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**LA THÈSE A ÉTÉ
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THE LAW OF BATTLE
AND
POLYGYNY
IN
THE REDWINGED BLACKBIRD

by

Christopher George Eckert

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

Department of Biology
Carleton University

1985

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ABSTRACT

Within populations of redwinged blackbirds (Agelaius phoeniceus) mating success varies widely among territorial males. The "polygyny threshold" model was advanced to explain such variation. It assumes that male quality becomes highly correlated with territory quality through intense competition between males for the best territories, such that females can choose mates by territory quality alone.

The results of a removal experiment failed to support the assumption that male quality, in terms of behavioural and morphological components of competitive ability, was highly correlated with territory quality.

A different approach involving wider variation in territory quality (across marsh and upland habitats) also failed to demonstrate that the relative competitive ability of males (measured by their dominance status in captive groups) dictated the relative quality of the territories they could defend.

Additional data combined with the results of other studies suggested that male parental quality could, and should influence female choice, in addition to but independently of territory quality.

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General Introduction

"The season of love is that of battle" (Darwin 1871)

Competition is a prevailing theme in ecological and evolutionary theory. It has been considered an organizing force at many levels, from that of the community (Wiens 1983) on down to the structure of the DNA itself (Dawkins 1982). The conceptual importance of competition stretches back to Darwin's (1859) conception of evolution through natural selection. The struggle for existence between individuals living in a finite world is the driving force of natural selection. Darwin was quick to point out that competition may not be confined to fighting over food, water, space, and other essentials of life, but that within a species, individuals of one sex (usually the males) may compete for the opportunity to mate with individuals of the other sex (usually the females). Individuals realizing greater success at obtaining mates leave a greater number of offspring to future generations. The genes of successful suitors are, thereby, favoured through this sexual selection. Later, Darwin (1871) expanded on how sexual selection could occur. Males could attract more mates by "out-charming" their less attractive rivals during courtship displays, or by virtue of their ornamentation (colourful plumage etc.). Males could also gain access to females by engaging their rivals directly in battle over females, or over resources needed by females for successful reproduction. Darwin's "Law of Battle" applied to this direct intrasexual selection. Females mate with winners because of what they have won. Consequently, males became larger, louder, and

more aggressive as "the result of the advantage gained by larger and stronger individuals over their rivals during many generations" (Darwin 1871).

Although intrasexual selection ("battle") and intersexual selection ("charm") need not ~~always~~ occur exclusively of each other, the dichotomy between the two persists in the modern theory of sexual selection. Intrasexual selection is viewed as being especially intense within species in which males attract mates by defending territories which contain resources essential to breeding females. Selection would favour males who use all facets of their competitive ability to secure as great a share of the critical resources as possible. As the potential for disproportionate success becomes greater, as in polygynous mating systems, the competition is thought to become more intense. The Law of Battle dictates that the competitively superior males should acquire the highest quality territories, while the competitively inferior males obtain only poor quality territories or none at all. When females choose mates, the victors realize a disproportionately high mating success.

The Verner-Willson-Orians "polygyny threshold" model explains the occurrence of variation in mating success among males in precisely this way (Orians 1969). Females choose among males by the quality of their territories. The male with the best territory attracts the largest harem of females. Although variation in the quality of territorial males may also be important to choosy females, the Verner-Willson-Orians model assumes the competition between males for the best territories results in a high correlation between male quality and territory quality. Consequently, a female choosing the

3
best territory will get the best male with it. In its 15 year history, this model has been subjected to a lot of empirical scrutiny (see review in Wittenberger 1980). Data from studies of the highly polygynous redwinged blackbird (Agelaius phoeniceus) have not provided conclusive tests of the model, calling for a reassessment of its fundamental assumptions.

The aim of this study is to test the assumption that male quality is highly correlated with territory quality in an eastern Ontario population of the redwinged blackbird.

In Chapter 1, I outline and apply an experimental approach designed to determine how strongly male quality is correlated with territory quality.

If male quality is not highly correlated with territory quality, then how should female redwinged blackbirds choose mates so as to maximize their fitness?

In Chapter 2, I set the results of the first chapter in the context of mate choice. Specifically, I ask: 1) What male characteristics might a female potentially assess in choosing her mate? 2) How do these characteristics vary with territory quality, each other, and the quality of parental care a male will provide for a female's offspring? 3) Does male parental quality affect female reproductive success?

If the best competitors do not regularly obtain the best territories, how can intrasexual selection be considered an important force in the evolution of male redwinged blackbirds? The experiment in Chapter 1 examines the distribution of males across a limited range of

territory quality. The effects of intrasexual competition may only become apparent across a steeper gradient of territory quality. In Chapter 3, I use a different approach to examine the distribution of males, in terms of their competitive ability, across two different habitats of widely different quality.

Chapter 1. Is male quality correlated with territory
quality in the redwinged blackbird?

Males of many species acquire mates through the defense of resources essential to breeding females (Emlen & Oring 1977). Within such resource-defense mating systems a male's success in recruiting a mate will depend upon both the quality of his territory, and his intrinsic qualities which, for one reason or another, attract females. Resource-defense by males is sometimes associated with considerable variance in male mating success. Polygynous matings occur such that, within a breeding season, some males attract more females than others. Such polygyny is interesting in terms of both the potential existence of sexual selection among males, and the compromises it involves for the females who choose to enter into polygynous matings. These two are related. Determining why a female chooses to mate polygynously rather than monogamously will indicate the nature, and strength of sexual selection acting on the males.

The Verner-Willson-Orians "polygyny threshold" model (Verner 1964; Verner & Willson 1966; Orians 1969) predicts that a female should choose to mate with an already mated male when the quality of his territory is high enough that she can raise at least as many offspring on his territory as on that of any available unmated male. The quality of males may also influence the quantity and/or quality of offspring a female can raise, so that both territory quality and male quality will influence female choice of mate (Verner 1964; Orians 1969; Wittenberger 1976; Weatherhead & Robertson 1977a, 1979). The Verner-Willson-Orians model, however, implicitly assumes that through intense competition between males for the best territories, male quality will become highly correlated with territory quality. In other

words, males will sort themselves out along a gradient of territory quality in an ideal dominance distribution (Fretwell & Lucas 1969; Orians 1980) so that a female choosing the best territory will get the best male with it. This assumption is intuitively pleasing, and as such, has remained untested. Applications of the Verner-Willson-Orians model to data from studies of the redwinged blackbird (Agelaius phoeniceus), however, have failed to produce conclusive results (e.g. Holm 1973; Weatherhead & Robertson 1977a, b; Lenington 1980), indicating the need for a reassessment of the model's fundamental assumptions. The aim of this study is to test the hypothesis that male quality is highly correlated with territory quality in an eastern population of the redwinged blackbird.

Redwinged blackbirds have been the subject of much research into mate choice (Weatherhead & Robertson 1977a; Searcy 1979b; Lenington 1980; Orians 1980; Yasukawa 1981), and sexual selection (Rohwer 1978; Payne 1979; Searcy 1979a, c, d, 1981; Searcy & Yasukawa 1981a; Weatherhead et al. 1984, see review in Searcy & Yasukawa 1983). It seems to be an ideal species for such research. Mating success varies greatly among males in a population (Payne 1979; Searcy & Yasukawa 1983). There is also ample evidence for the existence of intense competition between males for territories. Males return to the breeding grounds well before females (Orians 1961; Greenwood & Weatherhead 1982) during which time they compete for, and vigorously defend territories against frequent intrusions by conspecific males (Peek 1971). Associated with this competition are large groups of "floating" males who do not hold territories, but will quickly fill

vacancies created by the removal of territory owners (Orlans 1961; Rohwer 1982), or may wind up defending territories in sub-optimal habitats (Clark 1985; Greenwood 1985).

The relative importance of male quality and territory quality in influencing mate choice by female redwinged blackbirds has been the subject of much debate (Weatherhead & Robertson 1977a, 1979, 1981; Heisler 1981; Searcy & Yasukawa 1981b; Wittenberger 1981a; Weatherhead 1984). Simple univariate correlational analyses have failed to demonstrate consistent, strong associations between male mating success and either measures of territory quality (Holm 1973; Weatherhead & Robertson 1977a,b; Yasukawa 1981) or male quality (Weatherhead & Robertson 1977b; Searcy 1979a; Yasukawa 1981).

Interpreting the relative importance of male and territory quality from such analyses is clearly confounded by interactions between the two (e.g. Yasukawa 1981). Other critical tests of the relative importance of male and territory quality (Weatherhead & Robertson 1977b; Searcy 1979b; Yasukawa 1981) are also rendered equivocal if the two are highly correlated (Weatherhead & Robertson 1981; Wittenberger 1981a.).

The simplest way of determining to what extent male quality is correlated with territory quality would consist of measuring the various quality parameters in a group of territorial males, then measuring the relative quality of the territories they defend, and simply determining to what extent the two are statistically associated. However, past attempts at measuring territory quality have produced ambiguous results (Wittenberger 1980, 1981a; Lenington 1983).

Therefore, I have used an experimental approach that avoids the problematic measurement of territory quality.

A Removal Experiment

Male quality supposedly becomes highly correlated with territory quality through intense competition between males for the highest quality territories such that the best competitors obtain the best territories. That this actually occurs can be experimentally tested as follows: Competition between males for territories does result in some males being excluded from acquiring territories altogether. These unsuccessful males exist as transient "floaters", and will quickly fill any vacancy created by the removal of a resident male from his territory (Orians 1961). If competition between males also results in a high correlation between male quality and territory quality, then when a number of resident males are removed from their territories, floaters should likewise engage in competition for the highest quality vacancies such that the best floaters will obtain the best vacant territories. Therefore, if competition between males for territories resulted in the highest quality "Residents" acquiring the highest quality territories and the lowest quality Residents acquiring the lowest quality territories, then it should also result in the highest quality "Replacements" acquiring the highest quality vacant territories (from which the Residents were experimentally removed) and the lowest quality Replacements acquiring the lowest quality vacant territories. Since the same set of territories is occupied first by Residents then by Replacements, the highest quality Resident (relative

(to the other Residents) should be replaced by the highest quality Replacement (relative to the other Replacements), the lowest quality Resident by the lowest quality Replacement and so on across the group of experimental territories. A high positive correlation between male quality and territory quality will, therefore, be experimentally verified by a high positive correlation between the rank order of Residents, in terms of quality, and the rank order of their respective Replacements. It is important to reiterate two things about this experimental design. First, since the same set of territories are occupied by both contingents of males (Residents, Replacements), no measure of territory quality is required. Second, Residents are not compared to Replacements, rather the rank order of Residents, in terms of quality, is compared with the rank order of their respective Replacements. Such a removal experiment will indicate how strongly male quality is correlated with territory quality, but it will not reveal the direction of the correlation. A high correlation between the rank order of Residents and that of their Replacements could mean that male quality is either positively, or negatively correlated with territory quality.

In most previously studied populations of redwinged blackbirds, territorial boundaries are contiguous, such that the removal of a resident male often results in his neighbours expanding their territories to occupy the vacant space (Orlans 1961). For this experimental design to work as outlined, relative territory quality must not change between the removal of a Resident and the subsequent establishment of his Replacement. To overcome this problem I have

applied this experimental approach in a population of redwinged blackbirds in which males defend isolated territories centered around small roadside patches of cattail. The replacement of these males when removed, will not be confounded by resulting changes in territory quality.

Male Quality

Among the various components of male quality, those involved in territory acquisition and maintenance should be most strongly correlated with territory quality. Peck (1971) has shown a relationship between seasonal trends in the aggressive behaviour of territorial male redwinged blackbirds, and the frequency of intrusions by conspecific males. His additional experiments involving manipulations of aggressive behaviour (through tranquilization, Peck 1972a), and song (through temporary muting, Peck 1972b; see also Smith 1976), clearly indicated the importance of normal aggressive behaviour in successful territory maintenance. In addition, Searcy & Wingfield (1980) have shown that males treated with androgen implants become more aggressive, tend to be of high dominance rank in captive groups, and realize increased success in competition for territories relative to control males (Searcy 1981). Both male body size and epaulet size may also influence success in competing for and maintaining a territory. Body size (Searcy 1979c; Chapter 3) and epaulet size (Chapter 3) have both been shown to be associated with dominance status in captive groups. Peck (1972b), and others (Smith 1972; Morris 1975), have shown that males with blackened epaulets have increased

difficulty in maintaining their territories. Therefore, male competitive ability should be reflected by aggressive behaviour, body size and epaulet size, which as a result, should be highly correlated with territory quality.

There is an important distinction to make between aggressive behaviour and morphological characteristics with respect to the experimental approach I have outlined here. A positive relationship between territorial behaviour and territory quality may only reflect the influence of territory quality on male behaviour, and not that males with the better territories are of higher intrinsic quality (Parker 1974; Petrie 1984). A male defending a high quality territory may do so more vigorously than a male defending a lower quality territory simply because it is worth more (see Ewald 1985).

Morphological features, on the other hand, cannot be directly influenced by territory quality, and therefore, represent more reliable correlates of male quality. Consequently, the results of the removal experiment involving aggressive behaviour must be interpreted in light of those involving morphological characteristics. If male

quality is highly correlated with territory quality, I predict that the rank orders of resident males, in terms of both aggressive behaviour, and body size and epaulet size will be highly correlated with those of their respective Replacements.

