetic features) is highly

correlated with territory quality. If this is true, then some features of males (behavioural or morphological) should affect female RS for the reasons outlined below. Male behaviour should affect female RS because males may be important in defending the nest against predators or in feeding nestlings (Verner 1964). Male behaviour should also affect female RS if more competitive males are able to secure the best territories (Verner 1964, Verner and Willson 1966). Male morphology should be correlated with female RS because larger males may be better at deterring predators and large size (up to some maximum size) may be correlated with experience (i.e. age) at feeding nestlings and defending the nest (Yasukawa 1981). Large males may also be more dominant (Searcy 1979b,c, Yasukawa 1981, Petrie 1984), which may indicate they are better competitors. These features will be examined for yellow-headed blackbirds in this study.

A basic premise of the sexy son hypothesis (Weatherhead and Robertson 1979) is that females choose males for their quality, in addition to the quality of the territory, which would maximize females' inclusive fitness through the high pairing success of their sons. Features of males which enhance recruitment and are passed on to sons would be genetically determined. Many studies have found that females choose males based on characteristics that are genetically determined (e.g. Maynard Smith 1956, Lowther 1961, Mason 1964, O'Donald 1973, Ayala and Campbell 1974). If some males are more successful at recruiting females than others then it would be expected that some male characteristics (morphological or behavioural) should be positively correlated with harem size. For instance, males may differ in their courtship intensity (Weatherhead and Robertson 1977b, Yasukawa 1981), plumage characteristics (Andersson

1982), size (Yasukawa 1981), or vocalizations (Loffredo and Borgia 1986), all of which have been shown to affect recruitment of females. Features of male yellow-headed blackbirds and the effect on recruitment of females will be examined in this study.

If competition among males is more important than female choice in maintaining polygyny and sexual dimorphism in yellow-headed blackbirds (the null hypothesis), then some features of males should be correlated with their competitive abilities. It was found in chapter 2 that the pattern of female settling did not correspond to that expected if they chose mates based on the territory or the male and that the largest territories had the most females, therefore differences in male competitive abilities should be expressed by differences in territory size. Competitive abilities of males have been observed to be correlated with body size (Thompson 1960, Rand 1967, Bouissou 1972, Drickamer et al. 1973, Barlow and Ballin 1976, Searcy 1979c, Yasukawa 1981), male age (experience) (LeBoeuf 1974, Lill 1974, Searcy 1979b, Yasukawa 1981), colouration (Peek 1972, Smith 1972, Harrington 1973, Rohwer 1975, Roskoff and Rohwer 1985), and aggression (Allee et al. 1939, Rose et al. 1971, Eaton and Resko 1974, Spurr 1974). The effect of these features of male yellow-headed blackbirds on their ability to maintain a territory and on territory size will be determined in this study.

Methods

In addition to that which follows, see also General Methods.

Features of territories and nest sites were measured in 1983 and 1984. Territory features were measured at four sites per territory which were randomly selected by placing a grid over a map of the territory and using a random numbers table to choose the number of grid lines north and east from the southwest edge of the territory. In a 1 m² quadrat placed at each sample site, the following measurements were made within 3 days during the female settling period: water depth (used as a measure of accessibility to terrestrial predators, done by placing a metre stick on a board resting lightly on the substrate), mean stem height and number of stems (both used as a measure of potential concealment from predators or adverse weather) and proximity (m) to open water (to determine whether the territory was central or toward the edge of the habitat, near the uplands and terrestrial predators). Human activity on the marsh during the habitat measurement period did not affect female settling. Territory area (excluding open water), and amount of vegetation-water edge (a measure of food availability, since insects frequently emerge from the edge area) was also determined from aerial photographs and observations from the ground. The following features of nest sites were measured in a 1 m² quadrat with the nest in the centre: water depth (as above), mean stem height, number of stems, proximity to open water, number of stems supporting the nest, nest height above the water (a measure of accessibility of nest to ground predators), and vegetation height above the nest (a measure of nest concealment from aerial predators).

Measurements at nest sites were done in a period of two days after all nests had been initiated.

Arbitrary territories the size an average male's territory (0.04 ha) were drawn on maps of the marsh. This was done by plotting squares corresponding to 20m by 20m side by side on the maps beginning at the east side of the map and continuing to the far west side. The arbitrary territories did not correspond to actual territories held by males. The order that arbitrary territories were settled by females, the RS of females, and the number of females nesting simultaneously on each arbitrary territory were recorded for each year and compared using G tests of association (Sokal and Rohlf 1969). The order that territories were settled was only compared between 1984 and 1985.

The following morphological measurements were made on territorial males: weight (g), tarsus length (mm), bill length (mm), flattened wing length (mm) (measured from wrist to tip of primaries), and male head colouration was scored on an integer scale from 1 (dark, abundant black flecks in the yellow) to 5 (bright yellow, no dark flecks).

Behaviour of males was recorded by daily observations from 6 am to 12 noon and from 4 pm to 10 pm throughout the breeding season. Males were not observed in the early afternoon because overall bird activity was low at this time. Each male was observed for a 1 hour period and the nature of his activity was recorded every 15 seconds. Up to three males could be observed at once if their territories were adjacent. From this information, the amount of time a male spent in each activity could be determined to produce a daily 'time budget'.

To assess male courtship abilities, male behaviour toward a taxidermic mount of a female in a copulatory position, placed in the centre of their

territory, was recorded for a 5 minute period. An overall response score was calculated as the sum of the score for each behavioural act (Table 3) multiplied by the duration each behaviour was performed.

To assess male behaviour toward intruding males, the behaviour of territorial males toward a taxidermic mount of an adult male was recorded and an overall aggression score determined (as for the female mount).

Results

Territory quality

If females choose mates based on the quality of their territories, then some territory and nest site features should be correlated with female RS and harem size. Table 5 shows that there were a few correlations between territory features and either female RS or harem size. It is unlikely that any of the significant correlations were meaningful since some correlation coefficients were significant in one year but far from significant in the other year. Data from 1983 and 1984 are presented in table 5 separately to illustrate the lack of consistency of correlations in each year. In addition, only one of the significant correlations was greater than 0.5 (stem density in 1983, although in 1984 the coefficient was < 0.1), which indicates that the relationships were weak. No features of the nest site were correlated with female RS in either year (Table 5).

An indirect way to determine whether territory quality influences female choice of where to nest is by examining the attractiveness (number of females settling, date of settling) of arbitrary portions of the habitat year to year, and the RS of females on those arbitrary territories. There was no association in the order that the territories were settled by females between 1984 and 1985 (east end: $G = 12.06$, $df = 15$, $P > 0.5$; west end: $G = 8.22$, $df = 7$, $P > 0.1$) or in the eventual number of females nesting at the same time within an arbitrary territory (east end: $G = 21.94$, $df = 34$, $P > 0.9$; west end: $G = 21.51$, $df = 26$, $P > 0.5$, Table 6). In addition, there was no association across years in female RS (y/n) on arbitrary territories (east end: $G = 7.8$, $df = 8$, $P > 0.1$; west end: $G = 12.1$, $df = 10$, $P > 0.1$, Table 6). The relative mean water depth, vegetation height,

vegetation density within arbitrary territories was similar in all three years (G tests, all $P < 0.5$ for east and west ends). From this result it can be assumed that the relative quality of the habitat did not change in an obvious manner over the three years. These results indicate that territory quality (at least as measured) did not influence where females settled.

Male quality - effects on female RS

If females choose mates based on male qualities such as nest defense abilities or parental care, then some features of males that females could assess when settling should serve as cues to their parental abilities and hence should be correlated with nest success. No morphological or behavioural features were observed to be correlated with female RS (Tables 7 and 8). In addition, no male behaviours which should deter predators, such as time spent on the territory or the amount of time the male was on his territory alert were found to correlate with female RS (Table 8).

If male quality is correlated with territory quality, then the best males (as measured by parental and competitive abilities) would hold the best territories. Males should have the ownership of territories established by the time females settle and should not switch territories after females have started nesting because this would change the correlation between male and territory quality. Since females are assumed to choose the combination of male and territory quality that would maximize their expected RS, then if switches in territory ownership do happen, it should be detrimental to a female's RS. This loss in RS would arise because new males would not be expected to offer any parental care to offspring that they did not sire (see Rutberg and Rohwer 1980). It was observed that many territory boundaries shifted after females had built their nests.

Often the new boundary would exclude a nest that was previously inside, or include a new nest that was previously in an adjacent territory. There was one case in 1983 and one in 1985 where a male abandoned his territory after females had started incubating. These males were observed occasionally in adjacent fields. In these two cases, no new male moved in, nor did adjacent males expand their territories to incorporate part of the abandoned territory. If male quality (as measured by parental abilities) was important then these females should have suffered reduced RS. The RS of females mated to males with stable territory boundaries was no different from that of females on territories where a new male moved in, or took over a portion of their previous mates' territory, or for females whose mates abandoned them (Table 9). There were few behavioural differences among the three groups of males. Males which moved in or took over portions of other territories were more aggressive than males that moved out or males that were stable, yet the females on these territories did not have higher RS (Table 9). Stable males spent slightly more time alert than either males that moved in or out, but this did not affect female RS (Table 9). These results do not support the idea that male quality (as measured by parental and competitive abilities) was correlated with territory quality.

