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SEXUAL SELECTION AND PLUMAGE VARIATION
IN FEMALE RED-WINGED BLACKBIRDS

by

© Katherine Elizabeth Muma

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

1987

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January 1988

ABSTRACT

Sexual selection acting through intrasexual competition and mate choice is thought to have led to the bright red epaulets of male red-winged blackbirds (Agelaius phoeniceus). However, little attention has been given to the significance of the dull orange epaulets that are found on females. This study was conducted to determine if plumage variation in female red-winged blackbirds could be explained due to sexual selection acting on females or if it is due to genetic correlation with the male trait.

In a field study, I found that females with brightly coloured epaulets did not settle on territories first and were not more aggressive. Furthermore, there was no difference in the response of males or females to models of females with brightly coloured or dull epaulets. I also examined variation in the chin colour of females and found no behavioural differences between brightly coloured females and dull individuals.

In captive groups, females established dominance hierarchies when competing for food. However, there was no relationship between plumage colour and dominance. When I altered epaulet or chin colours of females the hierarchies changed indicating that plumage may be involved in individual recognition.

I concluded that variation in epaulet colour of female red-winged blackbirds does not function as a signal of status and is not maintained through sexual selection acting on females. Instead I propose that it is a genetic correlate of male plumage.

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GENERAL INTRODUCTION

One of the most striking features of birds is their extensive variation in plumage colouration. Nearly all research into plumage variation has focussed on males. Plumage patterns of male birds may have evolved through sexual selection by male-male competition and female choice or through selection for characters that aid in competition for resources other than mates (Darwin 1871). However, some females also exhibit bright plumage similar to males of their species. The purpose of this study is to determine if variation in female plumage could have resulted from direct selection due to female-female competition. If not, then variation may be due to genetic correlation with the characters found in males (Lande 1980).

Plumage badges

Selection could lead to the development of plumage patterns that reflect competitive ability. The status-signalling hypothesis has been suggested to explain the evolution of plumage badges of winter flocking species. (Rohwer 1975, 1977, 1982, 1985). Plumage badges are conspicuous patches of feathers usually located on the head, throat or wings that are often displayed during aggressive interactions between birds. For badges to signal competitive ability they must differ consistently between dominant and subordinate individuals. The

advantage of a signalling system is that subordinate individuals will recognize dominants without requiring a contest and possible risk of injury (Rohwer 1985). Rohwer (1982) proposed that badges of social status will evolve when individuals engage in interference competition for resources and are likely to interact repeatedly with the same competitors.

Rohwer (1977) found that in winter flocks, male Harris' sparrows (Zonotrichia querula) having large, solid black bibs, were dominant over individuals with less black on their throats and breasts. When immature birds were dyed to resemble adults with large bibs they became dominant over control individuals of the same sex and age class (Rohwer 1985). However, Shields (1977) argued that status may be conveyed by a variety of behavioural cues and that plumage variation could simply be the result of differences in age or sex. Stable hierarchies could be formed in winter flocks due to individual recognition (Shields 1977, Watt 1986, Balph et al. 1979).

Sexual selection and male-male competition

Contests over food in winter switch to contests for mates in the breeding season. In his "law of battle", Darwin (1871) proposed that there is selection on males for the development of strength and weaponry for the purpose of obtaining access to females. Darwin (1871) noted that many of the bright colours and elaborate plumes of male birds

did not confer a survival advantage and therefore could not have evolved through natural selection. Instead, these characters aided in the acquisition of mates and have developed through sexual selection either through male-male rivalry or female discrimination. The major types of sexually selected characters in birds outlined by Darwin (1871:257) include such diverse features as weaponry used in male-male competition, ornaments, and structures for producing sounds. These characters are usually restricted to males and often are not fully expressed until the male reaches sexual maturity and begins to compete for mates (Wittenberger 1981).

Males are generally the more competitive sex, especially in polygynous mating systems. Because one male can monopolize resources that allow access to more than one female, there will be high variance in male mating success and hence strong selection on male morphology, behaviour and physiology (Selander 1965, Emlen and Oring 1977).

Floating populations of non-breeding sub-adult males may exist if there is low probability that young males can acquire territories and hence obtain mates (Selander 1972).