METHODS

Study Sites

I studied male redwinged blackbirds defending territories along roadsides in eastern Ontario during the spring and summer of 1984 and 1985. The study sites were located along the sides of paved highways within a 20 km radius of the Queen's University Biological Station, located 40 km north of Kingston (Figure 1-1). The structure and species composition of the vegetation on these sites varied widely. However, most had some common features regularly used by the resident males, including a patch of cattails (Typha latifolia) located within 5 m of the road, a fence running through or adjacent to the cattail patch, and in many cases, telephone poles and wires running parallel to the road. The cattail patches varied in size, and were set in a variety of habitat types, including uncultivated "old field", hayfield, pasture, mixed shrubland, cornfield, and mixed deciduous forest (in order of occurrence). The activities of territorial residents were centered around the cattail patches. However the defended areas were quite large, averaging approximately 5816 m², and ranging up to 29000 m² (Eckert unpublished data). Suitable habitat seemed to be patchily distributed along the roadsides, and as a result, neighbouring males were relatively isolated from one another. Neighbours were usually in visual contact with each other, but did not share contiguous territorial boundaries.

Figure 1-1. Location of study sites in eastern Ontario.
Triangles represent sites used only in 1984, squares:
1985, circles: both years.

General Methods

Males were captured using mist nets and decoy traps (Smith 1976; Picman 1979), individually colour banded, measured, and released back on to their territories. Some of the males whom I was unable to trap could be identified by distinct song types, and/or unique patterns of missing feathers. When the identity of a male could not be consistently confirmed, he was excluded from further study.

Male Qualities

Males were ranked in terms of body size by wing length, measured (to the nearest 0.5 mm) from the bend of the wing to the tip of the longest primary. Since wing length is highly correlated with fat-free weight in some bird species (Connell et al. 1960), and does not fluctuate greatly with nutritional status, it has become a conventional index of size in this species (Searcy 1979a, c, d; Yasukawa 1979, 1981; Greenwood 1985).

Males were ranked in terms of epaulet size by epaulet length, measured as the distance (to the nearest 0.5 mm) from the bend of the wing to the furthest extent of yellow plumage (Searcy 1979c).

Aggressive behaviour was assessed by quantifying the responses of territorial males to a model intruder consisting of a stuffed adult conspecific male mounted in an upright posture with epaulets fully exposed, affixed atop an aluminum pole, and accompanied by a playback of territorial song (see Orians & Christman 1968) broadcast from a cassette recorder hanging off the pole 0.5 m below the mount (see Rohwer 1978; Yasukawa 1978 for use of similar techniques). The model

was placed within the cattail patch on each male's territory so that it was clearly visible from all directions, and the volume of the playback adjusted slightly so that it could be heard throughout the territory.

To accurately quantify individual differences in aggressive behaviour, it is important to minimize differences between males resulting from variation in behaviour with time of day and season (Peck 1971), weather conditions, male reproductive stage (Dabelsteen 1984), and length of residency on territory (Rohwer 1982). Variation in male response with time of day was standardized among individuals by presenting the model three times to each male over a period of about ten days: once in the early morning (sunrise to 0800 hours EST), once in the late morning (0800 to 1000 hours), and once in the early evening (1630 hours to sunset). Individuals were never tested more than once a day. In 1985, this schedule was further refined by presenting the model for the first time in the early morning, the second time in the late morning, and the third time in the early evening. To minimize the effects of variation in weather conditions no model presentations were conducted during periods of snow, rain, or high winds. To minimize variation resulting from differences in the length of residency, model testing was begun after males were on territory for at least ten days. In an attempt to minimize variation in male response resulting from differences in reproductive stage, most model presentations were conducted in the early spring before the onset of breeding. In 1984, the Residents were tested before the onset of nesting by females. Although model testing of their Replacements

was conducted after breeding had started, all males had an incubating female on their territory. Therefore, this effect should be minimized, because all the males within each group (Residents, Replacements) were at the same reproductive stage. In 1985 model testing of both Residents and Replacements was completed before the onset of nesting on any of the territories. The presence of females could affect the results of the 1984 experiments in another way. Females generally settled on male territories well before they began nesting. The presence of a settled female on a territory, vacant due to the removal of the original Resident, may influence its apparent quality in the eyes of incoming Replacements, independent of its intrinsic quality. This problem was avoided in 1985 by removing all settled females along with resident males. The actual effect of both these female-related factors on the outcome of the 1984 experiments could be assessed by comparing the 1984 results with those from 1985.

Response of Males to The Model

Male response to the model was quantified during a 15 minute observation period, with the aid of binoculars; a portable tape recorder, and an electronic metronome, by an observer concealed inside a car parked on the roadside 20-30 m distant. Time budgets were estimated by instantaneously sampling the male's behaviour at five second intervals (Wiens et al. 1970). All discrete behavioural displays occurring during the observation period were tallied and classified following Orians & Christman (1968). Song spread displays were classified with respect to intensity, on the basis of wing

extension and epaulet exposure following Peek (1972b). Peek recognized four categories: incipient, low, medium, and high (in order of increasing intensity). I have added a fifth category not clearly described by Peek: "simple". This intensity class consisted of songs given with neither wing extension nor epaulets exposure, and seemed to be functionally distinct from Peek's incipient category.

In some cases when a male attacked the model, observations had to be stopped because the male had damaged the mount to such an extent that it could no longer be considered a standard stimulus. In these cases, the response of the male up until destruction of the model was recorded and used in the subsequent behavioural analysis.

The Removal Experiments

In 1984, the aggressive responses of 19 resident males were tested with the male model. Ten of these (group 1984I) were removed on 3 May, and the remaining nine (group 1984II) on 13 May. In 1985, 22 Residents were tested with the model. All of these were removed on 25 April. Model presentations were subsequently repeated for all the replacement males.

If the non-territorial males are to sort themselves out among vacant territories on the basis of male quality it is important that all Replacements have the opportunity to assess all the experimental sites. In the early spring, male redwinged blackbirds gather in communal roosts at night, and make forays during the day to either look for, or defend territories (Greenwood & Weatherhead 1982). The distribution of experimental sites must, therefore, be within the

range of the daily excursions of floating males. In 1984 the sites in each experimental group were all within 10 km of each other; and in 1985 the sites were all within 25 km. Although the movements of males roosting in the spring have not been studied, the spatial separation of experimental sites was within the size of home ranges reported for fall-roosting blackbirds (Meanley 1971 (cited in Heisterberg et al. 1984); Somers et al. 1981; Heisterberg et al. 1984). The effect of spatial scale in this regard may be further investigated by comparing the results from 1984 with those from 1985, and by looking at subsets of sites within each experimental group.

Detecting a correlation between male quality and territory quality requires that both parameters vary to some extent. The degree of variation in male quality will become apparent as a result of the behavioural and morphological measurements. Variation in territory quality is much more difficult to assess, hence the rationale for this experimental approach. If male pairing success is any indication of relative territory quality (Searcy 1979a; Yasukawa 1981), then variation in territory quality may be revealed by variation in harem size. Therefore, I followed reproduction on the experimental sites throughout the summer in 1984. Harem size was estimated as the maximum number of simultaneously active nests per territory.

Behavioural Variables

Aggressive behaviour can be described in terms of many different variables. The nine variables used below were selected so as to describe the full range of male response to the model, and most are

common to other studies of the aggressive behaviour of male redwinged blackbirds (Rohwer 1978; Yasukawa 1978). Four time budget variables were used. Two of these describe male response in terms of proportion of the observation time spent either less than 5 m ("Time <5m"), or greater than 50 m ("Time >50m") from the model. Another two describe the proportion of time spent attacking the model ("Time attacking"), and time spent territorially vigilant ("Time vigilant"). The values for each of these variables were calculated as follows. The males used in this study were isolated. However, response to the model was sometimes interrupted by conspecific male and/or female intrusions. To minimize the differences between males resulting from variation in intruder pressure among sites, the time a male spent reacting to intruders was recorded and removed from the total observation time. The remaining time was subdivided into time spent less than 5 m, 5-50 m, and greater than 50 m from the model. Fifty metres was arbitrarily chosen as the point beyond which a male was essentially no longer responding to the model. This distance also corresponded to the average limit of the observers' visual acuity. Time spent less than 50 m from the model was divided into time in, and out of view. Time less than 50 m and in view was further subdivided into time spent attacking the model and time spent in other activities. An attack on the model represented the ultimate aggressive response. Since not all males attacked the model, it was important to quantify the time spent in other activities so that the resulting variables could be related in a standard way to the tendency to attack. Therefore, time spent attacking was calculated and removed from the total time less than 50

m and in view. The remaining time was subdivided into time spent vigilant (territorially alert with epaulets fully exposed), and the time spent in other activities (e.g. displaying, foraging, flying, preening). In this way, four variables (Time ≥ 50 m, Time < 5 m, Time attacking, and Time vigilant) were calculated as proportions of the relevant total times.

Another four variables represent the rate at which the various stereotypical advertisement displays ("Song spreads", "Bill-ups", "Flight songs", and "Alarm calls", see Orians & Christman 1968) were given during the time spent in view, less than 50m from, but not attacking the model. Particular attention was given to the song spread, as it is a graded display, the intensity of which is thought to provide information on a male's motivational state (Yasukawa 1978). The ninth variable, therefore, estimates the average intensity of the song spreads given during presentations of the model, and was calculated by weighting each song spread with respect to its intensity class (simple to high = 1 to 5).

Statistical Analysis of Behaviour

The aggressive response of each male can be described using all nine variables. However, as is often the case in behavioural systems, the different variables may be inter-correlated. Ranking the males in terms of aggressive behaviour using each variable separately would be redundant and very cumbersome. To overcome this problem, I used a principal-components analysis (PCA) with the orthogonal varimax rotation to objectively reduce the original nine variables to a

smaller number of mutually uncorrelated, composite variables, or factors. The use of PCA in behavioural analysis has become quite common (see Rohwer 1978; and Yasukawa 1978 for applications of similar techniques to aggressive behaviour in male redwinged blackbirds), and is explained in detail by Huntingford (1976); Aspey & Blankenship (1977); and Frey & Pimental (1978). Each factor describes a dimension of the variation in male aggressive response not accounted for by any of the others, and can be interpreted on the basis of the relative loadings of the original variables. A PCA was, therefore, used to extract factors from a 9 by 9 Pearson correlation matrix based on the behavioural responses of 51 males. These 51 consisted of the resident males from both years, plus a number of non-experimental males tested in the pre-breeding season of 1985. These non-experimental males were included to increase the power of the PCA in accurately describing the variation in male aggressive behaviour. The replacement males were excluded from this analysis so as to provide an independent set of factors with which to rank both the Residents and Replacements in terms of aggressive behaviour. The analysis was further limited to those principal-components with eigenvalues of at least 1.0 (i.e. those accounting for at least as much of the variation as one of the original variables, see Aspey & Blankenship 1977). Scores for each Resident and Replacement male on each factor were computed by multiplying the factor score coefficients for each variable by the standardized value of each variable for each male (standard values were calculated as deviation from the within-group mean, expressed as number of standard deviations). Standardization was necessary because

not all variables were measured in terms of the same units (Aspey & Blankenship 1977).

Multivariate techniques are usually based on the assumption that the original variables are normally distributed. Time budget variables, however, were expressed as proportions, and as such, tended to be binomially distributed. These variables were normalized using the arc-sine transformation (Zar 1976). Average intensity and rate variables could not be transformed but were for the most part normally distributed. However, as only relatively few males spent any time attacking the model, Time attacking remained negatively skewed. Similarly, rate of bill-up displays was also negatively skewed. Although PCA is a robust technique and can accommodate deviations from normality (Frey & Pimental 1978), the relationships involving these two skewed variables should be interpreted with caution.

All analyses were performed using the programs in SPSS-X (release 1.0, SPSS, Inc. 1984) on the Carleton University Honeywell CP-6 computer. Statistical significance was accepted at the 0.05 level. In some correlational analyses, samples were small and could not be pooled. In these cases I considered the consistency of correlation coefficients in terms of both sign and magnitude as well as statistical probability values in assessing significance. Complete data were not available for all males, therefore, sample sizes vary for different analyses. All means are presented $\pm$ standard error.

RESULTS

The response of males to the model was usually rapid, yet varied from apparent disinterest to repeated vigorous attacks. Of the 91 males tested, all responded with at least some song spread displays ($\bar{X} = 2.99 \pm 0.31$ song spreads/minute), and 23% spent some proportion of the observation time attacking the model ($\bar{X} = 0.034 \pm 0.012$, $N=91$).

Analysis of Response to The Model

The nine behavioural variables were generally inter-correlated, with 19 of 36 correlations (53%) being statistically significant (Table 1-1). A PCA produced three new composite factors, which together accounted for 66.3% of the total variation in male response. In addition to being mutually uncorrelated, these factors turned out to be intuitively interpretable (Table 1-2). Factor 1 is characterized

by high positive loadings of Time <5m, Time vigilant, Song spreads, and Average SS. This factor represents a behavioural response that consisted of spending a high proportion of time territorially vigilant and close to the model while giving frequent song spreads of relatively high intensity. I will call it "Display". Factor 2 is characterized by high positive loadings of Time attacking and Bill-ups, and moderate positive loadings of Time <5m, and Average SS (but a low negative loading of Song spreads). This factor clearly represents an attack response, and will be called "Attack". Those males who did attack the model, regularly, preceded an attack with numerous close-range bill-up displays accompanied by relatively few

Table 1-1. Pearson correlation¹ matrix of nine variables² describing the responses of 51 male redwinged blackbirds to a series of conspecific male model presentations.

	Time > 50 m	Time < 5 m	Time attacking	Time vigilant	Song spread	Average SS	Bill- ups	Alarm calls
Time < 5 m	-0.547*							
Time attacking	-0.310*	+0.469*						
Time vigilant	-0.310*	+0.633*	+0.194*					
Song spreads	-0.151	+0.361*	-0.037	+0.382				
Average SS	-0.384*	+0.684*	+0.285*	+0.714*	+0.321*			
Bill-ups	-0.370*	+0.466*	+0.564*	+0.083	+0.157	+0.352*		
Alarm calls	+0.192	-0.073	-0.097	+0.148	-0.084	-0.039	-0.184	
Flight songs	+0.198	-0.357*	-0.103	-0.299*	-0.085	-0.290*	-0.180	+0.097

1-Statistical significance at the 0.05 level denoted by: *

2-See text for a description of each variable.