Male quality - attractiveness

— If the sexy son hypothesis is true and females choose combinations of males and territories so as to maximize their fitness through having sons that will attract large harems, then some males should be better at recruiting females than others. No morphological features of males were found to affect recruitment of females (harem size and density of females, Table 7). In addition, males which spent a lot of time courting

females did not recruit more females (Table 8a).

Another way of assessing male courtship abilities was by the female mount presentations. All males responded to the female mount in the first half of the breeding season. Many males attempted to copulate with the mount, but responses varied enormously. Response scores of males were not correlated with eventual harem sizes or with the density of females on the territory (Figure 17), indicating that males which were more vigorous courters did not recruit more females. By the time most nests contained nestlings, many males failed to respond to the mount. One notable exception was a 2-year old male that had been banded on the study area as a juvenile the year before. He maintained the highest response score for the first mount presentations before females had arrived, and continued to have this high response after many nestlings had fledged. Despite his vigorous response, this male had a harem of only three females (which was the average harem size) and the density of females was low ($0.008 \text{ females/m}^2$).

Females mating polygynously are expected to recoup the loss in RS from mating polygynously by having sons which will inherit some of their father's ability to recruit females. Males which can attract large harems are assumed to be of high quality because these males will have many grandoffspring. If this assumption is true, it follows that females in large harems should be faithful to their mates and should not solicit copulations from other males. Over the three years, 32 copulations were observed and of these 16 were extra-pair copulations. Of females in large harems (≥ 4), 7 of 19 copulations were extra-pair copulations. These cases of infidelity usually occurred when a male on a nearby territory intruded on a territory when the owner was off the marsh. Additionally,

females assumed a pre-copulatory position to any male that landed nearby or flew overhead. This behaviour of females would not be expected if they were choosing to mate polygynously so as to maximize their fitness through having sons that resemble their fathers in their ability to attract large harems. /

If the null hypothesis is true and females do not choose males or territories, but settle without regard to other birds, then there should be competition among males for territories to gain access to females. A measure of the relative competitive abilities of males is their response to an intruding male mount place in their territory. Mount presentations were done until females arrived on the study areas. The response of territorial males to the mount was variable, with only three direct attacks observed. Response scores of males were significantly, positively correlated with their territory size and eventual harem size (Figure 18). Other measures of male aggression included how long it took them to approach the mount after having noticed it, and how close they came to it. Males which approached quickly and came closer were assumed to be the most aggressive and were observed to have the largest territories (Spearman correlation with territory area: minimum distance to mount, $r = -0.77$, $P < 0.01$, time to approach mount $r = -0.78$, $P < 0.02$). As mentioned earlier, males which moved in or took over portions of territories where females had already started nesting were more aggressive than those which moved off territories or whose territory boundaries were stable (Table 9). It appears that male aggression was important in securing a territory.

Discussion

Female yellow-headed blackbirds do not appear to be influenced by territory or male quality when settling on the breeding area, contrary to the VWO and sexy son hypotheses. The VWO hypothesis assumes that the quality of a territory should affect female RS and therefore its attractiveness to females. A territory provides nest sites, shelter, and for some species, food, thus it would be expected that some territory features available when females settle would serve as indicators of future territory quality and would be correlated with female RS, harem size and the order territories were settled by females. In the present study, there were no consistent significant correlations with territory features, contrary to what would be expected if females chose where to settle based mainly on territory quality.

Several other studies have also failed to demonstrate a relationship between territory features and harem size or female RS (Zimmerman 1966, Haigh 1968, Verner and Engelson 1970, Bédard and LaPointe 1984). However, other studies have shown that some territory features did affect harem size (Wilson 1966, Martin 1974, Monahan 1977, Lenington 1980, Catchpole et al. 1985) or female RS (Martin 1974, Weatherhead and Robertson 1977a, Searcy 1979a, Shipley 1979). Caution is required when using correlations as evidence for the importance of territory quality because they can be spurious. The lack of correlations between territory features and female RS, harem size and the order that territories were chosen in the present study supports the idea that these features are either not important to females or not variable. It could be argued that the lack of correlations merely indicates that the features which are

important to females were not measured. This may be true, but all the features that had been measured in other studies and found to be important were measured in the present study. It is possible that there were no cues available at the time females settled regarding the quality of the territory during the nestling stage (Wittenberger 1981b). If future territory quality was unpredictable, then females could not choose territories based on qualities which would affect nestling growth and survival.

Another feature of territories that may affect female RS is food abundance. Differences in food levels within territories have been suggested to influence the occurrence of polygyny in other populations of yellow-headed blackbirds (Willson 1966), bobolinks (Wittenberger 1980), and great reed warblers (Catchpole et al. 1985). However, the amount of water-vegetation edge was not correlated with female RS or harem size. Additionally, the birds in the present study rarely fed on the territory. Therefore the fact that food abundance on territories was not measured could not be considered to be the missing critical variable affecting females. Since all the territories were within 200 m of the upland feeding areas, it cannot be argued that some territories are superior to others because they are closer to food.

An indirect way to assess the importance of territory features in a female's choice of where to settle is to look at the attractiveness of arbitrary portions of the marsh and female RS on these arbitrary territories. Searcy (1979a) found that harem sizes of red-winged blackbirds were the same year to year on arbitrary territories, and suggested that territory quality was important in influencing where females settled. However, several of the same males returned to the arbitrary territories each year, and therefore the influence of male quality

cannot be ruled out (Searcy 1979a, Yasukawa 1981). The confounding effects of site fidelity by males were not important in the present study because males did not return to their former territories. Mayfield (1960) suggested that female Kirtland's warblers (*Dendroica kirtlandii*) chose territories and not males because females returned to the same territory year to year even though their previous mate was nearby on a different territory. This same result was found by Nolan (1978) for prairie warblers (*D. discolor*). In the present study, no association was found in female yellow-headed blackbirds' RS, the order that arbitrary territories were settled, or the number of females nesting on arbitrary territories across three years. This lack of association was not due to the habitat changing year to year. It is possible that the relative importance of male or territory quality on a female's choice of mate varies among species and perhaps a generalized hypothesis is not appropriate.

The VWO hypothesis assumes that male quality is highly correlated with territory quality and that male quality can influence a female's RS, and hence a female's choice of mate. Females may choose males based on features which serve as markers of their parental abilities, as in red-winged blackbirds (Searcy and Yasukawa 1981b, Eckert 1985), cichlids (Perrone 1975), and scorpionflies (Thornhill 1976). In other studies, male vigilance has been observed to decrease the likelihood of a nest being preyed upon (Patterson et al. 1980), and male help in feeding young has been found to decrease the amount of nestling starvation (Dyrce 1977, Catchpole et al. 1985). However, parental investment is a male feature that females would not be able to assess directly when choosing a mate. Therefore, it would be expected that some behavioural or morphological feature would serve as a cue to male quality (as measured by parental

abilities). Some features of male red-winged blackbirds that have been found to be correlated with their parental abilities are courtship intensity (Searcy and Yasukawa 1981b), epaulet size and dominance status (Eckert 1985). In the present study, there were no features of males during female settling that affected female RS. This may be due to two reasons. Firstly, perhaps no male features that were measured were cues as to male parental abilities. Secondly, it is possible that male parental investment does not even influence female RS since no male behaviours (feeding of nestlings and behaviours that should deter predators) during the nestling period affected predation or the number of young fledged per nest (see chapter 4).

Even if male quality does not influence female RS in the immediate breeding season it is possible that male help in feeding nestlings is beneficial in other ways. Nestlings which are fed by two parents may weigh more at fledging (Martin 1974, Patterson 1979, Patterson et al. 1980, Wittenberger 1980, Richter 1984, but see chapter 4) and as a result may survive better (Perrins 1965; Howe 1979, Fiala 1981). Male help may also reduce the amount of work a female does in feeding nestlings, as in bobolinks (Martin 1974), and therefore she may be in better condition at the end of the breeding season. This may enable a female to survive better to reproduce in future years, thus male help may affect a female's lifetime RS (Elliott 1975). These aspects of male help do not apply to the population of yellow-headed blackbirds used in the present study because males did not provide much assistance in feeding nestlings (see chapter 4).

Another aspect to male quality is genetic quality (e.g. their survival abilities, the quality of their sperm). Female choice based on males' genetic quality may be influenced by male characteristics that increase

the viability of young, or the pairing success of their sons (Weatherhead and Robertson 1977a, 1979). If females choose males based on their attractiveness, some males should be able to recruit more females than others. Females have been observed to choose males based on features that may be markers of the male's genetic quality. Borgia et al. (1985) observed that female bowerbirds choose males based on the males' courting area and bower, which may be markers of the males' genetic quality since males only contribute genes and no parental care. Weatherhead and Robertson (1977a) observed that males which courted more intensely were able to recruit a higher density of females (more females per territory area, not larger harems) than males which courted less. They argued that if females are induced to nest densely, suffering a reduced RS, then they must receive some form of compensation, possibly through having offspring that are more viable or sons with high pairing success. Yasukawa (1981) found that males which courted more had larger harems but suggested that this was a cue to males' experience on the breeding area. He argued that females prefer experienced males possibly because experienced males are better at feeding young or defending the nest. Several other studies have found that females prefer larger, older, or more experienced males (Searcy 1979b, Noonan 1983, Winkel and Winkel 1984). However, Weatherhead (1984) presented evidence that the conclusion that females prefer older males because they provide superior parental care is not warranted. He argued that it was possible that females prefer older males because older males may be genetically superior, as evidenced by their having survived longer (Trivers 1972). The effect of male age or experience was not assessed in the present study. This does not appear to be important as the females were not attracted to

males based on their morphology or behaviour. Possible reasons for this are that males do not affect females' RS and/or male features were not very variable (see chapter 4).