If plumage patterns are related to displays given in intrasexual aggression or in courtship, sexual selection acting on these characters may lead to bright plumage in adult males. In some species, competition with older males has lead sub-adult males to delay the acquisition of

typical adult male plumage until their second year and instead they resemble females in their plumage. Selander (1965, 1972) suggested that female-like sub-adult males may experience lower predation due to crypticity and decreased aggression from adult males since males are less likely to attack female-like individuals. Delayed plumage maturation represents a compromise between survival and reproduction brought about by male-male competition (Greenwood 1985). Polygyny and female-female competition

Females may also be competing in polygynous systems. Since polygyny is generally thought to be advantageous to males, most theories for the evolution of polygyny have focussed on the potential costs and benefits for females (Verner and Willson 1966, Weatherhead and Robertson 1979). The polygyny threshold model (Verner 1964, Verner and Willson 1966, Orians 1969) states that when there is variation in the quality of male territories, a female may do better settling with an already mated male on a good territory than she would if she settled with an unmated male on a poor territory. The evolution of polygyny depends on the immediate and future costs and benefits associated with intrasexual competition for both males and females.

A prediction from the polygyny threshold model is that the average reproductive success of a female will decrease as more females are added to the harem (Orians 1969). The

competitive female choice version of the model assumes that polygyny is costly to the female (Altmann et al. 1977).

These costs could include decreased food, increased predation due to higher nesting density, or a decrease in male parental care (Yasukawa and Searcy 1981). If females are competing due to costs imposed by polygyny, then sexual selection could act on female characters such as plumage variation. The alternative to the competitive model is that females within a harem cooperate. In the cooperative female choice version, benefits gained through group living (*i. e.* through improved defense against predators) outweigh the costs imposed by increased nest density (Picman 1981). Wittenberger (1981) stressed that it is the magnitude of the costs and benefits that determines whether primary females (those that settle first on a territory) will be aggressive toward secondary females.

Aggression in red-winged blackbirds

It has long been known that male red-winged blackbirds (Agelaius phoeniceus) will attack and destroy conspecific male models placed on their territories (Noble and Vogt 1935). Furthermore, females are aggressive toward other females and exhibit territorial displays similar to the male displays. These include exposing epaulet (upper wing coverts) and chin feathers as well as direct attacks and chases. LaPrade and Graves (1982) placed conspecific female models near red-winged blackbird nests. Females

were highly aggressive and made at least one attempt to drive off the intruder. In fact, it is not uncommon for females to dive at and strike a model female placed on their territory (Hurly 1982). Nonetheless, more than one female often settles on a given territory.

Hurly and Robertson (1984) suggested that aggression between females may be an attempt to deter settlement of later arriving individuals. They demonstrated that females defended areas within their male's territory against intrusions by other females. In addition, newly arriving females were more likely to settle on territories where the resident female had been removed than on control territories (Hurly and Robertson 1985). This was likely due to the aggression exhibited by residents toward these newcomers. However, females may not be successful in driving away intruders because males may intervene and begin courtship displays directed at the new female (Searcy 1986). These observations suggest that female-female competition may be a factor influencing polygyny in this species.

Several studies have found additional support for the competitive female choice model in red-winged blackbirds. In one investigation, females settled according to territory quality and reproductive success decreased with increasing harem sizes (Lenington 1980). Similarly, Weatherhead and Robertson (1977 a) found that female

reproductive success decreased with increasing nesting density. Lenington (1980) proposed that an interaction between female choice of mates, limited high quality breeding habitat and direct competition between females have all determined the red-winged blackbird mating system. Yasukawa and Searcy (1981) found that the intervals between nest starts were similar within and between territories in a population where males provided little or no assistance in feeding the young. In a population where males did feed the young of the primary female, nest starts within territories were spaced apart in time suggesting that females were competing. In another study, Yasukawa and Searcy (1982) noted that the primary female was most aggressive toward intruding female models presented in the precopulatory posture. The precopulatory posture would signal the intent of the intruder to mate with the territorial male. Since primary females received the most assistance from the male, Yasukawa and Searcy (1982) proposed that aggression between female red-winged blackbirds was an attempt to ensure male parental investment.

Plumage variation

A number of studies have documented the importance of plumage colouration in male red-winged blackbirds. These birds have bright red and yellow epaulets that are exposed during territorial and courtship displays (Nero 1956 a, b).

Yearling males can be easily identified because they have delayed plumage maturation (Selander and Giller 1960).