Table 1-2. Factor loading matrix for principal-components analysis of nine response variables¹.

variable	Factor 1 ²	Factor 2	Factor 3
Time > 50 m	-0.413	-0.512	+0.230
Time < 5 m	+0.730	+0.536	+0.004
Time attacking	+0.042	+0.872	+0.082
Time vigilant	+0.853	+0.100	+0.301
Song spreads	+0.673	-0.196	-0.267
Average SS	+0.782	+0.328	+0.104
Bill-ups	+0.139	+0.788	-0.204
Alarm calls	-0.003	-0.133	+0.914
Flight songs	-0.446	-0.139	+0.149
label:	"Display"	"Attack"	

1- Based on the responses of 58 males to a series of three presentations of a conspecific male model intruder. See text for description of the variables.

2- The three factors together account for 66.3% of the total variation in male response.

song spreads of moderate to high intensity. In spite of Time attacking and Bill-ups being negatively skewed, this factor is highly interpretable with respect to my observations of male behaviour. Factor 3 is characterized by a very high positive loading of Alarm calls, and low positive loadings of Time vigilant, and Time >50m. This factor is more enigmatic than the previous two. It appears to represent an alarm response of some sort, and will not be considered as a component of aggressive behaviour.

The Removal Experiment

Resident males were usually replaced quite rapidly. Of the 41 Residents, 23 were replaced later the same day, seven the morning after, two within the same week, and four were not replaced until much later in the season. All four of these late replacements occurred in 1984 (3 in group 1984I, and the other in group 1984II). Due to a general decline in aggressive behaviour with the season (Peck 1971) these late Replacements could not realistically be ranked along with the others in their group, and were removed from the analysis. Of the remaining 39 resident males, two were replaced by more than one male, and one was replaced by expansion of a neighbour's territory. These males were also removed from the analysis. In all other cases the replacement males occupied the entire vacant space, and demonstrated striking fidelity to the original song posts and boundaries.

The Verner-Willson-Orians model assumes that male quality is highly correlated with territory quality and, in terms of this experimental design, predicts that the rank orders of resident males

with respect to aggressive behaviour, body size, and epaulet size should be highly correlated with those of their respective Replacements. The results of the three experiments I have conducted failed to support this prediction. Spearman rank correlations involving the two components of aggressive behaviour produced coefficients that were consistent in sign and magnitude over the three experiments. However, none of them indicated a strong correlation. The ranks of Residents in terms of Display were correlated to a moderate extent with those of their Replacements (Figure 1-2), and the correlation coefficient for the 1985 experiment is statistically significant. The ranks of Residents in terms of Attack, however, were virtually uncorrelated with those of their Replacements (Figure 1-3). None of the coefficients were greater than 0.100, and none approached significance. Similarly, ranks of resident males in terms of the morphological features associated with dominance status, were not highly correlated with those of their Replacements. Ranks based on body size (as indexed by wing length) were only weakly correlated, and coefficients for the three experiments varied in sign and magnitude (Figure 1-4). Ranks based on epaulet length were consistently correlated, with coefficients ranging from 0.385 to 0.454, inferring a weak correlation (Figure 1-5). The results were generally consistent from 1984 to 1985, suggesting that the potentially confounding female-related factors present in 1984 (but not 1985) had no significant effect on the outcome of the experiments.

In 1984, four males were not replaced until much later in the breeding season. That these territories remained vacant in spite of

Figure 1-2. Display scores of resident males and their respective Replacements.

Different symbols represent each experimental group:

open circles = 1984I, closed circles = 1984II, closed triangles = 1985. Circled points lying along the x-axis represent the scores of residents that were not replaced until much later in the breeding season.

r_s = Spearman rank correlation coefficient.

Statistical significance is denoted by: ns = $\underline{P} > 0.10$.

$** = \underline{P} < 0.01$.

Figure 1-3. Attack scores of resident males and their respective Replacements.

Different symbols represent each experimental group:
open circles = 1984I, closed circles = 1984II, closed
triangles = 1985. Circled points lying along the x-axis
represent the scores of residents that were not
replaced until much later in the breeding season.

r_s = Spearman rank correlation coefficient, $\underline{p}$

0.50 for all correlations.

Figure 1-4. Relative body size of resident males and their respective Replacements (as measured by wing length, in mm).

Different symbols represent each experimental group: open circles = 1984I, closed circles = 1984II, closed triangles = 1985. Circled points lying along the x-axis represent the scores of residents that were not replaced until much later in the breeding season.

r_s = Spearman rank correlation coefficient. P

> 0.50 for all correlations.

Figure 1-5. Relative epaulet size of resident males and their respective Replacements (as measured by epaulet length; in mm).

Different symbols represent each experimental group: open circles = 1984I, closed circles = 1984II, closed triangles = 1985. Circled points lying along the x-axis represent the scores of residents that were not replaced until much later in the breeding season.

r_s = Spearman rank correlation coefficient. P
> 0.50 for all correlations.

the apparent existence of a contingent of floating males (as evidenced by rapid replacement of removed residents later on, and intrusions by conspecific males during subsequent model presentations on other territories) suggests that these Residents were defending the worst of the experimental territories. If male quality was highly correlated with territory quality, these four males should rank the lowest within their groups, in terms of the four measures of male quality. The data presented in Figures 1-2 through 1-5 did not support this prediction, thereby corroborating the results of the correlational experiments.

The Effect of Spatial Scale

The results of these experiments are consistent from 1984 to 1985. This indicates that a two-fold increase in spatial scale between years had no significant effect on how precisely replacement males sorted themselves out on the basis of relative male quality. The effects of spatial scale may be further assessed by examining the rank correlations of Residents with their Replacements within subsets of the experimental sites. Of the 20 sites used in the 1985 analysis, some were within a very short distance of each other. Six sites (group A) were within 1.75 km of each other, and another four sites (group B), were all within 1.25 km. Repeating the rank correlation analysis for each of these two groups, indicates that the ranks, in terms of Display are still only weakly correlated (group A: $r_s = 0.200$; group B: $r_s = 0.400$), but that the ranks in terms of Attack seem to be more strongly correlated (group A: $r_s = 0.314$; group B: $r_s = 1.000$) than in the large-scale experiment. Unfortunately,

complete morphological data are not available for the males in these groups. The results of this analysis still do not indicate that male quality is highly correlated with territory quality, though they do allude to the possibility that large spatial scale may have weakened the apparent correlations between territory quality and some of the components of male quality.

Variation in Male Quality and Territory Quality

For male quality to be correlated with territory quality, both parameters must vary to some extent. Results from the behavioural analysis indicated that male quality, in terms of aggressive response is highly variable (see Figures 1-2 and 1-3). The functional significance of variation in the morphological indices is more difficult to assess. Coefficients of variation for wing length, calculated for each group of residents and each group of replacements, ranged from 1.3% to 3.9%. Coefficients of variation for epaulet length were slightly higher, ranging from 4.1% to 7.2%. A similar degree of variation in both variables (wing length: 2.7%, $N=28$; epaulet length: 5.3%, $N=28$) was associated with the formation of linear dominance hierarchies in groups of captive male redwinged blackbirds (see Chapter 3). This suggests that the estimated variation in body and epaulet size amongst males in groups of residents and groups of replacements is significant with respect to competition for resources.

Although variation in territory quality cannot be assessed directly, harem sizes varied amongst the 1984 experimental sites,

ranging from zero to two in group 1984I ($\bar{X} = 1.1 \pm 0.23$, $N=10$), and zero to three for group 1984II ($\bar{X} = 1.5 \pm 0.33$, $N=8$). Similar data were not available for the 1985 experimental group, however the sites were in the same locale, and included some of the same sites used in 1984. It seems, therefore, that there was significant variation in both the quality of males, and the quality of territories used in these experiments.

DISCUSSION

Orians' (1969) version of the polygyny threshold model implicitly assumes that, through intense competition between males for territories, male quality will become highly correlated with territory quality. In terms of the experimental approach I have used, it predicts that the rank orders of resident males, in terms of the components of male quality important for acquisition and maintenance of territory, will be highly correlated with those of their respective Replacements. The results, presented here, did not support this prediction. The ranks of Residents in terms of one component of aggressive behaviour (Attack), and body size (as indexed by wing length) were not correlated at all with those of their Replacements. The rank correlations of Residents with their Replacements in terms of another component of aggressive behaviour (Display), and epaulet size (as measured by epaulet length) were moderate and weak, respectively, but consistently positive. These results suggest that the different components of male quality vary independently of each other with respect to territory quality. However, together they clearly indicate

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that male quality is not highly correlated with territory quality in this population of redwinged blackbirds.

Limits to the Effect of Intrasexual Competition

Why might male quality not be highly correlated with territory quality? I will discuss three possibilities.

1) Quality perception

Males will only be able to sort themselves out along a gradient of territory quality with respect to their competitive abilities if they can perceive the variation in territory quality. Fretwell (1972) suggests that this assumption may often prove to be false. Moreover, if males cannot predict relative changes in territory quality over the breeding season, then the correlation between male quality and territory quality will become increasingly weak as the season progresses (Wittenberger 1981b). Ideal quality perception may be limited in male redwinged blackbirds. They acquire territories in early spring when much of the habitat is still covered in snow. As yet, there is no evidence with which to assess either of these possibilities, though both are consistent with the results of this study.

2) Site dominance

Assuming males can accurately assess and predict the relative quality of the territories available to them, a vacant territory may be secured not by the highest quality male, but by the male who gets to it first and establishes some sort of site dominance. Site

dominance may be a result of asymmetries in competitive ability between territory owners and intruders. However, the results presented above suggest that this is not the case with male redwinged blackbirds. Site dominance may also be a result of conflicts between territory owners and intruders being resolved on the basis of an arbitrary convention regardless of their relative competitive abilities (Maynard-Smith & Parker 1976). The convention, in this case, is that the owner always wins, and the intruder always loses. This type of strategy should evolve when the risk of fighting to both parties is very high regardless of their relative fighting abilities, as it may well be in male redwinged blackbirds (Rohwer 1982). Site dominance of this sort would weaken the correlation between both the quality of Residents and Replacements, and territory quality. Lastly, site dominance may result from asymmetries in knowledge between owners and intruders; The owner may know a lot about his present territory (Williams 1966), and very little about the existence of other potential territories (Rohwer 1982). Therefore, the subjective value of the territory would be greater for the owner than the intruder, so that if both are of the same quality the owner should be more willing to escalate in fighting than the intruder. The owner wins due to a pay-off related asymmetry in his favour (Parker 1974). This type of site dominance would weaken the correlation between the relative quality of Residents and the relative quality of their territories, but should not affect the distribution of Replacements across territories. Because Replacements settled more or less simultaneously, little time would have elapsed during settlement, thus limiting the

development of knowledge-related asymmetries between one Replacement and another.

Krebs (1982) has distinguished among these three types of site dominance in a removal/release experiment with great tits (Parus major). His results suggest that territory owners win because of a pay-off related asymmetry rather than an asymmetry in competitive ability or an arbitrary convention. Rohwer (1982) provides data suggesting that site dominance in redwinged blackbirds is a result of all three types of asymmetries, although arbitrary conventions seem to be of considerable importance. Yasukawa (1979) has also demonstrated what could be a sort of convention- or pay-off-related site dominance in redwinged blackbirds. Males who were successful in acquiring territories for the first time had, more often than not, been captured in the general vicinity of the territories during the previous year's post-breeding season whereas most unsuccessful males had not.

3) Territory fidelity

The correlation between male quality and territory quality may also be weakened if males return to the same territories in successive years (Krebs 1971; Searcy 1979a; Weatherhead & Robertson 1981). If male competitive ability increases with age (Krebs 1971; Searcy 1979c) or breeding experience, and if males would be more successful on a territory different from that which they held in the previous year, we would expect males to shift to progressively higher quality territories as they got older and more experienced. However, such is not the case with redwinged blackbirds. Adult males show strong between-year territory fidelity (Nero 1956a; Searcy 1979a). Of 17 non-experimental males banded in 1984 and who returned in 1985, 14

reclaimed their old territories. Territory fidelity would have an even more pronounced effect if males establish territories as subadults, as do some male redwinged blackbirds. Most subadult males do not breed. Those that do, have to compete with adults for territories, and as a result, wind up obtaining very low quality territories (Greenwood 1985). These territorial subadults are presumably the highest quality males of their cohort. If they return to their original territories in subsequent years, then some of the highest quality males will be on the lowest quality territories (Weatherhead & Robertson 1981).

Conclusions

The conclusion that male quality is not highly correlated with territory quality has implications for both the study of female mate choice, and that of sexual selection in redwinged blackbirds.

If variation in male quality affects female fitness (see Searcy 1979b), female choice of mate may be influenced by the inherent qualities of males in addition to, but independently of the quality of the territories they defend. Recent evidence indicates that male quality may well influence the reproductive success of female redwinged blackbirds (Patterson 1979; Searcy & Yasukawa 1981a; Yasukawa & Searcy 1982; Muldal et al. in press; Chapter 2). While I have not measured those male qualities which directly influence female fitness, I have measured those which should be most highly correlated with territory quality. I suggest that the male qualities related to female fitness will likewise be weakly correlated with territory quality. Future studies should consider both male quality and

territory quality to clearly elucidate the patterns of female mate choice in this, and other species in which resource-defense polygyny occurs.