One further line of evidence which supports the idea that females do not choose mates on the basis of the genetic quality of males comes from behavioural observations of females toward other males. Female yellow-headed blackbirds in large harems (mated to the most attractive males) frequently copulated with males other than their own mate and solicited copulations from any male that flew over the territory. If females were concerned with mating with males of high quality such that their sons would inherit some of the father's recruitment abilities, it would not be expected that they would solicit copulations. It was also noted that red-winged blackbird females mated with males other than their mates (Bray et al. 1975, Roberts and Kennel 1980). Both these studies observed a high percentage of fertile eggs in nests of females mated to experimentally vasectomized males. Eggs of female bobolinks have been found to have multiple paternity, based on electrophoretic and behavioural evidence (Gavin and Bollinger 1985). Male quality does not seem to influence female choice in collared flycatchers (*Ficedula albicollis*) either, as a high degree of cuckoldry was observed in this species (Alatalo et al. 1984).

If female choice of mates is a relatively unimportant component of sexual selection in the maintenance of polygyny in the yellow-headed blackbird, then an alternate hypothesis that competition among males is important may be true. The VWO hypothesis assumes that there is competition among males for high quality territories because females choose mates on the basis of territory quality. The null hypothesis also

assumes that males compete for territories, but differs from the VWO in that males are not competing for high quality territories because females do not choose mates on the basis of territory quality. Instead, males are assumed to be competing to secure a territory in the first place (because there were many males which did not hold territories), and secondly to secure a large territory.

In an attempt to test the VWO hypothesis, Searcy (1979b) failed to find any strong correlation between harem size and characteristics of male red-winged blackbirds that should affect their ability to secure good territories. Searcy (1979b) did not determine the aggressiveness of males, which may be a characteristic that would affect competition for territories. Yasukawa (1979) found that aggressiveness of male red-winged blackbirds had no effect on their ability to establish territories. However, Searcy (1981) observed that males injected with testosterone tended to take over portions of other males' territories and Peek (1972) found that trespassing occurred more frequently on territories of tranquilized males. These latter two results indicate that aggression may be important in the establishment and maintenance of territories. Aggression by males has been found to be important in territory establishment in greater prairie chickens (*Tympanuchus cupido*, Robel 1972), red grouse (*Lagopus l. scoticus*, Watson and Miller 1971), but not for sharp-tailed grouse (*Pediacetes phasianellus*, Trobec and Oring 1972, Rippin and Boag 1974).

The results from the present study support the idea that males which secure or take over portions of other males' territories are more aggressive than those which cannot hold onto a territory. Additionally, males which were more aggressive held larger territories (and hence had

larger harems) than less aggressive males. It was mentioned earlier that there may be no basis for female choice in this population of yellow-headed blackbirds because there is little variation among males in their behaviour or morphology. If there is variation in the aggressiveness of males, which affects the number of mates they acquire, then it could be argued that there is a basis for female choice since their sons would also be able to acquire large harems (as in the sexy son hypothesis). However, it is unlikely that aggressiveness of males would affect female choice because their sons would have high pairing success for two reasons. Firstly, fitness may not be very heritable (Williams 1975, Maynard Smith 1978), and secondly, aggressiveness may not be genetic. Aggressiveness may be learned and thus increase with age and experience (Yasukawa 1981). It is unknown whether differences in male aggression were related to differences in age or experience in the present study.

The evidence gathered in this study supports the null hypothesis that female yellow-headed blackbirds settle in the breeding area without being influenced by other females or by male or territory quality, and males compete to gain access to females. Because no male or territory features that were measured affected female RS or recruitment it appears that there was no basis for female choice. Why female choice may not be important in the maintenance of polygyny will be examined in more detail in chapter 4.

Chapter 4

Introduction

In most species of birds the female is the sex which chooses a mate. This occurs because females stand to lose more than males for making an error in their choice of mate due to the large initial investment in gametes by females (Trivers 1972). Females may choose mates based on the abilities of males to defend the nest from predators or to help care for offspring, and in territorial species females may base their choice of mate on the quality of resources they hold (Verner 1964, Verner and Willson 1966, Orians 1969). These aspects of males and the quality of their territories are assumed to affect the number of young that fledge (a female's reproductive success, RS, Verner 1964, Verner and Willson 1966). Because territory resources and the time a male can spend feeding offspring are limited, it is assumed that polygyny is costly to females as it means they would have to share these features (Verner 1964, Verner and Willson 1966, Orians 1969).

In addition to the above aspects of male quality, females may choose mates based on some less proximate genetic quality of the males, which could affect the viability or pairing success of offspring (Orians 1969, Wittenberger 1976, Weatherhead and Robertson 1977b, 1979). Mate choice based upon males' genetic quality would affect the fitness of females rather than their RS. This would occur since their offspring would be of high quality and hence have high RS (Wittenberger 1976, Weatherhead and Robertson 1977b, 1979).

Verner (1964) and Verner and Willson (1966) presented the hypothesis that a female should only choose to mate with an already mated male when

the quality of the territory is high enough that the RS a female could expect would be no lower than the RS she could expect by mating with a bachelor on a poorer quality territory. That is, the difference in quality between the better and poorer territories must exceed the 'polygyny threshold' for polygyny to occur (Verner and Willson 1966). Orians (1969) elaborated on this idea and proposed some assumptions and predictions of the hypothesis (referred to as the VWO hypothesis in the present paper). One assumption of this hypothesis is that, through competition among males, the best quality males come to hold the best territories. Therefore a female only needs to base her choice of mate on the quality of his territory to maximize her expected RS.

Weatherhead and Robertson (1977b, 1979) proposed a modification of the VWO hypothesis. They suggested that male quality is not highly correlated with territory quality. In this case, females are assumed to base their choice of mate on the quality of the male as well as on the quality of the territory. Females are assumed to recoup the loss in RS from mating polygynously with an attractive male by producing sons that will inherit some of the father's ability to recruit a large harem (the sexy son hypothesis). Therefore, females mated to attractive males will have a higher fitness by having more grandoffspring.

Many studies have attempted to examine the validity of the VWO and sexy son hypotheses and neither hypothesis has ever been unambiguously supported (e.g. Searcy 1979a, Wittenberger 1979, Alatalo et al. 1981, Yasukawa 1981, and see Garson et al. 1980). Part of the reason for this is that few studies have tested accurate predictions of the hypotheses. Another reason is that no study has examined in detail all the basic assumptions of both hypotheses.

This study tested accurate predictions of the VWO and sexy son hypotheses in chapters 1, 2, and 3 using data on the yellow-headed blackbird (*Xanthocephalus xanthocephalus*). From chapters 1, 2, and 3 it appears that female yellow-headed blackbirds did not choose mates based on the quality of the territory or the male. An alternate "null" hypothesis, proposed and supported, was that females settled without regard to other females or to males or territory boundaries and males competed to hold territories in order to gain access to females (the null hypothesis). It is unclear why the polygyny threshold hypotheses did not explain the maintenance of polygyny in this population of yellow-headed blackbirds. Therefore, it was of interest to examine the assumptions underlying the VWO and sexy son hypotheses. There are several assumptions (modified after Orians 1969) inherent in the polygyny threshold (VWO) hypothesis and its modification, the sexy son hypothesis.

1. Polygyny is costly to females because territories provide food for females and their offspring that are not shareable among females. Territories also provide nest sites and high quality sites may be limited so that polygyny occurs on territories with many good sites.
2. Polygyny is costly to females because males assist in feeding the offspring, and this assistance is not shareable among females.
3. There is variation in quality among territories upon which females can base their choice of mate. This variation is necessary because it is through differences in territory quality that females are compensated for mating polygynously.
4. There is variation in the quality (in parental care and the ability to recruit females) of males upon which females can base their choice of mate. This variation is necessary because it is also through

→ differences in male quality that females are compensated (by having higher RS, as in the VWO, or fitness, as in the sexy son) for mating polygynously.

5. When females are settling, they can accurately assess the relative qualities of territories and males (i.e. there are cues available regarding male and territory quality, and females have time to assess several situations before deciding where to settle), and females choose so as to maximize their RS (VWO) or fitness (sexy son).

In this paper the assumptions of the VWO and sexy son hypotheses are examined in order to determine why evidence from yellow-headed blackbirds does not support the VWO and sexy son hypotheses. The data will be used to support the idea that the above assumptions may be too unrealistic to apply to natural populations, as suggested by Davies and Houston (1986).

Methods

In addition to the methods explained below, see General Methods.

Polygyny may occur if males monopolize a limited number of high quality nest sites. To determine whether features of nest sites differed from features of territories, features of both were measured (as in chapter 3) and compared using paired t-tests. If nest sites differed from the territory in general, then the potential exists that nest sites were limited.