Young males have plumage patterns intermediate between adult males and females with mottled orange epaulets and black body feathers tipped with buff (Meanley and Bond 1970). Sub-adult male plumage appears to have developed due to strong sexual selection on males. By having dull plumage, yearling males decrease the risk of predation and aggression from adult males while at the same time gaining experience in courtship and territory acquisition (Selander 1965, 1972). Furthermore, female-like males may actually be able to deceive territorial males and sneak copulations with resident females and thereby breed without having to maintain a territory (Greenwood 1985).

Apparently, both vocalizations and the characteristic red epaulets are necessary for males to maintain territories (Peek 1972). Smith (1972) blackened the epaulets of males and found that these males were more likely to lose their territories than were control individuals. Roskoff and Rohwer (1987) found that intruding males avoided models of males with large, bright epaulets when compared to models with blackened epaulets. Dominant males in a group of captive red-winged blackbirds were not only larger than subordinates but also had longer epaulets (Eckert and Weatherhead 1987 a). Thus, many studies have been conducted addressing the function of red

epaulets on male red-winged blackbirds. However, no one has tested the functional significance of variation in female plumage.

In contrast to adult males, adult females are brown with dark brown streaking on the breast and back. Females have epaulets which are duller than those found on males and range in colour from pale yellow to vivid orange. Chin plumage varies from pale yellow to strong yellowish pink. Payne (1969) stated that females having significant red colouration on the epaulets were invariably adults and thus these plumage characteristics have been used to age individuals (Selander and Giller 1960, Payne 1969).

Is plumage variation functionally significant ?

In male red-winged blackbirds, the bright red epaulets of adults are thought to be a product of sexual selection (Selander 1965). The dull sub-adult male plumage is a tradeoff between sexual selection for bright plumage and breeding in the first year and natural selection for cryptic plumage and delayed reproduction (Selander 1965, 1975, Greenwood 1985). Similarly, bright plumage in female red-winged blackbirds may be a balance between sexual selection resulting from female-female competition for resources or mates and natural selection for cryptic colouration. This will be referred to as the direct sexual selection hypothesis. It is similar to the status-signalling hypothesis that bright individuals signal

experience and fighting ability except it is specific to females during the breeding season.

The indirect hypothesis proposes that variation in female epaulet colour is genetically correlated with the character in males. Here selection is acting on males and only affects the female indirectly. Darwin (1871) believed that characters (i.e. bright plumage) exhibited by the male could be "transferred" to the female. The character need not have a selective advantage for the female and may actually be limited by natural selection. For example, selection against conspicuous females could act through predation pressure (Baker and Parker 1979). In fact, characters first expressed equally in both sexes may become limited to one sex due to natural selection against it in the other sex (Fisher 1930). Fisher (1930) expanded Darwin's ideas on sexually limited traits and placed them within the context of Mendelian genetics. He stated that if modifications are not strictly limited to the male then selection acting on males will lead to a corresponding change in the character in females.

We now know that genetic correlation between characters is due to pleiotropy (one gene affecting multiple traits, Lewin 1985) and if male and female characters are correlated they do not evolve independently (Lande 1980, Lande and Arnold 1985). Lande (1980) noted that selection acting on one sex may result in a

corresponding change in the character in the opposite sex. Correlated characters may restrict the rate of evolution of sexual dimorphism (Lande 1980). Due to different selection pressures acting on males and females there will be a different optimal phenotype for each sex.

Genetic correlation can involve behavioural or morphological traits. For example, Halliday and Arnold (1987) suggested that this genetic correlation between the sexes is a possible explanation of the evolution of multiple mating in females. Promiscuous mating is seen as a trait which is highly selected for in males but not advantageous for females. However, females exhibit the trait because selection against it is not strong enough to limit it to males. Multiple mating in females of some species may not be adaptive but may simply be a genetic correlate of male behaviour (Halliday and Arnold 1987). In the same way, plumage patterns expressed in both sexes may be selected for only in one sex.

The purpose of this study is to determine if plumage variation in female red-winged blackbirds is under direct sexual selection or if plumage colouration is instead a correlate of traits selected for in the male. In Chapter One I present results from observations and experiments on females in the field. In Chapter Two I examine interactions among females kept in groups in aviaries. If female plumage is under direct sexual selection I predict a

strong positive correlation between plumage colouration and aggression in the field and dominance in the aviary. On the other hand, if plumage patterns in females are due to indirect selection through correlation with male characters I predict no correlation between plumage and status.