The results of this study suggest that male competitive ability is not the primary factor determining the distribution of males across territories of different qualities. Perhaps the effect of intrasexual selection on male redwinged blackbirds is not as strong as previously thought (see also Searcy 1979a). The results I have presented above are only suggestive. The striking sexual size-dimorphism (Searcy 1979d), the delayed plumage maturation of subadult males (Greenwood 1985), and the abundant evidence of intense (and not always successful) competition between males for territories (see above), all imply that intrasexual selection has been, and continues to be, a prime mover in the evolution of males in this species. This study has considered the distribution of males across a restricted portion of the global array of territory quality. The effects of intrasexual competition may be more pronounced in determining the distribution of males across habitats of widely different qualities (see Chapter 3), or determining which males, within an age class, obtain territories and which do not. Alternatively, intrasexual selection may only operate during restricted periods in the history of populations (see Wiens 1977), such that short-term studies will fail to reveal its occurrence. This may be especially true of redwinged blackbirds, whose recent history has seen many changes involving their distribution and abundance across many different habitats (Clark 1985). However, I point out these possibilities as lines of further investigation, not as explanations for an anomalous result.

The notion that individuals choose mates so as to maximize their fitness has recently received much scrutiny. While theoretical developments concerning the evolution of mate choice have been substantial, clear demonstration that adaptive mate choice actually occurs has proved more difficult (Arnold 1983; Halliday 1983). One of the greatest challenges in this regard lies in determining the role of mate choice in situations where territorial males acquire mates through monopolizing resources essential to breeding females. In some species a resource-defense mating system (Emlen & Oring 1977) is associated with considerable variance in male mating success. Polygynous matings occur such that, within a breeding season, some males acquire more mates than others. The Verner-Willson-Orians "polygyny threshold" model (Verner 1964; Orians 1969) proposes that variance in male mating success is a result of adaptive mate choice on the part of females. Females choose the highest quality "breeding situations" available to them. The quality of each breeding situation is determined by the quality of the territorial male and/or the quality of the territory he defends (Wittenberger 1976). Sufficient variation in the quality of breeding situations results in variation in male mating success. Since the polygyny threshold model is based on adaptive female choice, testing it requires clear predictions as to the order in which females should rank available breeding situations so as to maximize their fitness (Lenington 1980). The purpose of this paper is to illustrate the complexity involved in making such predictions concerning female mate choice in a polygynous passerine bird: the redwinged blackbird (Agelaius phoeniceus).

Chapter 2. Male quality, territory quality, and the
study of mate choice in redwinged
blackbirds.

Determining the relative quality of breeding situations in resource-defense mating systems may be difficult. Territories may vary in the abundance of food as well as their vulnerability to predators (Lenington 1980, 1983). The owners of these territories may vary in the quality of their genes (Fisher 1958; Weatherhead & Robertson 1979), as well as the amount and quality of parental care they can or will give. Orians' (1969) conception of the "polygyny threshold model" simplifies the situation somewhat. While recognizing the potential importance of male quality, he implicitly assumes that, through intense competition between males for territories, male quality will become highly correlated with territory quality. This notion is intuitively pleasing. Because the relative quality of a male's territory is the outcome of intense competition, it will be a predictor of his quality on which inferior males cannot cheat. Consequently, females, and researchers studying mate choice, need only rank breeding situations by territory quality alone. However, tests of the polygyny threshold model involving only territory quality have produced equivocal results (Holm 1973; Weatherhead & Robertson 1977b; Lenington 1980, 1983; Wittenberger 1981a).

Variation in male quality may be of considerable importance in explaining the patterns of polygyny within populations of the redwinged blackbird. I have presented the results of a removal experiment which suggest that male quality is not highly correlated with territory quality in an eastern population of this species (Chapter 1). Therefore, females may be considering male quality in

addition to, but independently of territory quality in choosing mates. Searcy (1979b) has pointed out that male quality will influence female choice of mate only if 1) a male trait affects the quantity and/or quality of young a female can raise; 2) this trait varies among males to such an extent that a female choosing the best male with regard to the trait will realize a higher fitness than if she chose her mate randomly, and 3) a female can accurately predict the quality of a male with respect to the trait before mating with him. There is evidence that some aspects of male parental quality may fulfill all of these criteria (Patterson 1979; Searcy & Yasukawa 1981b; Muldal et al. in press).

If male quality is not strongly correlated with territory quality, then females may have to predict male parental quality by assessing a limited number of male characteristics. These may include courtship behaviour, territorial aggressive behaviour, social dominance, and any morphological correlates of male parental quality. The results of my removal experiments indicate that neither of the two components of aggressive behaviour, or of the two morphological correlates of dominance status (body size, and epaulet size, see Searcy 1979c; Chapter 3) is highly correlated with territory quality. In this paper I 1) use the results of a removal experiment to determine the relationship between courtship behaviour and territory quality, 2) determine how strongly male characteristics are correlated with each other, and how well they predict male parental quality, and 3) review the evidence that male parental quality influences female fitness to arrive at an idea of what factors should be considered by

females, and researchers in making good mate choice decisions in this species.

METHODS

I studied male redwinged blackbirds defending territories along roadsides in eastern Ontario during the breeding seasons of 1984 and 1985. All the sites were within a 20 km radius of the Queen's University Biological Station, located 40 km north of Kingston.

The structure and species composition of the vegetation on these sites varied widely. However, all sites were on the sides of paved highways, and all included a patch of emergent cattail (Typha latifolia) located within 5 m of the road (see Chapter 1 for details). Since suitable habitat was patchily distributed along the roadsides, neighbouring males were relatively isolated from one another. Neighbours were usually in visual contact with each other, but did not share contiguous territorial boundaries.

Males were captured using decoy traps (Smith 1976; Picman 1979) and mist nets, and individually colour-banded. Some of the males that I was unable to trap could be identified by distinct song types, and/or unique patterns of missing feathers. When the identity of a male could not be consistently confirmed, he was excluded from further study.

Courtship Behaviour and Territory Quality

The extent to which courtship behaviour is correlated with territory quality can be determined through an experimental approach

involving the removal of resident males from isolated territories. A detailed outline of this approach, plus discussion of its assumptions and limitations can be found in Chapter 1. Briefly, if courtship behaviour has become highly correlated with territory quality as a result of intense competition between males for the best territories, the removal of a number of resident males from isolated territories should likewise result in competition between the non-territorial "floating" males for the highest quality vacancies. Each "Replacement" should, therefore, be of the same quality, in terms of courtship behaviour, relative to the other Replacements as the male he replaced was relative to the other "Residents". This pattern will be manifest in a high correlation between the rank order of Residents, in terms of courtship, and the rank order of their respective Replacements.

Male Behaviour and Morphology

I have assessed male behaviours by performing a principal-components analysis (PCA) on variables describing male responses to a series of conspecific model presentations (see Chapter 1 for details). Aggressive behaviour was previously assessed by analysing the responses to a conspecific male model of the 22 resident and 20 replacement males involved in a 1985 removal experiment (see Chapter 1), as well as 16 non-experimental ("Control") males. Courtship behaviour was assessed for these 58 males in essentially the same way. Each male was presented once with a stuffed adult conspecific female mounted in an upright posture, and affixed atop an aluminum pole (see Weatherhead & Robertson 1977a; Rohwer 1978 for use

of a similar technique). The mount was placed within the cattail patch on each male's territory so that it was clearly visible from all directions. Observations were made from a distance of 15-25 m, using a car as a blind, for a period of 15 minutes. Time budgets were constructed for each male by instantaneously sampling his behaviour and location at 5 second intervals (Wiens et al. 1970). All discrete behavioural displays given by the male during the observation period were tallied and categorized following Orians & Christman (1968). Because the female mount was a purely visual stimulus, it was important that response be recorded only after it was certain that the male had seen it. I assumed that the male had seen the mount only after he had perched within 10 m, and turned to face towards it.

I have attempted to minimize differences between males resulting from variation in response with time of day, weather conditions, male reproductive stage (see Dabelsteen 1984), and length of residency on territory (see Rohwer 1982). Mount presentations were conducted during a restricted period in the mid-morning (0700 to 1000 hours EST) before breeding had begun on any of the territories, and never during periods of snow, rain, or high winds. All males had been resident on their territories for at least ten days.

The response of each male was described using eight variables; proportion of time greater than 50 m from the mount ("Time > 50 m"), proportion of time less than 5 m from the mount ("Time < 5 m"), proportion of time territorially vigilant with epaulets fully exposed ("Time vigilant"), rate of song spreads ("Song spreads"), rate of flight songs ("Flight songs"), rate of alarm calls ("Alarm calls"),

and proportion of time in crouch ("Time in crouch"). The song spread is a graded display, the intensity of which may be related to a male's motivational state (Yasukawa 1978). Therefore, I estimated the average intensity of song spreads ("Average SS") given by each male by weighting each song spread by the degree of wing extension and epaulet exposure (simple-high = 1-5, see Peek 1972b; Chapter 1). All these variables, except Time in crouch, were also used to describe the responses of males to a conspecific male model. All variables were calculated as outlined in Chapter 1.

During three of 58 mount presentations, a female who was settling on the territory attacked the mount. In all these instances, the resident male was treating the female mount with apparent disinterest both before and after response by the female. Nevertheless, a courtship response to the mount could be inhibited by the female attacking it. Therefore, I have only used the data recorded before the attack in the subsequent behavioral analysis.

Because these eight variables were generally intercorrelated, I used a PCA with the orthogonal varimax rotation to produce a smaller number of mutually uncorrelated composite variables (factors) (see Huntingford 1976; Aspey & Blankenship 1977; Frey & Rimental 1978; Rohwer 1978; Chapter 1). A PCA extracted three factors from an eight by eight Pearson correlation matrix based on the responses of 38 males (22 Residents and 16 Controls). The 20 replacement males were excluded from this analysis so as to provide an independent set of factors with which to rank both Residents and Replacements in terms of their courtship responses. Proportional variables tended to be binomially

distributed and were, therefore, normalized using the arc-sine transformation (Zar 1976). Average intensity and rate variables were not greatly skewed. Scores for each male on each factor were computed as detailed in Chapter 1.

Relative body size was estimated by wing length, measured as the distance (in mm) from the bend of the wrist to the tip of the longest primary, a conventional index of size in this species (Searcy 1979a, c; Chapter 1).

Relative epaulet size was estimated by epaulet length, measured as the distance (in mm) from the bend of the wing to the furthest extent of yellow plumage (Searcy 1979c).

Male Parental Care

1) Nest defense effort

I measured the nest defense effort of territorial males in two ways. The first involved scoring their response to a human intruder. An observer walked directly from a car to within 2 m of an active nest, and scored the territory owner's behaviour after allowing him 30 seconds to respond. The scoring system used was similar to Searcy's (1979b). Values from 0 to 7 were assigned to each response based on the following criteria:

0. Male flew off his territory in response to the observer.
1. Male remained silent, and greater than 10 m from the observer.
2. Male gave alarm calls from a distance of greater than 10 m.
3. Male remained silent within 3 to 10 m of the observer.

4. Male gave alarm calls from within 3 to 10 m.
5. Male silently circled within 3 m of the observer's head.
6. Male gave alarm calls and circled within 3 m of the observer's head.
7. Male made physical contact with the observer.

In 1985, nest defense effort was also assessed by recording the responses of territorial males to a model predator. Each male was presented with a life-sized plastic crow decoy, affixed atop an aluminum pole, and placed within 1 m of an active nest. Response was quantified during a 3 minute observation period by an observer using a car as a blind. Alarm calls ("Alarms"), "Dives" (swooping flights passing within 1 m of the decoy), and "Strikes" (contacts with the decoy) were tallied and expressed as number per minute.

A male's nest defense effort may vary throughout the breeding season, with stage of nest development and weather conditions (Regelmann & Curio 1983). His apparent response to an intruder may also vary with the number of times an intruder is presented (Knight and Temple 1985). In addition, a polygynous male may be expected to alter his nest defense effort according to the number of active nests on his territory. To control the effects of these factors males were only tested once; in the morning (0800 to 1200 hours EST), during the first three days of incubation of the first nest of the season, and never during inclement weather. All males had only one female nesting on their territory at the time, and had only been visited once before, during egg-laying, after the onset of breeding.

2) Feeding of nestlings

I determined whether or not a male was feeding his nestlings by watching him from inside a car, parked 30-40 m distant, during the late morning (1000 to 1200 hours EST) at specific times during the development of his nestlings. Male redwinged blackbirds usually begin to feed their young after the nestlings are four days old (i.e. day 5 of nestling development)(Patterson 1979). In 1985, each male was observed for one hour when his nestlings were five days old (day 6), and again when they were seven days old (day 8). In 1984, I observed males for approximately one hour on day 8. I also recorded any evidence that a male was feeding his young (i.e. carrying food or fecal sacs) during visits to his territory before and after the observation period. I never saw any indications that a male who did not deliver food to the nest during the observation period was doing so at any other time.

Statistical analyses

All statistical analyses were performed using the programs in SPSS-X (release 1.0, SPSS Inc. 1984) on the Carleton University Honeywell CP-6 computer. Statistical significance was accepted at the 0.05 level. In some correlational analyses samples were small and could not be pooled. In these cases I considered the consistency of correlation coefficients in terms of both sign and magnitude, as well as statistical probability values in assessing significance. Complete data were not available for all males; therefore, sample sizes vary for different analyses. All means are presented $\pm$ standard error.

RESULTS AND DISCUSSION

Statistical Analysis of Courtship Behaviour

Response to the female mount varied widely among males. Some appeared to be uninterested in the mount. Others spent a lot of time in the crouch display, and performed numerous flight songs. Of the 58 males tested with the mount, nine gave pre-copulatory displays, and five attempted to copulate with it. Generally, responses to the female mount differed from those to the male model. Paired comparisons of responses to the first presentation of the male model with those to the single presentation of the female mount reveal a number of significant differences (Table 2-1). On average, males responding to the female mount, spent less time vigilant, spent more time further away from the mount, gave half as many song spreads (but of the same intensity), but about five times as many flight songs than in response to the male model.