Polygyny may be costly to females if they must share food available on the territory. To assess whether territories were important as sources of food for nestlings, the location at which parents gathered food for nestlings was determined during the daily time budget sessions. To determine the types of foods fed to nestlings by the parents, a total of 25 food boluses were extracted from nestlings in 7 different nests. This was done by twisting a small piece of pipe cleaner around a nestling's throat just below the head tight enough that the nestling could not swallow but loose enough that it could still breathe. The nest was observed from a distance and as soon as a parent had made a trip to the nest with food, the nest was visited. The bolus was removed from the nestling's throat with tweezers and placed in a vial of 70% ethanol. The invertebrates in the bolus were identified at a later date.

Polygyny may be costly to females if they have to share male help in feeding offspring. To determine whether male help was important, the relative numbers of feeding trips made by the male and female to each nest in a territory were recorded by cameras set at the nests. Five cameras were set out from 6 AM until 8 PM throughout the nestling period.

Each nest was monitored once in each of three times during the nestling period, when the nestlings were 1-3, 5-7, and 9-10 days old. The cameras were triggered remotely by a switch placed on the rim of the nest bowl which was tripped when an adult landed on the nest. The camera was camouflaged by a cover of burlap. Neither the switch nor the sound of the camera appeared to disturb the birds.

Nests were visited each day during laying and the eggs were numbered in the order they were laid. Nests were also visited at hatch and nestlings were marked with small leg bands made of tape identifying nestlings according to the egg from which they had hatched. It was possible to identify which egg each nestling came from because the eggs hatched asynchronously. The growth of nestlings was monitored from hatch to fledging. Every two days, beginning at hatch, the following measurements were made on nestlings: weight (g) using a Pesola spring scale, bill length (mm, measured from the first feather on the forehead to the tip of the bill, using calipers), and tarsus length (mm, measured on a bent leg from the distal end of the tarsometatarsus to the distal end of the femur, using calipers).

Results

One aspect of territories that could be limited, and hence induce females to nest polygynously, are suitable nest sites. If the structure of vegetation at nest sites was different from that of the territory in general, then the potential exists that nest sites were limited. Therefore, features of both were compared. There was only one difference in the mean values for several features of nest sites and territories and that was the stem height on territories was greater than that at the nest sites in 1983 (Table 10). This indicates that nest sites were not very different from the territory in general and hence were probably not in short supply.

The VWO and sexy son hypotheses both assume that it is detrimental to females to mate polygynously because they will have to share territory resources and male assistance in feeding nestlings. An aspect of territories that could be limited is food. However, from daily time budget information, it was observed that birds did not use the territory for food very often, either for themselves or for nestlings. Of 147 feeding trips to nestlings observed, 89% were made to low lying wet areas of fields surrounding the marsh and only 11% of the time did birds forage on their territories. It is possible that the foods were gathered off the territory because the preferred food types were not available on the marsh. However, all the invertebrates identified from food boluses were inhabitants of marshes (Table 11).

If male assistance in feeding nestlings is important for nestling survival then females which feed nestlings alone should have lower RS than those that receive male help. Males were observed mainly to feed nestlings of the primary female, but occasionally fed nestlings of females

2 OF 2

MICROCOPY RESOLUTION TEST CHART
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(ANSI and ISO TEST CHART No. 2)

that settled later on the territory. The percentage of the total feeding trips made to nestlings by males did not affect the number of young that fledged per nest (Table 12). An indirect way to assess the importance of male assistance is to determine the survival of nestlings relative to the order the nest was initiated, because the amount of assistance a male gave in feeding nestlings was negatively correlated with the order in which the nests were initiated on the territory (personal observation). Female RS (number of young fledged per nest, y/n , number of young fledged per successful nest y/s , percent of nests successful %) was not related to the order in which they settled on the territory (Figure 19), which indicates that male assistance did not affect nestling survival to fledging. It is possible that nestlings fed by two parents grew faster and were larger at fledging, which may affect their survival after fledging. However, growth was no different among nestlings relative to the order the nest was initiated on a territory (Table 13). The average weight of juvenile females at fledging was 36.5 ± 7.0 g. and of males 48.5 ± 8.5 g., which is within the range of that reported by Willson (1966) and Richter (1984).

Discussion

It appears that the population of yellow-headed blackbirds studied in this paper does not fit the existing hypotheses which attempt to explain the maintenance of polygyny. Instead, the maintenance of polygyny in this population seems best explained by the null hypothesis that females settle without being influenced by other females or by males and their territories and males compete for territories to gain access to females. The reason why the yellow-headed blackbirds did not fit the VWO and sexy son hypotheses is that the assumptions of the hypotheses were not met.

A basic assumption of the polygyny threshold hypotheses is that polygyny is costly to females. This study failed to demonstrate that polygyny was costly to females in any way. If it was detrimental to a female to nest polygynously, then females should behave competitively toward one another. This prediction was not met, as tested in chapter 1.

Polygyny is assumed to be costly to females because it means females will have to share territory resources. When the hypothesis was first proposed Verner (1964) considered the long-billed marsh wren (*Telmatodytes palustris*), a species that uses the territory for food. Verner and Willson (1966) suggested that polygyny would be more common in marshes and prairies because these habitats are likely to have sufficient differences in food among territories. However, it is possible that the range of differences is not sufficient to affect female RS, and this possibility was not discussed.

Many studies have determined whether or not females used the territory for food in an attempt to support or refute the idea that territory quality influences female choice of mate in polygynous species (as in the

VWO version of the polygyny threshold hypothesis). Willson (1966) observed that one population of yellow-headed blackbirds used the territory for food while another did not. Wittenberger (1980) found that bobolinks (*Dolichonyx oryzivorus*) foraged on the territory. Zimmerman (1966) concluded that there was little support for the polygyny threshold hypothesis because dickcissels (*Spiza americana*) fed off the territory. Haigh (1968) found that territories which had the highest production of invertebrates did not attract the most females for red-winged blackbirds (*Agelaius phoeniceus*). Holm (1973) argued that the main difference in territories of red-winged blackbirds was food because the vegetation appeared the same but clutch size increased with harem size. She reasoned that territories must differ in the amount of food they contain because clutch size is influenced by food availability (Lack 1968). However, she had no data on food abundance, only this indirect measure. Savannah sparrows (*Passerculus sandwichensis*) did not use the territory for food, although food was abundant on territories (Bédard and LaPointe 1984). The corn bunting (*Emberiza calandra*) also does not use the territory for food (Ryves and Ryves 1934). In the present study, it was found that neither males nor females used the territory for food, but rather they foraged in nearby fields. Given that five polygynous species do not always feed on their territories, it leads one to question whether the assumption of the polygyny threshold hypothesis that differences in food abundance among territories are responsible for polygyny is generally applicable.

Searcy (1979a) suggested that the polygyny threshold hypothesis could also apply in species which do not use the territory for food because differences in territory quality could be related to how close they are to

foraging areas. The distance to foraging areas in the present study was unlikely to be significantly variable, since all territories were within 200 m of the fields where the birds foraged. For most territorial species, it does not seem that variation in the distance to food sites would affect female RS unless territories were very isolated. The reason for this is that territories are most often close together so that even the territory farthest from foraging sites would be only several hundred metres farther than the closest territory. This does not seem to be a great enough difference to be costly to females.

It is difficult to predict how great a variation in food abundance on territories or distance to foraging areas is necessary to affect female RS. The critical differences may become evident only in bad years or bad weather as found in pied flycatchers (*Ficedula hypoleuca*, Alatalo and Lundberg 1984). If the distance to food was important to females, then high quality territories would be those that are close to foraging areas. Therefore it would be expected that polygyny would be more frequent on territories close to foraging areas than on territories farther away. In the present study, polygyny occurred on territories throughout the marsh, with no areas consistently having a higher incidence of polygyny than any other.

It has also been suggested that good nest sites that are sheltered from severe weather and concealed from predators may be limited (Verner 1964). If by holding territories some males can monopolize several nest sites, then some females will have to settle polygynously if they are to nest. Verner (1964) and Verner and Willson (1966) considered this to be an assumption of the polygyny threshold hypothesis because variation in the number of nests on territories would be one of the critical aspects of territory quality necessary for polygyny to occur. Females would settle

polygynously on a territory with many high quality nest sites in preference to settling monogamously on a territory with poor nest sites.

It appears that nest sites were not in short supply for the population of yellow-headed blackbirds in the present study. Features of the territory in general were no different from those of nest sites, which indicates that there were suitable nest sites available on the territory in addition to the nest sites already established. Thus, the assumption that females are polygynous because nest sites are limited and monopolized by males is not valid for this population of yellow-headed blackbirds. This was also observed in the savannah sparrow (Bédard and LaPointe 1984) and used as evidence against the idea that differences in territory quality are responsible for polygyny. In a study on long-billed marsh wrens, Verner and Engelson (1970) found no evidence that nest sites were limited. This result leaves open to question the validity of the polygyny threshold even as an explanation for the maintenance of polygyny in the species on which it was developed. The assumption that territories with high quality nest sites compensate females for settling polygynously may not be a valid test of the VWO hypothesis. The pattern of settling suggested by Verner and Willson (1966) could occur without female choice of mates and evaluation of the mated status of males. If females choose nest sites, then they are simply exhibiting habitat selection. Females could settle randomly at the good nest sites, thus polygyny occurs because of competition among males to hold territories with good nest sites.