The eight response variables were generally intercorrelated (Table 2-2). A PCA produced three mutually uncorrelated factors, which together account for 70.8% of the total variation in male response (Table 2-3). Factor 1 clearly represents a courtship response, as indicated by the high positive loading of Time in crouch. The crouch display is used primarily in courtship (Nero 1956b; Orians & Christman 1968), and was never observed during presentations of the male model. Furthermore, factors 2 and 3 had negligible loadings of Time in crouch. Factor 1 (which I will call "Courtship") was also characterized by high positive loadings of Time < 5 m, Flight songs,

Table 2-1. Paired comparison¹ of the responses of 58 males to conspecific male and female models.

variable ²	male model ³		female model		2-tailed <u>P</u>
	$\bar{X}$	SD	$\bar{X}$	SD	
Time > 50 m	0.075	0.184	0.130	0.219	<u>P</u> < 0.05
Time < 5 m	0.405	0.418	0.169	0.240	<u>P</u> < 0.001
Time vigilant	0.625	0.253	0.409	0.234	<u>P</u> < 0.001
Song spreads	3.760	1.650	1.708	1.304	<u>P</u> < 0.001
Average SS	2.499	0.792	2.305	0.869	<u>P</u> > 0.50
Alarm calls	0.445	0.717	0.537	1.123	<u>P</u> > 0.50
Flight songs	0.099	0.142	0.461	0.600	<u>P</u> < 0.001

1-Paired comparisons made using Wilcoxon matched-pairs signed-ranks test.

2-See text for a description of the variables.

3-Statistics for male model variables calculated using data from one early morning presentation.

Table 2-2. Pearson correlation matrix of variables² describing the responses of 38 male redwinged blackbirds to presentations of a female mount.

	Time > 50 m	Time < 5 m	Time in crouch	Time vigilant	song spreads	Average SS	Alarm calls
Time < 5m	-0.332*						
Time in crouch	-0.156	+0.672*					
Time vigilant	-0.136	+0.080	-0.053				
Song spreads	-0.048	-0.293*	-0.280*	+0.191			
Average SS	-0.496*	+0.485*	+0.594*	+0.423*	-0.082		
Alarm calls	-0.265	-0.154	-0.024	-0.023	+0.070	+0.257	
Flight songs	-0.156	+0.412*	+0.662*	+0.014	-0.337*	+0.460*	-0.032

1-Statistical significance at the 0.05 level denoted by : *

2-See text for a description of each variable.

Table 2-3. Factor loading matrix for a principal-components analysis¹ of eight variables describing male responses to a presentation of the female mount.

variable	Factor 1	Factor 2	Factor 3
Time > 50 m	-0.267	-0.659	-0.273
Time < 5 m	+0.809	-0.004	+0.132
Time in crouch	+0.883	+0.078	-0.049
Time vigilant	+0.051	-0.006	+0.889
Song spreads	-0.557	-0.122	+0.505
Average SS	+0.643	+0.477	+0.451
Alarm calls	-0.158	+0.883	-0.152
Flight songs	+0.784	+0.054	-0.085

label: "Courtship"

1. PCA based on the responses of 38 males. The three factors together account for 70.8% of the total variation in male response.

and Average SS (but a negative loading of Song spreads). This factor represents responses which consisted of spending a relatively large proportion of time close to the mount, in the crouch display, while giving high intensity song spreads at a relatively low rate, and flight songs at a relatively high rate. Rohwer (1978) presented territorial male redwinged blackbirds with female mounts and observed a similar response.

Factor 2 appears to represent an alarm response. A PCA of responses to the male model also produced an alarm factor (Chapter 1). Factor 3 is similar to the Display factor describing responses of males to the male model (Table 2-4). However, it does not seem to represent a component of courtship behaviour. Its very low loading of Time < 5 m, and its similarity to Display suggests that it represents a response that consisted of being uninterested in the female mount, while performing normal territorial advertisement on other parts of the territory.

This multivariate analysis of the responses to male and female models has identified three distinct suites of male behaviour (Table 2-4). These together with dominance status may all be assessed by females in choosing among prospective mates. Because Courtship is directed specifically towards females, it is likely to convey some information on the relative quality of the courting male. Aggressive behaviour and social dominance, although involved primarily in intrasexual interactions, may also influence a female's choice of mate. Females are often the object of group sexual chases involving a number of different males, including the territory owner, his

Table 2-4. A multivariate description¹ of male aggressive and courtship behaviour.

variable	Display	Attack	Courtship
Time > 50 m	-0.413	-0.512	-0.267
Time < 5 m	+0.730	+0.536	+0.809
Time attacking	+0.042	+0.872	-
Time in crouch	-	-	+0.883
Time vigilant	+0.853	+0.100	+0.051
Song spreads	+0.673	-0.196	-0.507
Average SS	+0.782	+0.328	+0.643
Bill-ups	+0.139	+0.788	-
Alarm calls	-0.003	-0.132	-0.159
Flight songs	-0.446	-0.139	+0.784

¹Factor loadings from PCA's of variables describing the responses of 58 males to a series of three male model presentations, and the responses of 38 males to a single presentation of the female mount.

neighbours, and any number of incidental males (Nero 1956b; Orians & Christman 1968; personal observation). Often these chases wind up as group rumbles amidst the vegetation. Consequently, a male's aggressive behaviour and/or dominance status may be quite important in the successful recruitment of females. Whether these male characteristics are actually used by females in choosing mates will depend on the extent to which they are correlated with territory quality, with each other, and with those components of male parental quality which actually influence female fitness.

Correlations with Territory Quality

Orians' (1969) version of the polygyny threshold model implicitly assumes that male quality is highly correlated with territory quality, such that a female choosing the best territory will enjoy the best overall breeding situation. Using an experimental approach I obtained results for two experiments in 1984, and another in 1985 which suggest that male quality, in terms of aggressive behaviour and dominance status, is not highly correlated with territory quality. A high correlation between male quality and territory quality should be manifest in high correlations between the rank orders of resident males, in terms of the various components of male quality, and the rank orders of their respective Replacements. Rank correlations involving Display, and caudal length (a good predictor of dominance status in captivity, Chapter 3) produced moderate and weak positive coefficients, respectively. Ranks in terms of Attack, and body size (another predictor of dominance status in captivity, Searcy 1979c;

Chapter 3) were essentially uncorrelated between Residents and their Replacements. I can determine how strongly Courtship is correlated with territory quality in the same way. In 1985 I tested the responses of 20 Residents and 20 Replacements to the female mount. The rank order of Residents, in terms of Courtship, was significantly correlated with that of their Replacements ($r_s = 0.554$, $p = 0.01$, $N=20$, see Figure 2-1). However, the magnitude of the coefficient indicates that a considerable amount of the variation in Courtship is left unexplained by territory quality. The result of this experimental approach reveals the magnitude of the correlation between Courtship and territory quality, but not its direction. Intensely courting males could have tended to be on relatively high quality territories or on relatively low quality territories.

Correlations Among Male Characteristics

The extent to which each male characteristic will influence female choice of mate will depend on its relationship with the other characteristics, and its relationship with male parental quality. In general, the four male characteristics I have measured are not consistently correlated with each other (Table 2-5). Courtship and Attack, however, are significantly correlated with each other, but only among the Residents and Controls. The coefficient for the Replacements is weakly negative and non-significant. Prior to the removal of the Residents, these Replacements were probably "floaters" with little or no previous breeding experience. That Courtship is not correlated with Attack in this group

Figure 2-1. Courtship scores of resident males and their respective Replacements.

r_s = Spearman rank correlation coefficient.

Table 2-5. Spearman rank correlations^{1,2} among behavioural and morphological features of male redwinged blackbirds.

variable	group	Display	Attack	wing length	epaulet length	corr. with terr. qual. ³
Courtship	Residents	+0.182 (22)	+0.427*(22)	+0.393 (15)	+0.393 (13)	moderate
	Replacements	+0.250 (20)	-0.360 (20)	-0.131 (18)	+0.108 (17)	
	Controls	+0.244 (16)	+0.500*(16)	0.000 (10)	+0.141 (10)	
Display	Residents	+0.162	+0.214	+0.296		moderate
	Replacements	+0.120	-0.278	-0.254		
	Controls	-0.150	+0.061	+0.047		
Attack	Residents		-0.211	+0.177		very weak
	Replacements		+0.338	-0.145		
	Controls		+0.751*	-0.047		
wing length	Residents			+0.393		weak
	Replacements			-0.131		
	Controls			0.00 (8)		
epaulet length						weak to moderate

1-Sample sizes are in parentheses in top row unless otherwise indicated.

2-Probability values denoted as: *: $P < 0.05$, all others: $P > 0.10$.

3-Strength of correlation with territory quality.

of males suggests that the positive correlation between these two in the other groups is an indirect result of both Courtship and Attack having a common correlation with breeding experience. Searcy & Yasukawa (1981b) found a significant positive correlation between time spent courting (per female in the harem) and number of years breeding ($r_s = 0.489$, $p < 0.01$, $N=54$) in an Indiana population of redwinged blackbirds. Courtship may also be related to male breeding experience in this population.

Considering that Courtship appeared to be only moderately correlated with territory quality, and that Attack appeared to be uncorrelated with territory quality implies that breeding experience was only weakly correlated with territory quality in this population. Yasukawa (1981) measured several features of male territories, and found that they were, at best, only moderately correlated with breeding experience in his Indiana population of redwinged blackbirds. Moreover, these results are consistent with the notion that the strong between-year site fidelity shown by adult male redwinged blackbirds may limit any increase in the quality of a male's territory with the number of years he breeds (Searcy 1979a; Weatherhead & Robertson 1981; Chapter 1).

Overall, the various male characteristics which a female may potentially assess before choosing a mate are, in most cases, not correlated with each other, and are not highly correlated with territory quality.

Male Parental Quality and Female Choice

The quality of male parental care should only influence female choice of mate if it fulfills the three criteria outlined above. It must vary among males, be accurately predictable before mating, and influence female fitness (Searcy 1979b). Male redwinged blackbirds do not help with incubating the eggs. However, they do defend their territories against predators and, in some populations, assist their mates with feeding the young. I will begin by considering these two components of male parental care separately.

1) Nest defence effort

Male redwinged blackbirds are notorious for their vigorous nest defense behaviour. This is not surprising considering that predation of eggs and young is the single most important factor influencing the reproductive success of both males and females (e.g. Holm 1973; Caccamise 1976; Weatherhead & Robertson 1977b; Lenington 1980; Picman 1980). In this population, 41% of all broods (N=73 broods; eggs or nestlings) were taken by predators in 1984 and 1985. Moreover, nest defense effort varies widely among males in a population (Searcy 1979b). Are there any male characteristics that a female could use to predict how vigorously a male will defend her nest?

Nest defense effort was measured as the response to a human intruder (RHI) during early incubation for 20 males (8 Controls and 12 Replacements) in 1984, and 11 different males (Controls) in 1985.

(Table 2-6). Although RHI did not vary much among the eight 1984 Controls, it varied widely among the 12 1984 Replacements and 11 1985 Controls. The three variables describing the responses of males to the crow decoy also indicated considerable variation in nest defense effort among the 1985 Controls. Of the 11 males tested, nine responded with some alarm calls ($\bar{X} = 9.33 \pm 1.87$ alarm calls/minute; range = 0.7 - 18.0 alarm calls/minute, $N=9$), six dove at the decoy ($\bar{X} = 5.23 \pm 2.13$ dives/minute, range = 1.0 - 15.4 dives/minute, $N=6$), and four struck the decoy at least once ($\bar{X} = 2.00 \pm 1.24$ strikes/minute; range = 0.3 - 5.7 strikes/minute, $N=4$). Of these three response variables, Strikes probably represents the most direct measure of risk to a defending male, and deterrence to a potential predator. Strikes was highly correlated with RHI ($r_s = 0.864$, $P = 0.001$, $N=11$), suggesting that the measures I have used accurately reflect relative nest defense effort.

Spearman rank correlations between the morphological and behavioural characteristics of males and the four nest defense variables reveal that epaulet size is the best predictor of relative nest defense effort (Table 2-7). Epaulet length was positively correlated with all four variables, particularly Dives ($r_s = 0.931$, $P < 0.01$, $N=8$). That epaulet length was as strongly correlated with RHI among the 1984 Replacements as among the 1985 Controls suggests that its relationship with nest defense effort is not affected by male breeding experience. Attack was also significantly correlated with Dives ($r_s = 0.601$, $P < 0.05$, $N=11$), but uncorrelated with RHI ($r_s = 0.00$, $N=11$).

Table 2-6. Frequency distribution¹ of male nest defense effort scores.

group	response score ²								N
	0	1	2	3	4	5	6	7	
1984									
Controls	0	0	7	0	0	0	1	0	8
Replacements	0	1	5	0	3	0	3	0	12
1985									
Controls	0	2	5	1	3	0	0	0	11

1-The values shown are the number of males in each response category.

2-Response scores estimate the nest defense effort of males in response to a human intruder.

Table 2-7. Behavioural and morphological correlates¹ of male nest defense effort.

correlate	RHJ	Alarms	Dives	Strikes	N
1984					
wing length					
Replacements	+0.313				12
Controls	+0.599				8
epaulet length			not measured		
Replacements	+0.526+				12
Controls	+0.255				8
1985, Controls					
wing length	-0.088	-0.025	+0.435	+0.278	6
epaulet length	+0.542	+0.651	+0.931**	+0.658+	8
Courtship	-0.222	+0.542+	+0.210	-0.053	11
Display	-0.043	+0.156	-0.048	-0.047	11
Attack	0.000	+0.524+	+0.601*	+0.296	11

¹-Spearman rank correlation coefficients, probability values denoted by: +: $P < 0.10$, *: $P < 0.05$, **: $P < 0.01$.

These results suggest that females should be able to predict the relative nest defense effort of a prospective mate, through either assessment of his dominance status, or its morphological correlate, epaulet length. Since Attack is correlated with Dives, but not with epaulet length, females may be able to increase their accuracy in predicting future nest defense effort of prospective mates by simultaneously assessing their dominance status as well as their responses to conspecific male intruders. Whether or not choosing a male who vigorously defends her nest will decrease the probability of a female losing her brood to a predator is less clear. High nest defense effort has been related to increased survivorship of broods in both Stonechats (Saxicola torquata) (Greig-Smith 1980), and eastern kingbirds (Tyrannus tyrannus) (Blancher & Robertson 1982). However, Searcy (1979b) failed to demonstrate a similar relationship in a Washington population of redwinged blackbirds, and argues that predictable variation in the vulnerability of territories to predation will be more likely to influence female choice of breeding situation. Detecting a direct relationship between male nest defense effort and brood survivorship will be difficult. The young and eggs of redwinged blackbirds are eaten by a diverse and variable array of predators, such that the effectiveness of nest defense behaviour in deterring predation will vary within and between habitats, locales, and breeding seasons (Wittenberger 1981a). A direct assessment of the effectiveness of male nest defense behaviour will often be confounded by these factors. Nevertheless, the importance of predation as a potential selective agent clearly indicates the need for more research in this regard.

2) Feeding of nestlings

Prior to Patterson's (1979) work in Indiana, male redwinged blackbirds were thought to contribute little if any assistance to females in feeding their nestlings (Orians 1961, 1980; Holm 1973; Robertson 1973; Searcy 1979b; Weatherhead & Robertson 1981). Several recent studies have all shown that, in at least eastern populations, some males make consistent contributions to feeding their nestlings (Patterson 1979; Yasukawa & Searcy 1982; Muldal et al. in press). This component of male parental care varies widely among males within a population. Some males consistently assist with feeding their young. Some males do not assist with feeding at all. The amount of assistance also varies among those males who do assist in feeding their young (Patterson 1979; Muldal et al. in press). My observations indicate that male provisioning of young was quite common, and highly variable in this population as well. In 1984, I observed 15 males (seven Controls and eight Replacements) on day 8 of nestling development. Seven of these delivered food to the nest. In 1985, two of ten males delivered food to the nest on day 6, and four (including the previous two) of eight males delivered food to the nest on day 8 (two of the original ten broods were lost to predators).

Searcy & Yasukawa (1981b) have shown that the tendency for a male to assist with the feeding of his nestlings is correlated with the amount time he spent courting (per female in the harem), which in turn is correlated with breeding experience. There is evidence of a similar relationship in this population. I examined the relationship between

male characteristics and provisioning of nestlings by comparing "Feeding" and "Non-feeding" males. In 1985, the two males who delivered food to the nest on day 6 had significantly higher Courtship scores than those who did not (Mann-Whitney, $U = 0.00$, $P = 0.04$). The same trend was evident on day 8, but the difference is not significant (Mann-Whitney, $U = 5.00$, $P = 0.40$). Comparing the proportions of males seen delivering food to the nest between the 1984 Replacements and 1984 Controls suggests that the tendency for a male to feed his nestlings may indeed be related to his breeding experience. Five of the seven Control males were seen delivering food to the nest, while only two of the eight, relatively inexperienced replacement males were seen to do so (Fisher exact test, $P = 0.10$). This evidence is only suggestive; however, when combined with that provided by Searcy & Yasukawa (1981b) suggests that a female should be able to predict, to some extent, whether or not a male will assist with feeding her young. Moreover, a female choosing a Feeding male will, on average, realize higher reproductive success than if she chose a Non-feeding male. Both Patterson (1979) and Mørdal et al. (in press) have shown that male assistance increases the survivorship and body weight of nestlings (after five days of age), and that this is not a result of Feeding males holding higher quality territories.

General Discussion

The results of the removal experiments suggest that male quality is not highly correlated with territory quality, such that male quality may influence female choice of mate in addition to, but independently of territory quality. Moreover, I have presented some evidence that two components of male parental quality, nest defense effort and feeding assistance, vary among males, and are somewhat predictable by females before mating. Females should be able to predict the future nest defense effort of prospective mates by assessing their dominance status (or its morphological correlate, epaulet length), as well as their response to conspecific male intruders. Whether or not females will generally realize higher fitness by mating with top-notch nest defenders is, as yet, unclear. A female should also be able to choose the prospective mate most likely to provide assistance with feeding her nestlings by scrutinizing his courtship behaviour or some other correlate of breeding experience. The reproductive pay-off to females making such a choice has been clearly shown (Patterson 1979; Muldal et al. in press). However, Weatherhead (1984) has argued that since males who do feed their young, often feed only the brood of the primary female (Patterson 1979; Yasukawa & Searcy 1982), indicators of male assistance should not influence the choice of secondary and later-settling females. This will only be true if the probability of a later-settling female receiving no assistance from a Feeding male is the same as the probability that she will receive no assistance from a Non-feeding

male. However, this is unlikely for secondary females. Considering the high probability that the brood of any particular female (primary females included) will be lost to a predator suggests that, all other things being equal, a female should choose to become the secondary mate of a Feeding male rather than mate with a Non-feeding male. Furthermore, Muldal et al. (in press) have shown that males in an eastern Ontario population assisted with the feeding of both primary and secondary broods. Some secondary females were actually more likely to receive assistance when they engaged the male in courtship during the development of his primary female's nestlings. However, this advantage is restricted to secondary females, as those females settling later received little if any assistance from the male. I would, therefore, expect tertiary females to ignore cues indicating that a male might feed her nestlings, and pay more attention to cues indicative of high nest defense effort. This would result in a consensus in mate preference among primary, secondary, and tertiary females only if nest defense effort and feeding assistance tend to covary. However, Mann-Whitney comparisons of Feeding and Non-feeding males failed to reveal any differences with respect to any of the measures of nest defense effort, but did show that Non-feeding males tended to have longer epaulets (indicating greater prospective nest defense effort) than Feeding males (1984: $U = 9.5$, $P = 0.05$; 1985, day 6: $U = 4.0$, $P = 0.70$; day 8: $U = 0.05$, $P = 0.09$). This implies that a female choosing a male who appears to be "a good bet" in terms of nest defense effort will, more often than not, be a poor choice in terms of feeding assistance. It is reasonable that females

should vary their weighting of the different components of breeding situations depending on their prospective mating status. If the different components of male parental quality and territory quality vary independently of each other, as they seem to, then no straightforward female preference will exist.

These results and their implications will be important in deciding what factors to consider when predicting adaptive female mate choice in this species. A clear demonstration that females are choosing mates in an adaptive fashion will require researchers to consider both the manifold quality of breeding situations, and the mating status of the females in question. Investigations considering only a single component of the breeding situation (e.g. Weatherhead & Robertson 1977b) will be unlikely to produce conclusive results (for a remarkable exception see Pleszczynska 1978). A lack of consensus among females making mate choice decisions at different times will require that female preference be determined directly (see Lenington 1980, 1983), and not by an indirect "yardstick" such as harem size (e.g. Holm 1973; Orians 1980; Weatherhead & Robertson 1977b; Searcy 1979a; Yasukawa 1981).

Finally, predictions concerning optimal mate choice by female redwinged blackbirds should be tested in light of the possible constraints imposed upon females in making such choices. The assumption that females are free to mate with whomever they choose (see Orians 1980) can no longer be considered tenable. There is ample evidence that females compete for membership in harems (Nero 1956b; Lenington 1980, see also 1983; LaPrade & Graves 1982; Hurly &

Robertson 1984, 1985). Moreover, the outcome of this competition may vary with female age (Crawford 1977), and mating status with respect to features of both territories (Lenington 1980), and the parental quality of the males who own them (Yasukawa & Searcy 1982).

The evidence I have presented here suggests that the mating system of the redwinged blackbird may be much more complex than first imagined. The same may be true for other polygynous species in which males offer females more than just a one-dimensional resource.

Chapter 3. Male dominance and habitat quality in
breeding redwinged blackbirds.

Fretwell & Lucas (1970) recognized that territorial individuals could be distributed across habitats of varying quality such that individuals in the higher quality habitat exist at higher densities, and realize greater increases in fitness, than those in the poorer quality habitats. This "ideal dominance distribution" was assumed to arise through individuals recognizing and competing for territories in the highest quality habitats. Since all contestants would not be equally matched, socially dominant individuals would be able to exclude subordinates from the best areas. Fretwell's (1969) study of winter habitat distribution in juncos (Junco hyemalis) lent support to this assumption. Males inhabiting high density field habitat were larger than those in the lower density forests. Since dominance status increases with size in juncos he concluded that larger individuals were indeed despotic, forcing subordinates to reside in the sub-optimal habitat (see also Fretwell 1972).

This type of territorial distribution may have profound evolutionary consequences within species in which males acquire mates by defending resources essential to breeding females. Territorial resource-defense is sometimes associated with considerable variance in mating success among males. Polygynous matings occur such that, within a breeding season, some males attract more females than others (Orlans 1969). The quality of a male's territory may further enhance his reproductive success by influencing the reproductive performance of the females he mates with. In such mating systems, both natural and sexual selection should favour intense competition between males for territories in the highest quality habitat. This competition would

result in a clear ideal dominance distribution of territorial males. The best competitors should obtain the best territories. The purpose of this paper is to determine whether or not the habitat distribution of territorial males within a polygynous species is related to their relative competitive abilities.

There are two main problems confounding a direct demonstration that individuals defending territories in high quality habitat are dominant over, that is have a higher resource holding power (RHP, Parker 1974) than those defending territories in the relatively poorer quality habitats. First, habitats of various qualities may be spatially separated, making a direct assessment of the relative RHP of resident individuals logistically impossible. Secondly, in a situation where a territory of known higher quality abutts one of known lower quality, the dominance of the resident of the higher quality territory over the resident of the lower quality territory apparent during boundary disputes or other territorial activities, may only reflect the relative quality of the resources they are holding, and not their RHP's per se (Parker 1974). The apparently dominant individual may win simply because his territory is worth more, and his relative territorial effort is increased accordingly (Ewald 1985). Therefore, it is important to determine the relative RHP of territorial individuals in the absence of the territories in question (Petrie 1984).

In the study of avian territoriality, tests of the "dominance assumption" have involved monogamous species in which territorial individuals overwinter in flocks within the same locale as their

territories. Two studies have shown that the high-ranking individuals in groups of juveniles (Knapton & Krebs 1976), and transient non-territorial "floaters" (Smith 1978) were more likely to acquire vacated territories. However, only Smith (1976), working with black-capped chickadees (Parus atricapillus), and Petrie (1984), working with moorhens (Gallinula chloropus), have directly demonstrated that the relative dominance of males is correlated with the quality of the territories they wind up defending.

To date, the dominance assumption has remained untested with respect to species in which resource-defense polygyny regularly occurs. In this paper I report an experimental test of the hypothesis that dominance status is correlated with habitat quality in an apparent ideal dominance distribution of a polygynous passerine bird: the redwinged blackbird (Agelaius phoeniceus).

Habitat Quality and the Reproductive Success of Male Redwinged Blackbirds.

Male redwinged blackbirds can be found defending territories in a wide variety of habitat types, ranging from highly productive cattail marshes to urban hedgerows and gardens (Francis 1971; Albers 1978; Clark 1985). The relative dispersion and reproductive success of territorial males across two common habitats, cattail marshes and upland fields, appears to conform to two aspects of a classic ideal dominance distribution. The density of breeding males, as reflected by territory size, is much higher in marshes than upland fields (Table 3-1) (see also Albers 1978). This density distribution also appears to

Table 3-1. Density of territorial male redwinged blackbirds in marshes and upland fields in eastern North America.

area (m ²)				
location	habitat	per male ¹	range (m ²)	reference

Illinois	marsh	-	100-1000	Lenington (1980)
Indiana	marsh	1418	-	Patterson (1979)
New Jersey	marsh	-	350-1400	Lenington (1980)
Ohio	upland	4110	-	Dolbeer (1976)
Ohio	marsh	5335 *	-	Dyer (1970)
Ohio	upland	15458 *	-	Dyer (1970)
Ontario	marsh	1045	153-2890	Weatherhead & Robertson (1977b)
Ontario	upland	5816	2214-29235	Eckert, unpublished data

1-All areas represent average territory size except those marked with * which represent breeding density calculated as: area of habitat block divided by number of territorial males present.

covary with male fitness, in terms of reproductive success. The only three studies comparing the mating success of males in marshes to those in uplands within the same locale and during the same breeding season, all indicate that males defending territories in marshes acquire, on average, larger harems than those defending territories in the uplands (Table 3-2). Data collected by Dr. P. J. Weatherhead and myself, from an eastern Ontario population during the summer of 1985, reveal that this difference in harem size is associated with a difference in actual reproductive success. Males in marshes fledged approximately half again as many young per territory as males in the uplands (marsh: $\bar{X} = 3.83 \pm 0.74$, $N=28$; upland: $\bar{X} = 2.28 \pm 0.16$, $N=14$; $t = 1.38$, $0.20 > P > 0.10$).

The ideal dominance distribution model, therefore assumes that males defending territories in marshes should be generally dominant (have a greater RHP) over those defending territories in upland fields. I have tested this assumption by determining the dominance structure of captive groups consisting of previously territorial males from both high quality (marsh) and relatively sub-optimal (upland) habitats.

Male Morphology and Resource Holding Power

Dominance status of individuals in captive and free-living groups has been related to a number of different morphological characteristics thought to either advertise or directly enhance an individual's relative RHP (see reviews in Brown 1975; Wilson 1975; Morse 1980). Body size has been shown to be correlated with dominance

Table 3-2. Mating Success of male redwinged blackbirds in marshes and upland fields.

average harem size		location	reference
marsh	upland		
2.2	1.9	New York	Case & Hewitt (1963)
2.9	2.0	Quebec	Weatherhead et al. (1980)
1.9	1.5	Ontario	Weatherhead & Eckert, unpublished data

status in juncos (Fretwell 1969; Baker & Fox 1978; Ketterson 1979) and moorhens (Petrie 1984). More specifically, Searcy (1979c) has shown that dominance status is significantly correlated with an index of body size (length of flattened wing) in small groups of captive male redwinged blackbirds.