In some species, preferred nest sites are limited and do seem responsible for polygyny, but possibly not due to female choice, as assumed in the polygyny threshold hypothesis. Nest sites are not limited in the pied flycatcher (Alatalo et al. 1981), although some sites are

preferred over others and females are more successful at preferred sites (Askenmo 1984). In this species, it has been suggested that polygyny is related to males monopolizing good sites (Askenmo 1984), which is achieved through competition among males. Catchpole et al. (1985) observed that larger territories had more nest sites and hence larger harems in great reed warblers (*Acrocephalus arundinaceus*), which suggests that nest sites were limited. Nest sites have also been found to be limited in bell-magpies (*Gymnorhina tibicen*, Carrick 1963), village weavers (*Ploceus cucullatus*, Crook 1964), great-tailed grackles (*Quiscalus mexicanus*, Selander 1972), and dickcissels (Zimmerman 1966). In all these species, it appears that polygyny occurs due to competition among males to monopolize nest sites and not due to females choosing polygyny on good territories in preference to monogamy on poorer territories.

A similar observation was made by Davies and Lundberg (1984). They noted that female dunnocks (*Prunella modularis*) settled on ranges and males competed to monopolize these ranges. The idea that males defend resources that are critical for females to lay their eggs is not new. Resource defense polygyny has been discussed as being an explanation for polygyny in many species (see Emlen and Oring 1977, Davies 1978). However, most of the theoretical and empirical work has proceeded with the assumption that females choose mates on the basis of the resources they defend. It is possible that in some cases where territory and male features do not vary enough to affect female RS, females may settle without making a choice based on the male or his territory. Thus competition among males may sometimes be more important than female choice in the maintenance of polygyny.

Verner (1964) also assumed that polygyny is costly because females would have to share male assistance in feeding young. To demonstrate that sharing male help is costly, it is necessary to determine whether or not male help affects female reproductive success. Orians (1969) suggested that the main factor effecting differences in reproductive success between monogamous and bigamous females was male help. Male help in feeding nestlings has been observed to affect the number of young that fledge in great reed warblers (Dyrce 1977), Brewer's blackbirds (*Euphagus cyanocephalus*, Patterson et al. 1980), bobolinks (Wittenberger 1978, 1980, 1982), pied flycatchers (Alatalo et al. 1981), an Indiana population of red-winged blackbirds (Patterson 1979), and willow ptarmigan (*Lagopus lagopus*, Hannon 1984). Another measure of female reproductive success is the growth of nestlings, since it has been shown that heavier fledglings survive better than lighter fledglings (Perrins 1965, Howe 1979, Fiala 1981). When fed by both parents, nestlings fledged at a heavier weight in bobolinks (Martin 1974, Wittenberger 1980), yellow-headed blackbirds (Willson 1966, Patterson et al. 1980), and pied flycatchers (Alatalo et al. 1982).

In the present study, about 20% of male yellow-headed blackbirds were observed to feed nestlings, but this assistance did not affect nestling survival or growth. It appears that females did not need male assistance. Therefore, this non-shareable aspect of males was not costly to females. Male help has been observed not to affect the number of young that fledge in yellow-headed blackbirds by Fautin (1941), Willson (1966), and Patterson et al. (1980), in dickcissels (Zimmerman 1966), or in a Washington population of red-winged blackbirds (Searcy 1979a).

It is possible that females without male assistance had to work harder

feeding nestlings as in bobolinks (Martin 1974) and song sparrows (Smith et al. 1982) and thus have a reduced chance of survival because they may not be in good condition at the end of the breeding season. This was not determined in the present study, but it is unlikely this was the case. It would be expected that there would be some cues regarding the male's parental abilities available when females were settling, and that females would choose males based on their parental abilities. However, no male features that were measured were related to whether or not they fed nestlings. In contrast, features of male red-winged blackbirds have been found to be correlated with their parental abilities (Searcy and Yasukawa 1981b, Eckert 1985).

Patterson et al. (1980) suggested that males may be more important in defending the nest than in providing food. Searcy (1979a) found no evidence that nest defense by male red-winged blackbirds affected predation. The present study also found that male behaviour did not affect predation (chapter 3).

Another assumption of the VWO and sexy son hypotheses is that females can assess the quality of the territory and the male. It was shown in chapter 3 that no features of territories or males that were available when females were settling affected female RS or the recruitment of females by males. Thus, there may be no accurate markers of territory or male quality when females settled (Searcy 1979b, Wittenberger 1981b). This uncertainty sheds doubt as to the importance of female choice in polygynous species, as assumed in the VWO and sexy son hypotheses.

It is also possible that there was little variation among territories or males on which females could base their choice of mate. Both the VWO and

sexy son hypotheses assume that there is variation in the quality of breeding situation such that females only settle polygynously in high quality breeding situations (Verner 1964, Verner and Willson 1966, Orians 1969, Weatherhead and Robertson 1977a, 1979). Searcy (1979a) found that there was a basis on which female red-winged blackbirds should choose territories. He found that predation affected female RS, was variable among territories, and probably was predictable. He used these data to support the idea that territory quality could influence female choice of a mate. However, this is not a test of the VWO hypothesis. These data merely indicate that there is a basis for females to exhibit habitat selection. On the other hand, the null hypothesis can apply to situations where females select good nest sites. The null hypothesis states that females are not weighing the costs and benefits of nesting polygynously at good sites versus monogamously at poorer sites. Females are assumed to select the best nest sites available at the time they settle, without regard to male mated status or territory boundaries.

It was not evident in this study that territories or males were significantly variable. All areas of the marsh and all males appeared to be equal, as measured by female RS and the order in which territories were settled by females. Additionally, all territories were equal in terms of accessibility to predators. Predation was random throughout the marsh, as indicated by several lines of evidence. Predation was not affected by the density of nests (chapter 1), features of the territory or nest site (chapter 3), or male behaviour (chapter 3). In addition, there was no seasonal effect of predation (chapter 2). Finally, there were no "hot spots" of predator activity on the marsh, since predation on arbitrary territories was not similar in each of the three years (chapter 3).

The above evidence indicates that the VWO and sexy son hypotheses do not apply to this population of yellow-headed blackbirds because none of the assumptions of the hypotheses were met. It is not female choice which determined whether or not polygyny occurred in this population. Polygyny occurred because males competed for territories in the habitat where females nest, and by doing so excluded other males from breeding such that the operational sex ratio was skewed in favour of females. For all females to breed, some necessarily mated with the same male. Females did not need to choose between monogamous and polygynous situations because polygyny was not costly. Until it can be demonstrated that polygyny cannot be explained by competition among males, the null hypothesis is the most parsimonious explanation of why polygyny occurs.

The polygyny threshold hypothesis has persisted for over 20 years, despite much lack of support. Wittenberger (1976) suggested that the VWO hypothesis may not be generally applicable because the relative importance of factors favouring polygyny may differ in different habitats. Given all the ambiguous results from studies discussed in this thesis, it appears that a generalized hypothesis may not be appropriate.

The VWO and sexy son versions of the polygyny threshold hypothesis may be unlikely to apply to most polygynous species because they both ignore the possibility that there are conflicts of interest between males and females (Davies and Houston 1986). In some polygynous species male help in feeding nestlings does not affect female RS and thus the null hypothesis may explain why these species are polygynous. The null hypothesis certainly seems to explain why the population of yellow-headed blackbirds in this study were polygynous since there was no detrimental effect on female RS in being mated polygynously.

For the species and populations in which male help is important, then it may be detrimental to females to settle polygynously. Secondary female pied flycatchers suffer a reproductive loss for not having male assistance, but it appears that pied flycatchers are polygynous due to the inability of females to assess the mated status of males (Alatalo et al. 1981, 1982). It is also possible that later settlers may arrive later because they are not in good condition, or they may be younger or more inexperienced females; settling at the best nest site available may be the best choice for them. In some species, females may not need to be concerned with the quality of the male since all males that are able to hold territories are likely of high quality. The rationale for this is that in polygynous species there is a large population of males which do not hold territories, thus, males which do hold territories must be of higher quality or else they would be displaced. However, there have been several studies discussed in this thesis which support the idea that territory and male features affect female RS and thus provide a basis for female choice. It must be emphasized that there probably is no 'grand unified theory' of why polygyny occurs; different explanations may apply in different species.

Orians (1969) suggested that in species in which nest sites and food are not important attributes of territories, polygyny evolved because it was advantageous to males and neutral to females. In saying this he was referring to forest, frugivorous species that nest in colonies. In these species, a fraction of all the males can defend the nest sites in the colony (Wittenberger 1976). Based upon the observations in the present study on the yellow-headed blackbird, there is no apparent reason why this explanation cannot apply to marsh- and prairie-breeding polygynous species as well.

Conclusions

1. Female yellow-headed blackbirds in this population were not co-operative within harems.
2. Based on several predictions regarding the order that females should choose mates, the resulting reproductive success of females, and harem sizes, it was determined that the VWO and sexy son versions of the polygyny threshold hypothesis did not explain why polygyny occurred.
3. A null hypothesis was proposed that assumes females settle without regard to other females and males compete for territories in order to gain access to females. This hypothesis was supported for all predictions based on the settling patterns of females.
4. It was observed that neither male nor territory features affected female reproductive success or harem size. It was concluded that there was no basis for female choice. Data were presented that indicated that competition among males was the force maintaining polygyny.
5. The polygyny threshold hypothesis does not apply to this population because the assumptions of the hypothesis were not met. Unless it can be clearly demonstrated that polygyny is costly to females, that there is variation in territory and male features which affects female fitness, and that females choose mates, then the polygyny threshold hypothesis seems too restrictive to apply as a general explanation for why polygyny occurs.
6. The null hypothesis, which assumes that competition among males is more important than female choice of mate, was supported by the data in this study. This is a viable alternate hypothesis to the polygyny

threshold hypothesis which may apply in some situations.