The function of colouration or plumage characteristics as reliable signals of RHP is more controversial (Rohwer 1975, 1982; Shields 1977). Since colouration plays no part in physical combat, we would expect it to be related with RHP indirectly, through its correlation with other more tangible traits (e.g. Balph et al. 1979). However, plumage characteristics have been clearly related to dominance status in both Harris' sparrows (Zonotrichia querula) (Rohwer 1985) and white-crowned sparrows (Zonotrichia leucophrys) (Fugle et al. 1984). The bright red epaulets (shoulder patches) of adult male redwinged blackbirds have been repeatedly shown, through experimental manipulations, to serve some important role in territory maintenance (Peek 1972b; Smith 1972; Morris 1975; Roßkraft & Rohwer 1985). However, the relationship between natural variation in epaulet characteristics (size and colour) and dominance in captive groups of males seems to be a by-product of age-related dominance (Searcy 1979c).

The second aim of this paper is to determine what morphological features, if any, are correlated with dominance status, and to investigate their role in any apparent RHP asymmetry between marsh- and upland-breeding male redwinged blackbirds.

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MICROCOPY RESOLUTION TEST CHART
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STANDARD REFERENCE MATERIAL 1010a
(ANSI and ISO TEST CHART No. 2)

METHODS

During the summer of 1985 I captured 3 groups of territorial males using mist nets and decoy traps (Smith 1976; Picman 1979). All males were defending territories in either highly productive marshes or marginal upland fields within a 10 km radius of the Queen's University Biological Station, located 40 km north of Kingston in eastern Ontario. Each group consisted of a similar number of males from both habitats (marsh/upland: group I=5/3, group II=5/5, group III=4/6). Aside from habitat, and habitat-related differences in morphology, I wanted to minimize the effect of any other potentially confounding factors. To minimize the effects arising from differences in residency (Searcy 1979c; Yasukawa & Bick 1983) all males in each group were captured and introduced into the aviary on the same day (I: 6 June, II: 27 June, III: 9 July). To minimize any effects of prior acquaintance of some of the males within a group, males from the same habitat were captured from different sites so that no two males resided in the same marsh or field. However, all sites were within the same general locale, so that marsh and upland males would have become equally aware of the different habitats available during territory establishment in the early spring.

Each group was housed in separate aviary compartments (3 X 2 X 1.5 m) of a roofed aviary, provided with plenty of perches, two sources of fresh water, and dishes of feed (consisting of, approximately 4 parts cracked corn, 2 parts millet, and 1 part trout chow (Purina, #3, floating pellets) by volume). Upon introduction to

the aviary, each male was fitted with an aluminum leg-band (on the left leg of marsh birds, and the right of upland birds), weighed to the nearest 0.1 g using a 100 g Pesola spring scale (except for group 1), and measured with respect to various morphological features. The birds were given about 12 days ($\bar{X}=12.3$) to become accustomed to captivity after which they were reweighed, and marked with unique patterns of white acrylic paint on their tail and/or wing feathers to facilitate identification. Observations were begun 2 days later.

The dominance structure of each group was determined by recording the identity of winner and loser in encounters over food, which was restricted to a single small dish located on the aviary floor during the observation period. The outcome of conflicts over a resource such as food may be influenced by the relative hunger of contestants (Clutton-Brock & Harvey 1976). Each observation period was, therefore, limited to about 1.25 hours each morning (0830-1200 hours DST) to minimize hunger satiation of dominant individuals. Each group was observed using a video camera and recorder to eliminate the disturbing presence of a human observer. Observations were amassed for 20 hours ($\bar{X}=21.7$) or until 10 interactions were recorded for each pair of males (dyad), whichever came last. After each observation period the birds were fed ad libitum, from more dishes than birds, until about 1900 hours when all food was removed from the aviary until the next morning's observation period.

I estimated dominance structure in three ways. Dominance hierarchies were determined by constructing a winner-loser matrix for each group following Brown (1975). This method ranks the males in each

matrix from top to bottom in the order which minimizes the number of losses occurring below the diagonal. Relative dominance was also estimated for each male within a group by calculating the percent of encounters won. Within each dyad, dominant status was simply assigned to the male who won the majority of encounters between the two.

The relationships between morphological features and dominance status were assessed within each group using Spearman rank correlations of male characteristics with percent of encounters won. Because group size was small ($N = 8-10$) I considered consistency of correlation coefficients with respect to sign and magnitude, as well as statistical probability values in assessing significance. Probability values were pooled where appropriate (Sokal & Rohlf 1981, p.780).

Body size was estimated using the length of flattened wing ("wing length"), measured (to the nearest 0.5 mm) from the bend of the wrist to the tip of the longest primary. This measure has become a conventional index of size in redwinged blackbirds (Searcy 1979a, c, d; Yasukawa 1979, 1981; Greenwood 1985).

Epaulet size was measured as the distance (to the nearest 0.1 mm) from the bend of the wing to the furthest extent of yellow plumage ("epaulet length") (Searcy 1979c). Epaulet colour was assessed (following Searcy 1979c) by comparing the ~~red~~ portion of the epaulet of each male to Royal Horticultural Society colour sheets (Wilson 1938) and assigning the corresponding colour values (ranging from 15-19).

Body condition was indexed as body weight (in g) divided by wing

length. H. Greenwood (personal communication) has found this index to be a good predictor of proportional body fat in redwinged blackbirds.

Correlational analyses were performed using programs in SPSS-X (release 1.0, SPSS-X Inc. 1984) on the Carleton University Honeywell CP-6 computer. Chi-square and log-likelihood (G) tests were performed following Zar (1976) with the Yates correction applied in comparisons with only one degree of freedom. Statistical significance was accepted at the 0.05 level. All means are presented $\pm$ standard error.

RESULTS

The identity of winner and loser was recorded for 7198 (I:973, II:2801, III:3424) encounters around the food dish. Interactions ranged in intensity from almost indiscernible supplantings and avoidance, to all-out attacks. The data are summarized in the winner-loser matrices in Table 3-3 (a,b,c). In all 3 groups, the data indicate the existence of linear or near-linear hierarchies. Only two intransitive relationships occurred; one in each of groups I and III. For example in group III, male Y dominated male Z who dominated male AA who, in turn, dominated male Y. There were plenty of reversals and some pairs of birds appeared to have been very closely matched. For instance, in group I, male D was victorious over male F in 13 encounters, but lost to male F in 12 encounters.

Table 3-3. Winner-loser matrices for three groups of captive male redwinged blackbirds.

Table 3-3a. Group 1.

		--LOSER							
winner	habitat: ¹	M	M	U	U	M	M	U	M
	male: ²	A	B	C	D	E	F	G	H
	A	-	47	31	73	65	72	71	54
	B	0	-	22	18	30	24	45	20
	C	1	13	-	12	19	8	19	11
	D	1	8	2	-	11	13	26	8
	E	0	11	11	8	-	14	28	12
	F	0	20	5	12	9	-	9	20
	G	0	2	3	11	8	4	-	19
	H	0	6	1	2	13	16	5	-

1-Habitat is denoted as: M = marsh, U = upland.

2-Males are ranked within each matrix from top to bottom in the order which minimizes the number of losses occurring below the diagonal (see Brown 1975).

Table 3-3b. Group II.

		LOSER									
habitat:	U	U	U	M	M	M	M	U	M	N	
male:	I	J	K	L	M	N	O	P	Q	R	
WINNER	I	-	60	121	91	53	96	93	55	19	110
	J	23	-	69	70	55	69	65	55	32	72
	K	7	46	-	95	41	42	96	46	45	101
	L	8	7	46	-	21	79	78	26	26	103
	M	3	10	20	17	-	18	15	8	10	35
	N	3	7	29	19	9	-	67	39	27	68
	O	0	4	2	9	3	6	-	15	13	34
	P	0	0	5	4	2	9	9	-	4	23
	Q	0	2	5	9	4	10	11	8	-	15
	R	0	0	2	0	0	6	10	1	1	-

Table 3-3c. Group III.

LOSER											
habitat:	U	U	U	U	M	U	M	M	U	M	
male:	S	T	U	V	W	X	Y	Z	AA	BB	
WINNER	S	-	106	120	102	38	84	54	48	31	50
	T	87	-	98	118	63	133	91	49	40	97
	U	68	66	-	100	67	184	71	38	29	104
	V	39	11	50	-	26	90	40	26	20	80
	W	29	20	39	19	-	44	16	13	10	37
	X	46	18	35	31	30	-	34	27	14	92
	Y	12	12	15	25	11	25	-	16	5	27
	Z	3	5	4	20	7	17	13	-	16	11
	AA	5	1	2	2	4	10	7	5	-	12
	BB	5	2	7	9	10	15	3	4	4	-

Are Marsh Males Dominant to Upland Males?

Considering the ranks of marsh and upland males in the three hierarchies (Table 3-3) it does not seem that marsh males were generally dominant to upland males. I can test this by restricting the analysis to the dyads in which a marsh male was pitted against an upland male ("marsh/upland dyads") (64 of the 118 total dyads). The ideal dominance distribution model assumes that marsh males should dominate in a significantly greater proportion of these dyads than upland males. The data presented in Table 3-4 did not support this prediction, and in fact, imply the opposite. Upland males dominated marsh males in a significantly greater proportion (67.2%) of the marsh/upland dyads than marsh males. The magnitude of this dominance varied over the 3 groups, and was slightly reversed in group I. However, the overall result was significant ($\chi^2 = 6.891$, $\underline{p} < 0.01$).

The Morphological Correlates of Dominance.

What morphological features, if any, are associated with being dominant? Rank correlation analysis performed on each group separately indicated that epaulet length was positively correlated with dominance status (Table 3-5). Spearman correlation coefficients were consistently moderate and positive in sign (pooled $\underline{p} < 0.025$). Wing length was correlated only weakly with dominance status. Although the coefficients were consistently positive they were of generally low magnitude (pooled $\underline{p} > 0.50$). Epaulet colour, and body condition

Table 3-4. Habitat-related dominance within marsh/upland dyads¹

group	N of dyads	% in which dominant		χ^2	<u>P</u>
		marsh	upland		
I	15	53.3	46.7	0.00	<u>P</u> > 0.50
II	25	40.0	60.0	0.64	<u>P</u> > 0.50
III	24	12.5	87.5	12.04	<u>P</u> < 0.001
total	64	33.8	67.2	6.89	<u>P</u> < 0.01

¹-Dyads in which a marsh males was pitted against an upland male.

Table 3-5. Spearman rank correlations² between morphological features and dominance status¹ in captive groups.

group	N	wing length	epaulet length	epaulet colour	body condition
I	8	+0.293	+0.589	+0.594	-
II	10	+0.412	+0.665*	-0.241	+0.379
III	10	+0.142	+0.597+	+0.376	-0.534

1-Dominance status measured as percent of encounters won.

2-Two-tailed probability values denoted by: + : $0.05 < p < 0.10$, * $p < 0.05$.

index appeared to be ~~un~~associated with dominance status. Correlation coefficients for both varied in sign and magnitude between groups.

Correlations among the various morphological features were weak (Table 3-6) suggesting that they either did not vary with dominance status, or did so independently of each other.

If the relative size of two contestants with respect to a morphological feature influenced the outcomes of competitive interactions, then the male within each dyad who was the larger of the two with respect to the feature in question should have won the majority of encounters between the two. An analysis of asymmetric dyads (those dyads in which the two males are not tied with respect to the feature in question) revealed that relative epaulet length, and relative wing length are both associated with the outcome within dyads. The male with the longer epaulets dominated in 71.7% of all epaulet-asymmetric dyads, and the male with the longer flattened wing dominated in 60.9% of all size-asymmetric dyads. Both these proportions were significantly greater than those expected by chance (Table 3-7). Relative epaulet colour and body condition index showed no association with dominance within dyads (Table 3-7).

Why Are Upland Males Dominant Over Marsh Males?

The associations between dominance status within dyads and indices of relative body size and epaulet size did not change when the analysis was restricted to asymmetric marsh/upland dyads. Males with longer epaulets were dominant in a significantly greater number of epaulet-asymmetric marsh/upland dyads

Table 3-6. Spearman rank correlations^{1,2} between male morphological features.

	epaulet length	epaulet colour	body condition
wing length	+0.130	+0.287	-0.136
epaulet length	-	+0.033	+0.168
epaulet colour	-	-	+0.135

1-None of these coefficients is significant at $P = 0.05$, all P 's > 0.10 .

2- $N=28$ for all correlations except those involving body condition ($N = 20$).

Table 3-7. The relationship between morphological features and within-dyad dominance status.

% of dyads ¹ in				
feature	which dominant	N	χ^2	<u>P</u>

male with				
longer epaulets	71.7	106	19.10	<u>P</u> < 0.001
male with				
longer wings	60.9	105	4.61	<u>P</u> < 0.05
male with				
redder epaulets	52.5	101	0.16	<u>P</u> > 0.50
male in				
better condition	46.8	79	0.26	<u>P</u> > 0.50

1-Includes only those dyads in which the two males were not tied with respect to the morphological feature in question.

(44 of 57, $\chi^2 = 15.79$, $\underline{p} < 0.001$). Similarly, males with longer wings were dominant in a greater, but not significantly greater, number of size-asymmetric dyads (36 of 59, $\chi^2 = 2.441$, $\underline{p} > 0.10$). The general dominance of upland males over marsh males could, therefore, be explained by between-habitat differences in dominance-related morphology if upland males were, on average, larger and/or had larger epaulets than marsh males. Mean epaulet length, however, is almost identical between marsh ($\bar{X} = 43.5 \pm 0.69$ mm) and upland ($\bar{X} = 43.8 \pm 0.55$ mm) males ($t = 0.41$, $\underline{p} = 0.69$), and of the 57 epaulet-asymmetric marsh/upland dyads upland males had the longer epaulets in only 50.9% ($\chi^2 = 0.00$). The habitat-related dominance of upland males, therefore, was not associated with between-habitat differences in epaulet size. Mean wing length of upland males ($\bar{X} = 122.3 \pm 0.89$ mm) was significantly longer than that of marsh males ($\bar{X} = 119.5 \pm 0.91$ mm, $t = 2.19$, $\underline{p} = 0.038$). This was reflected in that upland males had the longer wings in 83% of the 58 size-asymmetric marsh/upland dyads ($\chi^2 = 21.97$, $\underline{p} < 0.001$).

The general dominance of upland males over marsh males was associated with upland males having been larger. However, further analysis reveals that the relationship between body size and dominance was not straightforward. Table 3-8 compares the outcomes of body and epaulet size asymmetries for males from each habitat. Marsh males dominated less often when they had a body or epaulet size advantage than did upland males (body size: $G = 5.15$, $\underline{p} < 0.05$; epaulet size: $G = 8.30$, $\underline{p} < 0.01$). This result was associated with an interaction between the two types of morphological asymmetries.

Table 3-8. Outcome of asymmetries in epaulet, or body size within marsh/upland dyads.

feature	larger	N	% of dyads in which dominant	marsh/upland comparison ¹
	male			
epaulet	marsh	29	62.1	G = 5.15
length	upland	28	93.8	$\underline{P} < 0.05$
wing	marsh	10	33.3	G = 8.30
length	upland	48	68.7	$\underline{P} < 0.01$

1-Comparison between marsh and upland males made using log-likelihood (G) test.

In the 52 marsh/upland dyads which were asymmetric in terms of both features, upland males had the "double advantage" of longer epaulets and longer wings in 25 (48.1%), while marsh males had this double advantage in only 6 (11.5%). Upland males had, what I will call, the "single advantage" of longer epaulets, but shorter flattened wings, in 2 (3.8%), while marsh males had this single advantage in 19 (36.5%). The association of epaulet advantage with size advantage was greater for upland males than for marsh males ($G = 28.34$, $P < 0.001$).

I can effectively partial out the effects of relative epaulet and body size on dominance status by comparing the outcomes of these double and single advantages between marsh and upland males. Upland males were dominant in 92% of the 25 marsh/upland dyads in which they had the double advantage. Marsh birds were dominant in only 50% of the 6 marsh/upland dyads in which they had the double advantage (Fisher's exact test, $P = 0.038$). A similar, but non-significant, result is apparent considering the outcome of single advantages. Upland males dominated in 100% of the 2 marsh/upland dyads in which they had the single advantage, while marsh males dominated in only 63% of the 19 marsh/upland dyads in which they had the single advantage (Fisher's exact test, $P = 0.43$). When the relative morphological advantages were the same, upland males still dominated more often than marsh males.

DISCUSSION

Before interpreting the results of this study in terms of the assumption that I have proposed to test, it is appropriate that I first address my own assumption.

Is Dominance Status in Captivity a Good Indicator of Resource Holding Power?

Is dominance status determined during food fights in groups of captive males a reasonable index of male RHP potentially involved in acquiring and maintaining a territory?

Rowell (1974) has criticized such extrapolation of captive dominance ranks on the grounds that hierarchical dominance relationships observed in caged groups may be a product of artificially high densities of animals in captivity. This should not be a problem here. Redwinged blackbirds roost and feed communally all year round except for the two month period during which some members of the population are raising young. They should be well adapted for competitive encounters at close quarters. Males engaged in competitive interactions in the aviary were frequently observed to display a number of behaviours, such as song spread and bill-up displays, common to agonistic interactions in feeding flocks, and on territories (Orlans & Christman 1968). Moreover, Weatherhead & Hoysak (1984) have shown that age-related dominance plays an important part in competition for roosting positions within a redwinged blackbird roost. Additional support comes from my observations of the behaviour of contestants during territory take-overs, or territory establishment

after the original resident has been removed (Chapter 1). These conflicts are accompanied by close-range bill-up duels which often escalate into attacks. Such behaviour is very similar to that observed around the food dish in the aviary. Therefore, I feel that it is safe to assume that the dominance relationships within these captive groups were not an artifact of high densities, but an extension of normal variation in RHP among males.

Another relevant criticism is that relative dominance status may be dependent upon the resource competed for, so that dominance status determined during food fights would be poorly correlated with RHP in terms of territoriality. This would be true when the costs and benefits of access to different resources varied among individuals and contexts (Clutton-Brock & Harvey 1976). Given that all males in the aviary groups were sexually mature adults (as assessed by plumage characteristics, Greenwood 1985) who were previously defending territories, and were all kept on the same nutritional regime, I would expect them to have had very similar cost/benefit schedules with respect to both breeding territories and aviary feed. Few studies have been designed precisely to address this problem. However, such an investigation can be approximated by comparing the results of studies of dominance carried out in different contexts. Adult male redwinged blackbirds generally dominate subadult males in both captive groups (Searcy 1979c), and communal roosts (Weatherhead & Hoysak 1984). In dark-eyed juncos (Junco hyemalis), large individuals enjoy a high dominance status in both captive (Baker & Fox 1978), and free-living groups (Ketterson 1979). Additional information comes from comparing

the importance of morphological features in captive and free-living situations. The results of this study suggest that the size of a male's epaulets was, in some way, associated with his RHP in captive groups. Peck (1972b) and others (Smith 1972; Morris 1975) have shown that the epaulets of male redwinged blackbirds are important in territory maintenance, and Roskafi & Rohwer (1985) have reported that transient non-territorial males avoid the "territories" of stuffed male redwings with supernormal epaulets relative to those of dummies with blackened epaulets. Although these lines of evidence do not constitute entirely unambiguous support, taken as a whole they do suggest that the relative dominance of male redwinged blackbirds in captivity should be closely correlated with RHP in terms of territoriality in the free-living situation.

Is Resource Holding Power Correlated with Habitat Quality?

The ideal dominance distribution model assumes that male dominance, or RHP, is positively correlated with habitat quality. Within a population of redwinged blackbirds, males defending territories in the high quality marshes should be generally dominant to those defending territories in the relatively low-quality upland fields. The results of this study did not support this prediction, and, in fact, imply the opposite. In captive groups, males from the uplands were generally dominant to those from marshes. This dominance was apparently associated with: 1) upland males having been generally larger than marsh males, 2) an interaction between relative epaulet size and relative body size in favour of upland males, and 3) some

other factor(s) which I was not able to identify. These results are surprising considering that I captured the birds from the apparently most productive of the local marshes and from the seemingly most sub-optimal upland fields. These two habitat types vary widely in appearance as well as quality so that males "shopping" for territories will be "ideal", in that they should be able to tell the difference between them. The assumption inherent in the ideal dominance distribution model that territorial males are ideal (Fretwell & Lucas 1970; Chapter 1) should, therefore, not be a confounding factor in the interpretation of these results. Furthermore, the marsh and upland sites from which I captured these males were all within the same locale, so that all males could have become aware of the different habitats available while flying to and from roosts and foraging areas in the early spring.

Given the same morphological advantages, why did upland males dominate more often than marsh males? I have attributed this result to some "unidentified" factor(s). One obvious possibility is that upland males are more suited to aviary life than marsh males. Males residing in uplands might be subject to a greater degree of human disturbance, and have a diet more similar to that provided in the aviary than marsh males. I can address this possibility by assessing adaptability to the aviary using body condition index measured after 12 days in captivity. Comparing marsh and upland males revealed no difference between them in terms of relative body condition (Mann-Whitney, $U = 88.5$, $P = 0.667$). Furthermore, McNicol et al. (1982) report that males from marshes and uplands in this area show a high degree of dietary overlap

during the breeding season, including significant proportions of waste corn and seeds. It seems unlikely that there was differential adaptation to captivity. The unaccounted-for dominance of upland males remains a mystery.

Before I can confidently dismiss the dominance assumption as being generally untenable, it is necessary to determine if the dominance-related size advantage of upland males in my aviary groups represents a real difference in the local populations of redwinged blackbirds. I have compiled data from several other samples of territorial males (Table 3-9). These data indicate that the size disparity present in the aviary groups is probably an artifact of sampling error, and further suggest that marsh males are, on average, larger than upland males. The interpretation of my results is, therefore, not completely straightforward. Based on the real average body size advantage of marsh males we might expect them to be generally dominant over upland males. However, epaulet length, a more reliable predictor of dominance status in captivity is virtually identical between marsh ($\bar{X} = 44.7 \pm 0.36$ mm, N=29) and upland (44.8 ± 0.32 mm, N=35) males in this population (Weatherhead & Eckert, unpublished data). Considering also the unaccounted-for dominance of upland males over marsh males suggests that marsh and upland males overlap widely in RHP. Taken together, the results of this study suggest that male RHP is not strongly correlated with territory quality in this population of redwinged blackbirds.

Table 3-9. Body size¹ of male redwinged blackbirds from marshes and upland fields in eastern Ontario.

Sample ³	Year	Marsh	upland	comparison ²
Aviary groups	1985	119.5 (14)	122.3 (14)	$\underline{P} < 0.05$
Local population ⁴	1985	123.1 (29)	120.6 (24)	$\underline{P} < 0.05$
Menard ⁵	1977	120.9 (37)	119.2 (29)	NS
	1982	122.1 (32)	121.1 (34)	NS
	1983	122.5 (32)	121.0 (30)	NS

1-Body size indexed as length of flattened wing (in mm).

2-Sample means compared using t-test; probability values are two-tailed; NS = $\underline{P} > 0.05$.

3-Sample sizes (N) are in parentheses.

4-Data for marsh sample courtesy of P. Weatherhead

5-Data courtesy of G. Menard; from three samples collected 30 km south of my study area.

Limits to Optimal Territory Selection?

Considering the substantial difference in mean reproductive success across the two habitats, and that the perception of quality should, in this case, not be difficult, why were some of these large dominant males defending territories in upland fields rather than marshes? Surely strong natural and sexual selection should favour males who acquire the highest quality territory possible.

The behavioural mechanisms involved in territory assessment and acquisition in male redwinged blackbirds are poorly understood. However, the limited investigation into this area has revealed some highly counter-intuitive results (Yasukawa 1979; Chapter 1). I have previously discussed how the strong territory fidelity shown by male redwinged blackbirds could considerably weaken the correlation between male RHP and territory quality within a habitat (Chapter 1; see also Krobs 1971; Searcy 1979a; Weatherhead & Robertson 1981), and that this effect may be especially pronounced in the case of males who manage to obtain territories as subadults (Weatherhead & Robertson 1981). If territory fidelity constrains the "upward mobility" of males across habitats of various quality, some males with very high RHP may wind up defending even worse quality territories than expected.

If early experience in the natal habitat affects habitat preference (Klopfer 1963; Catchpole 1974) or successful territory establishment later in life (Yasukawa 1979), then the sorting-out of males among territories may be even further influenced by stochastic processes.

Assuming these behavioural traits are acting in such a way that

some males are on worse territories than would be predicted on the basis of their relative RHP begs the question: how can apparently maladaptive traits such as these persist in a population of redwinged blackbirds in which both natural and sexual selection are thought to be intense? Surely any individual lacking these behavioural constraints would widely outflank his competitors in such a system. The answer to this question may involve the ever-changing natural history of the redwinged blackbird.

Redwinged blackbirds are thought to have been, at one time exclusively marsh-dwelling (Allen 1914; Graber & Graber 1963). Their widespread expansion into sub-optimal habitats is relatively recent and seems to be a result of increased population size which, in turn, is boot-strapped to increased food availability in agricultural landscapes during critical times in fall, winter, and spring (Clark 1985). Behavioural traits such as territory fidelity, and habitat preference influenced by natal experience, may have been adaptive in the ancestral habitat, and perhaps even valuable in competition for territories. Given the relatively short time period in which selection has been acting on multi-habitat populations, these traits still persist. If populations of upland- and marsh-breeding redwinged blackbirds represent somewhat different demes (Dyer 1964; Stone 1973 (both cited in Dyer et al. 1977); Hesse and Lustick 1972) then selection against these traits would be even slower than expected. These possibilities are advanced as speculations; not as explanations. The results of this study have failed to demonstrate that dominant males obtained the highest quality territories, and do

not support the notion that increased competitive ability is currently favoured by intrasexual selection. Further research is needed to determine why male competitive ability is not highly correlated with territory quality, and reveal the importance of intrasexual selection in the evolution of male redwinged blackbirds.

LIST OF CONCLUSIONS

- 1) In contrast with a common theoretical assumption, the results of a removal experiment failed to demonstrate that male competitive ability, in terms of aggressive behaviour, body size and epaulet size, was highly correlated with territory quality within an eastern population of breeding redwinged blackbirds.
- 2) A different experimental approach also failed to show that the distribution of males between high quality (marsh) and low quality (upland) habitats was associated with differences in their relative competitive abilities (as measured by dominance status in captive groups).
- 3) In reference to the above and current research on female mate choice in redwinged blackbirds:
 - a) Females should be able to assess the parental quality (nest defense effort, and provisioning of nestlings with food) of prospective mates before mating.
 - b) The morphological and behavioural correlates of male parental quality were not strongly correlated with territory quality or with each other.
 - c) Females should, therefore, be expected to assess male quality in addition to, but independently of, territory quality in making adaptive mate choice decisions.
 - d) The two components of male parental quality did not strongly covary, such that a female's criteria for mate choice may vary with her prospective mating status.

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