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Table 1 Scoring system for intruding female mount presentations to resident females and for female mount presentations to males. Scores were multiplied by the duration the behaviour was performed by the resident female or by the male then summed to give a grand total score for each 5 minute mount presentation.

<u>SCORE</u>	<u>BEHAVIOUR</u>
1	distant (> 5m) and non-attentive
2	close (< 5m) and non-attentive
3	distant, silent observation
4	close, silent observation
5	distant, agitation
6	distant, agitation and vocalization
8	close, agitation
10	close, agitation and vocalization
13	direct attack/mount

Table 2. Scores of resident female aggression to intruding female mounts in each of four nesting stages for females tested several times and females tested only once. Scores did not differ between the two groups of females. Means and (standard deviation, presented to illustrate variation) shown.

<u>GROUP</u>	<u>EGG LAYING</u>	<u>EARLY INCUBATION</u>	<u>LATE INCUBATION</u>	<u>MID NESTLING</u>
tested several times	10.8 (5.5) n = 12	15.7 (8.6) 12	25.9 (15.3) 10	22.6 (13.7) 9
tested only once	11.7 (3.2) n = 3	9.5 (0) 1	26.9 (7.2) 9	34.0 (7.5) 11
Mann-Whitney U =	20 $P > 0.2$	*	46 $P > 0.2$	48 $P > 0.2$

* not tested due to small sample size of females tested once

Table 3. Comparison of eventual harems sizes for males which chased or did not chase a resident female away from an intruding female mount.

<u>HAREM SIZE</u>	<u>NUMBER OF TIMES MALE</u>	
	<u>CHASED</u>	<u>DID NOT CHASE</u>
1	4	3
2	1	4
3	3	7
4	4	4
G = 1.83, $P > 0.05$		

Table 4. Comparison between the reproductive success (number of young fledged per nest) of later settling females and earlier settling females that ended up in the same sized harems. The columns indicate the number of times later settling females had higher, lower or the same reproductive success (RS) compared to earlier settling females.

SUCCESS FREQUENCY OF LATER SETTLING FEMALES
VERSUS EARLIER SETTLING FEMALES

<u>HAREM SIZE</u>	<u>FOR LATER SETTLING FEMALES</u>		
	<u>RS HIGHER</u>	<u>RS LOWER</u>	<u>RS EQUAL</u>
2	149	63	142
3	113	35	90
4	44	99	70
TOTALS	306	197	302

Table 5. Spearman rank correlation coefficients for territory features versus territory attractiveness to females (order that territory was chosen by females, harem size) and female reproductive success. Asterisks denote significant correlations ($P < 0.05$).

TERRITORY FEATURE	ORDER SETTLED <u>83 / 84</u>	HAREM SIZE <u>83 / 84</u>	Y/N ^a <u>83 / 84</u>	Y/S ^b <u>83 / 84</u>
water depth	-.322*/-.136	.456*/.298	-.095 /-.160	-.258 /-.129
stem height	-.267*/-.067*	.324 / .235	-.197 /-.009	-.122 /-.227*
stem density	.043 / .060	-.573*/-.069	.046 / .176	.303*/.148
edge ^c	.099 / .139	-.027 / .087	.113 / .083	.006 /-.137
prox. water ^d	.175 / .026	.185 /-.007	-.065 / .007	-.246 / .003
terr. size	.431*/.105	-.043 /-.177	.199 /-.125	.331*/-.023
NEST SITE FEATURE				
water depth			-.307 /-.077	-.223 / .091
stem height			-.214 / .082	-.013 /-.117
stem density			.051 / .112	.226 / .114
proximity to open water			-.151 /-.029	-.249 /-.071
nest height above water			-.249 / .065	-.048 / .059
stem height above nest			-.195 /-.012	.006 /-.159
number of support stems			-.068 /-.004	.242 /-.018

^a number of young fledged per nest

^b number of young fledged per successful (fledged > 0 young) nest

^c metres of vegetation-water edge

^d proximity to open water (metres)

Table 6a. Comparison of the order in which arbitrary territories in the east end of the marsh were settled in 1984 and 1985, the number of females nesting on each arbitrary territory in 1983, 1984 and 1985, and the number of young fledged per territory in each of the three years. Not all information was available for each arbitrary territory in each year.

TERRITORY	ORDER SETTLED		NUMBER OF FEMALES			NUMBER OF YOUNG FLEDGED		
	<u>84</u>	<u>85</u>	<u>83</u>	<u>84</u>	<u>85</u>	<u>83</u>	<u>84</u>	<u>85</u>
1	10	4	1	2	2	2	0	1
2	4	6	0	1	1			
3	4	1	1	2	3	0	3	0.3
4	2	4	6	5	3			
5	1	3	3	3	1			
6			1	0	3			
7	3	1	1	3	2			
8			1	1	0			
9	3	1	2	4	3			
10	3	3	1	1	1			
11	1	3	3	2	1			
12	4	4	1	1	3			
13	2	4	0	2	2			
14	4	3	0	2	1			
15	4	5	2	2	3	3	2	1.3
16	4	2	1	1	1			
17	7	4	2	1	1	2	2	2
18	7	4	1	1	2	2	2	1

Table 6b. Comparison of the order in which arbitrary territories in the west end of the marsh were settled in 1984 and 1985, the number of females nesting on each territory in 1983, 1984, and 1985 and the number of young fledged on each arbitrary territory in each year. Not all information was available for each year.

TERRITORY	ORDER SETTLED		NUMBER OF FEMALES			NUMBER OF YOUNG FLEDGED		
	<u>84</u>	<u>85</u>	<u>83</u>	<u>84</u>	<u>85</u>	<u>83</u>	<u>84</u>	<u>85</u>
19	4	3	3	2	2	2	0	1
20			0	1	0			
21	2	0	1					
22	14	5	0	1	2			
23	4	2	4	3	1	1.5	2	0
24	11	5	3	1	1	2	2	0
25			2	0	1			
26	7	4	0	2	1			
27	12	5	2	1	2	3	2	1
28	7	13	2	2	2	1	2	0
29			1	0	1			
30	5	4	1	2	1	2	2	0
31			1	0	1			
32			1	1	0			

Table 7. Spearman rank correlation coefficients for morphological features of males and their recruitment abilities (harem size, density of females on territory) and female reproductive success. There were no significant correlations.

MALE FEATURE	FEMALE DENSITY	HAREM SIZE	Y/N ^a	Y/S ^b	%s ^c	FEEDING RATE*
weight	.3212	.3791	.0158	.0177	.0205	0.011
bill length	.0197	.0081	.2954	.3118	.3040	0.251
wing length	-.1996	-.2057	.0199	.0206	.0291	-0.019
tarsus length	.0154	.0076	.0274	.0453	.0504	0.048
head colouration	.0098	.0165	.0319	.0023	.0029	-0.007

^a number of young fledged per nest

^b number of young fledged per successful (fledged > 0 young) nest

^c percent of nests successful

* number of feeding trips to offspring per hour

Table 8. Correlation coefficients for Spearman rank correlations between male behaviours and female reproductive success and harem size. a) male behaviours prior to the first egg hatched on the study area, $n = 42$ males, 182 hours of observation, b) male behaviours after there were nestlings on the study area, $n = 39$ males, 176 hours of observation. Asterisks indicate significant correlations ($P < 0.05$).

a						
MALE BEHAVIOUR	Y/N ^a	Y/S ^b	%s ^c	HAREM SIZE	FEMALE DENSITY	FEEDING RATE ^f
% off marsh	0.018	-0.004	0.106	-0.310	-0.188	0.082
% resting	-0.030	-0.032	0.002	-0.026	-0.044	-0.023
% alert	-0.026	-0.159	-0.060	0.159	0.005	0.173
* songs/hr.	0.345	0.323	0.210	-0.266	-0.157	0.270
* aggress./hr ^d	-0.004	-0.193	0.072	0.593*	0.274	0.098
* court/q/hr ^e	0.245	0.189	0.261	0.383	0.335	0.044
b						
% off marsh	0.402	0.541	0.311			
% resting	-0.315	0.281	-0.328			
% alert	0.421	0.278	0.480			
* songs/hr.	-0.292	0.178	-0.223			

^a number of young fledged per nest

^b number of young fledged per successful nest (fledged > 0 young)

^c percent of nests successful

^d number of aggressive interactions per hour

^e number of courtship interactions per female already settled on the territory per hour

^f number of feeding trips to offspring per hour

Table 9. Comparison of behaviours of males which moved into or took over part of another males territory, those which moved out of their territory or part of it, and those which were stable. The RS of females on territories of each type of male is also presented.

<u>BEHAVIOUR</u>	<u>IN</u>	<u>OUT</u>	<u>STABLE</u>
n (males)	7	4	24
n (hours obs.)	26	14	90
% off marsh	4.9	10.0	6.8
% resting	4.6*	7.5	2.8
% alert	77.0	77.7	83.9*
* songs/hr.	12.8	7.5	9.6
* aggress./hr.	4.3*	2.9	1.8
* court./hr.	0.4	0.45	0.39
* young/nest	1.1	1.0 ^a	1.1
* young/suc.nest	1.6	1.5	1.5
% nest success	64.3	60.5	58.2

* $P < 0.05$, Kruskal-Wallis oneway ANOVA

^a n = 2 males for success data, males never replaced

Table 10. Paired-t-test comparisons of features of nest sites and features of the territory the nest was in for all nests. Each value for a feature of the nest site was compared to the mean of four sample sites in the territory. Values in the table are the means over all nests and territories

<u>FEATURE</u>	<u>n</u>	<u>AT NEST</u>	<u>IN TERRITORY</u>	<u>p</u>
1983				
stem density ^a	25	104	110	> 0.1
stem height (cm)	25	60.2	64.5	< 0.05
prox. to water ^b	25	2.4	1.7	> 0.05
water depth (cm)	25	56.9	56.8	> 0.1
1984				
stem density	48	79.8	85.3	> 0.1
stem height	48	62.1	61.9	> 0.05
prox. to water	48	6.5	6.1	> 0.1
water depth	48	40.3	41.5	> 0.1

^a number of stems per m²

^b proximity to open water (metres)

Table 11. Identification of invertebrates from 25 food boluses taken from nestlings in 7 nests, and the percent of each food type.

ORDER	% (number)
Diptera	
suborder Nematocera	
family Chironomidae	58 (78)
Odonata	
suborder Zygoptera	22 (29)
suborder Anisoptera	
superfamily Libelluloidea	5 (7)
Trichoptera	
family Limnephilidae	14 (20)
Araneida	0.7 (1)

Table 12. The percentage of all feedings of nestlings given by males and the number of young fledged per nest. Feeding trips were recorded by cameras set on the nest triggered remotely by the adult landing on the edge of the nest bowl.

<u>MALE I.D.</u>	<u>HRS. OBS.^a</u>	<u>% TOTAL FEEDINGS</u>	
		<u>BY MALE</u>	<u>Y/N</u>
O-W nest 1	16	0	1
spock monog.	16	0	2
-Y nest 2	8	20	1
R-DG nest 1	24	40	2
<u>LG-LB</u> nest 1	8	0	1
0 nest 2	24	0	1
<u>-W</u> nest 1	16	45	2
LB nest 2	8	20	0
nest 3	16	0	2
UNM nest 1	8	33	3
nest 2	8	0	1
nest 3	8	0	2
nest 4	8	13	1

^a total number of hours the nest was monitored

Table 13. Comparison of growth of nestlings relative to the order that the female settled on the territory. The order that the female settled did not affect the growth of nestlings, measured as the percent change in size from the second day to the tenth day after hatch (Kruskal-Wallis, P 's > 0.1). Nestlings from nests of females to settle fifth on territories were excluded from the analysis due to the small sample sizes.

ORDER FEMALE SETTLED ON TERRITORY	<u>n</u>	PERCENT CHANGE		
		<u>WEIGHT</u>	<u>TARSUS</u>	<u>BILL</u>
female nestlings				
monogamous	12	302	139	76
1	44	354	133	68
2	26	318	145	70
3	9	280	126	71
4	3	299	150	77
5	1	326	146	71
male nestlings				
monogamous	10	457	175	85
1	35	452	178	86
2	26	458	188	93
3	12	427	171	85
4	5	494	161	90
5	2	521	176	80

Figure 1. Distribution of the number of days between a) first and second nests ($n = 55$ comparisons, mean days apart = 3.1 ± 3.3) and b) second and third nests ($n = 31$ comparisons, mean days apart = 3.7 ± 3.7) within a territory.

Figure 2. Distribution of the number of days between a) first and b) second nests within one territory and their respective consecutive nests on adjacent territories for all nests. a) $n = 55$ comparisons, mean days apart = 0.7 ± 1.1 and b) $n = 31$ comparisons, mean days apart = 0.5 ± 1.0 .

Figure 3. Distance to each of the nearest three nests (mean $\pm$ 1 standard deviation) for the first 25% of nests initiated (open bars) vs. after all nests were initiated (shaded bars). a) east end of the marsh, b) west end of the marsh. Asterisks indicate first 25% different from all nests (t-tests, all $P < 0.05$). Sample sizes are indicated over the first bars in each figure.

Figure 4. Scores of female aggression to an intruding female mount in four stages of the nesting cycle; I = egg laying, eI = early incubation, II = late incubation, mn = mid-nestling. Bars are means $\pm$ 1 standard deviation (presented to illustrate variation). Sample sizes are indicated above each bar. Similar letters above the bars denote significant differences; a, Mann-Whitney $U = 250.5$, $P < 0.002$; b, $U = 259$, $P < 0.002$; c, $U = 231$, $P < 0.002$; d, $U = 220$, $P < 0.002$.

Figure 5. Scores of female aggression to an intruding female mount for primary females (open bars) vs. secondary and tertiary females (shaded bars) during early nesting stages. Scores did not differ between the two groups of females in egg laying or in early incubation (Mann-Whitney $U = 31.5$, $P > 0.2$ and $U = 13$, $P > 0.2$, respectively). Bars are means ± 1 standard deviation (presented to illustrate variation). Sample sizes are indicated above each bar.

Figure 6. Females reproductive success in different sized harems. Means and 1 standard deviation (presented to illustrate variation) presented in a and b. Sample sizes are indicated above each bar.

Figure 7. The effect of female density on female reproductive success. The number of young fledged per nest did not vary with female density. Points are scattered vertically around each value of young per nest for clarity of presentation.

Figure 8. Female reproductive success as a function of nest density for a) the east and b) the west end of the marsh. The distance to the nearest 1 or 2 or 3 nests did not affect the number of young fledged per nest. Points are scattered vertically around each value of young per nest for clarity of presentation.

Figure 9. The effect of nest spacing in time on female reproductive success. The number of days between first (open bars) and second (shaded bars) nests within a territory did not affect success (Kruskal-Wallis, all $P > 0.1$). Means $\pm$ 1 standard deviation (presented to illustrate variation) are illustrated. Sample sizes are indicated above each bar. In a) the sample sizes for first and second nests are the same and are only shown once per time between nests.

Figure 10. The effect of nest spacing in time on female reproductive success. The number of days between second (open bars) and third (shaded bars) nests within a territory did not affect success (Kruskal-Wallis, all $P > 0.1$). Means $\pm$ 1 standard deviation (presented to illustrate variation) are illustrated. Sample sizes are indicated above each bar. In a) the sample sizes for second and third nests are the same and are only shown once per time between nests.

Figure 11. Relationship between expected female reproductive success (RS, the number of young fledged) and territory quality. Territory quality is assumed to be the main factor affecting female RS. The curve 'm' represents the RS of monogamous females and the curve 'b' that of females in harems of two on different quality territories. a) The case where male quality is highly correlated to territory quality. The 'polygyny threshold' (p.t.) is the minimum difference in quality between territories required to make the RS of a polygynously mated female (x) on the better territory equal to that of a monogamous female (y) on the poorer territory. b) The case where male quality is weakly correlated with territory quality. Female x may choose polygyny with the better male on the poorer territory in preference to polygyny with the poorer male on the better territory (female y) because she chooses a mate so as to maximize her fitness. Figure modified from Orrians (1969).

Figure 12. a) Predicted order of female settling on three territories if females base their decisions of where to settle on the quality of territory, and male quality is highly correlated with territory quality (the VWO hypothesis). b) Hypothetical order of female settling if they base their decisions on the quality of male and territory combined. Territory quality and male quality are only weakly correlated. A = highest, B = medium, C = lowest quality territory or male. The curve 'm' represents the RS of monogamous females, 'b' that of females in harems of two, and 'c' that of females in harems of three. Figure modified after Orians (1969).

Figure 13. Female reproductive success relative to the order that they settled on the study areas, for the last females to settle on each territory. There were no differences in y/n, y/s or %s vs. order (Kruskal-Wallis tests $P > 0.4$). Bars are means $\pm$ 1 standard deviation (presented to illustrate the high variation). Numbers above bars are sample sizes.

Figure 14. Relationship between the order that territories were settled by the first females and the order that those same territories were chosen by the second females to settle on them. The correlation was not significant (Spearman correlation $\rho > 0.05$).

Figure 15. Relationship between the order that territories were settled by the first females and the eventual harem size of the males on those territories. Several territories were settled on each day of the settling period. Males on the first territories settled had the largest eventual harems (Spearman correlation $P < 0.003$). Points with open circles around them indicate territories of equal size.

Figure 16. Relationship between harem size and size of territory. The correlation was significantly positive (Spearman correlation $\rho < 0.002$).

Figure 17. Relationship between scores for male responses to a taxidermic mount of a female placed in their territory and the eventual harem size of each male as well as the density of females on each male's territory. Higher scores indicate a stronger response.

Figure 18. Correlation between the size of a male's territory and scores for male responses to an intruding male mount placed in their territory and eventual harem size of each male. Higher scores indicate a stronger response. Both correlations were significant ($P < 0.001$).

Figure 19. Female reproductive success relative to the order they settled within each territory, or whether they were monogamous (m). There were no significant differences in female reproductive success (Kruskal-Wallis, all P 's > 0.2). Bars are means ± 1 standard deviation (presented to illustrate variation). Numbers above bars are sample sizes.

APPENDICES

APPENDIX I. Spatial nest distributions for the first 25% of nests initiated and after all nests were initiated. The east and west ends of the marsh were analysed separately because distances differed between ends.

1984	MEAN DISTANCE (m) TO		
	NEAREST NEST <u>east/west</u>	NEAREST 2 NESTS <u>east/west</u>	NEAREST 3 NESTS <u>east/west</u>
first 25% n	14 / 13	14 / 13	14 / 13
mean	12.5 / 25.4	20.4 / 35.3	34.6 / 51.8
s.d.	5.0 / 10.9	5.7 / 12.6	13.6 / 21.5
all nests n	58 / 51	58 / 51	58 / 51
mean	9.2 / 11.3	10.8 / 13.7	12.9 / 16.1
s.d.	9.3 / 5.4	5.2 / 6.1	5.1 / 6.3
1985			
first 25% n	15 / 9	15 / 9	15 / 9
mean	18.1 / 25.4	29.1 / 38.9	36.8 / 60.6
s.d.	9.6 / 13.4	14.2 / 15.0	14.7 / 26.3
all nests n	59 / 37	59 / 37	59 / 37
mean	11.5 / 14.8	13.6 / 17.3	16.2 / 20.6
s.d.	4.1 / 9.8	4.3 / 10.0	4.5 / 10.0

APPENDIX II. Harem size versus female reproductive success. Mean $\pm$ s.d.

YEAR	HAREM SIZE	y/n ^a	n	p ^b	y/s ^c	n	p	%s ^d	clutch
1983	1	1.4 (1.2)	8	0.7	2.2 (0.4)	5	0.3	62	4.0 (0.3)
	2	1.7 (1.0)	15		2.0 (0.7)	13		87	3.8 (0.4)
	3	1.1 (1.1)	18		2.0 (0.7)	10		56	3.9 (0.3)
	4	1.5 (1.5)	8		2.4 (1.1)	5		62	4.1 (0.4)
	5	1.4 (0.5)	5		1.4 (0.5)	5		100	3.8 (0.4)
	7	1.1 (0.9)	7		1.6 (0.5)	5		71	4.0 (0.4)
1984	1	1.2 (1.1)	16	0.2	1.9 (0.7)	10	0.2	62	3.7 (0.4)
	2	1.4 (1.1)	22		2.0 (0.7)	15		68	3.7 (0.5)
	3	1.1 (0.9)	30		1.6 (0.7)	21		70	3.5 (0.5)
	4	1.6 (1.0)	31		2.0 (0.7)	25		81	4.0 (0.5)
	5	0.9 (0.9)	10		1.5 (0.5)	6		60	4.0 (0.4)
1985	1	0.4 (1.0)	13	0.4	2.5 (0.7)	2	0.4	15	3.2 (0.4)
	2	0.7 (1.0)	42		2.0 (0.7)	15		36	3.1 (0.3)
	3	0.3 (0.7)	18		1.5 (0.6)	4		22	3.2 (0.4)
	4	0.4 (0.7)	17		1.5 (0.6)	4		24	3.2 (0.3)
	5	1.6 (0.9)	5		1.6 (0.9)	5		100	4.0 (0.4)
	6	0.7 (1.0)	6		2.0 (0)	2		33	3.8 (0.5)

^a number of young fledged per nest^b significance level for Kruskal-Wallis one-way ANOVA^c number of young fledged per successful nest^d percent of total nests that were successful (fledged at least one young)

Appendix III. Correlation coefficients for Spearman rank correlations between male behaviours up until eggs hatched and female reproductive success and harem size.

MALE BEHAVIOUR	Y/N	Y/S	%s	HAREM SIZE	FEMALE DENSITY
1983					
% off marsh	-0.463*	-0.531*	-0.204	-0.260	-0.385
% resting	-0.487*	-0.488*	-0.453*	-0.303	-0.082
% alert	0.354	0.287	0.314	0.192	0.213
* songs/hr.	0.074	0.156	0.154	-0.148	-0.032
* aggress./hr.	-0.253	-0.211	-0.199	-0.144	-0.288
* court./♀/hr.	0.411	0.454*	0.391	0.486*	0.368
1984					
% off marsh	0.381	0.380	0.068	-0.279	-0.033
% resting	0.000	0.000	0.000	0.000	0.000
% alert	-0.299	-0.299	0.061	0.322	0.227
* songs/hr.	0.488	0.501	0.199	-0.390	-0.142
* aggress./hr.	-0.267	-0.269	-0.083	0.611*	0.489*
* court./♀/hr.	-0.038	-0.036	0.110	0.813*	0.366
1985					
% off marsh	0.218	0.229	0.131	-0.327	-0.142
% resting	-0.028	-0.056	0.007	-0.041	-0.076
% alert	-0.537*	-0.439*	-0.542*	-0.157	-0.183
* songs/hr.	0.257	0.163	0.250	-0.258	-0.277
* aggress./hr. ^a	0.249	0.181	-0.246	0.053	0.157
* court./♀/hr. ^b	0.222	0.092	0.278	0.051	0.175

^a number of aggressive interactions with other males

^b number of courtship interactions

* correlation significant at $P < 0.05$

APPENDIX IV. Correlation coefficients for Spearman rank correlations between male behaviours after eggs hatched and female reproductive success. Asterisk indicates significant correlation ($P < 0.05$).

MALE BEHAVIOUR	Y/N	Y/S	%s
1983			
% off marsh	0.283	0.377	0.032
% resting	-0.504	-0.272	-0.375
% alert	0.179	-0.188	0.632*
* songs/hr.	-0.402	-0.299	-0.544
1984			
% off marsh	0.772*	0.771*	-0.376
% resting	-0.769*	0.765*	-0.713*
% alert	0.710*	0.711*	0.776*
* songs/hr.	-0.056	0.243	-0.097
1985			
% off marsh	0.533*	0.471*	0.444*
% resting	0.045	0.099	0.079
% alert	0.298	-0.142	0.091
* songs/hr.	-0.127	0.041	-0.167

APPENDIX V. Comparison of nestling growth versus the order that the female settled on a territory and for nestlings of monogamous females. Growth was measured as the percent change in size from the second to the tenth day after hatch. Male and female nestling growth were analysed separately. None of the differences were significant (Kruskal-Wallis, all P 's >0.1).

ORDER FEMALE SETTLED		PERCENT CHANGE (female nestlings)		
	<u>n</u>	<u>WEIGHT</u>	<u>TARSUS LENGTH</u>	<u>BILL LENGTH</u>
1984				
monogamous	10	305	144	76
1	35	372	133	69
2	22	331	144	73
3	8	266	126	71
4	2	288	155	74
5	1	326	146	71
(male nestlings)				
monogamous	8	463	175	85
1	20	452	175	86
2	19	459	182	88
3	10	423	170	84
4	2	497	146	96
5	1	425	160	94
1985				
(female nestlings)				
monogamous	2	290	117	77
1	9	280	131	65
2	4	251	145	55
3	1	393	*	*
4	1	320	139	83
(male nestlings)				
monogamous	2	432	173	85
1	15	450	184	86
2	7	451	205	108
3	2	445	178	90
4	3	491	175	86
5	1	518	192	85

* not measured

APPENDIX VI. Reproductive success (mean $\pm$ s.d.) of females versus the order females settled on each territory. There were no significant differences in success among females (Kruskal-Wallis, all P 's > 0.1).

ORDER FEMALE SETTLED	n	Y/N ^a	n	Y/S ^b	%s ^c	CLUTCH SIZE
1983						
monogamous	8	1.4 (1.2)	5	2.2 (0.4)	62	4.0 (0.0)
1	25	1.6 (1.2)	18	2.1 (0.8)	72	4.0 (0.5)
2	16	1.4 (0.9)	13	1.8 (0.6)	81	3.9 (0.3)
3	9	0.9 (1.1)	5	1.6 (0.9)	56	3.8 (0.4)
4	3	1.3 (1.2)	2	2.0 (0.0)	67	4.0 (0.0)
1984						
monogamous	16	1.2 (1.1)	10	1.9 (0.7)	62	3.7 (0.4)
1	35	1.5 (1.1)	25	2.1 (0.7)	71	3.8 (0.5)
2	28	1.4 (1.0)	22	1.7 (0.7)	79	3.6 (0.6)
3	19	1.2 (0.9)	15	1.5 (0.6)	79	3.9 (0.7)
4	9	0.8 (1.1)	4	1.7 (0.5)	44	3.9 (0.3)
5	2	1.0 (0.0)	1	2.0	50	4.0 (0.0)
1985						
monogamous	13	0.4 (1.0)	2	2.5 (0.7)	15	3.2 (0.6)
1	34	0.9 (1.0)	16	1.9 (0.6)	47	3.5 (0.2)
2	32	0.4 (0.9)	8	1.7 (0.9)	25	3.0 (0.5)
3	12	0.2 (0.6)	2	1.5 (0.7)	17	3.1 (0.7)
4	8	0.6 (0.9)	3	1.7 (0.6)	37	3.2 (0.4)
5	1	1.0	1	1.0	100	3.0
6	1	0.0	0	0.0	0	3.0

^a number of young fledged per nest

^b number of young fledged per successful nest

^c percent of nests successful (fledged > 0 young)

END

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FIN