Chapter 1. Settlement, aggressive behaviour
and plumage variation

INTRODUCTION

The development of elaborate ornaments and colouration of male birds is often attributed to sexual selection involving male-male competition and female choice (Darwin 1871). In some cases, females have bright plumage patterns similar to the males of their species. Bright plumage may have evolved in females due to intrasexual (this time female-female) competition in the same way that it has evolved in males. On the other hand, females may express male characters due to genetic correlation with traits that have evolved due to selection on males (Lande 1980, Halliday and Arnold 1987). In this case the characters would be selectively neutral in females.

Male red-winged blackbirds defend exclusive territories in marsh or upland habitats and often attract more than one female. As with the males, older females return to the breeding area before younger females and settle on these established territories (Nero 1956 a). Weatherhead and Robertson (1977 b) found that males that engaged in courtship displays most vigorously, ended up with the highest density of females on their territories. Females may be able to use such cues as courtship intensity to predict whether a male will assist in feeding nestlings (Eckert and Weatherhead 1987 b). However, several studies have found that female reproductive success decreased with increased nesting density or harem size (Weatherhead and

Robertson 1977 b, Lenington 1980). Therefore, females may be forced to compete with other females for access to the best breeding situations. Females that arrive and nest first or second on territories have a better chance that males will assist in feeding nestlings (Muldal et al. 1986) and will also have more time to reneest if their first attempt is unsuccessful. Since there is no evidence for a floating population of non-breeding females (Holcomb 1974), competition through aggressive interactions may simply force some females to settle on sub-optimal territories.

Female-female aggression has been documented in many studies (Nero 1956 a, b, Orians and Christman 1968, Lenington 1980, Yasukawa and Searcy 1981, Hurly and Robertson 1984). Most females will attempt to drive off intruding females through displays, vocalizations, and attacks (Hurly 1982), and may inhibit the settlement of later arriving females on their territories (Hurly and Robertson 1985). Because nest sites do not appear to be limiting, and feeding often occurs off the territory, female competition might serve to ensure male parental investment in populations where males help to feed the nestlings of the primary female (Yasukawa and Searcy 1982).

Competition among females could lead to selection on behavioural, morphological or physiological traits. Patches of coloured feathers are located on the epaulets and chins of females and there is extensive variation in

the brightness of these patches between females (Payne 1969). These feathers are accentuated in aggressive displays and thus may be subject to sexual selection. Although bright epaulets are characteristic features of males, only females exhibit bright chins. Hurly and Robertson (1984) suggested that the bright chin may be selected for because it would be most noticeable in a display where the bill is pointed upward (bill-tilt).

The purpose of this field study was to determine if plumage variation in female red-winged blackbirds could be accounted for by direct sexual selection due to female-female competition. If not, then plumage in females may be a genetic correlate of variation in male plumage and hence be affected indirectly (through the male) by sexual selection. If bright females have a competitive advantage, I predicted that bright females would settle on territories first. I also expected epaulets to become brighter with age.

Since females are aggressive, those that are dominant may have a competitive advantage when it comes to settlement. Since male courtship may indicate whether a male will provide parental care, bright females may obtain better nesting situations by settling with these males. Also, if female plumage signals competitive ability, I predicted that bright females would be more aggressive than dull females. Bright females could also be seen as more of

a threat to settled females. Therefore, I predicted that bright individuals would elicit a stronger aggressive response from already settled females than would dull individuals.

Males may use plumage cues to distinguish between experienced (bright) and inexperienced (dull) females. Older females have higher reproductive success (Crawford 1977). Therefore, given a choice, I predicted males should prefer bright females.

STUDY SITES

I conducted my research between April and July 1986 and 1987 along the paved roads within 30 km of the Queen's University Biological Station north of Kingston, Ontario. Red-winged blackbirds nested in cattails (Typha latifolia) or willows (Salix sp.) found in discrete patches in low lying areas along roadsides. Later in the season they also nested in the grasses of adjacent fields. All territories were located in agricultural areas and contained a fence running parallel to the road. These roadside territories did not share boundaries with other territories and therefore it was easy to monitor individual activities of the birds without interference from neighbouring individuals, as might be the case in a marsh-nesting population. Males return in March and hold exclusive territories at these sites while females do not return until late March or early April (Hurly 1982). When birds first returned to the study area, both males and females gathered nightly in large roosts in nearby willow or cattail marshes.

Behavioural interactions

When on their territories both males and females exhibit aggressive behaviour toward conspecifics in the form of displays and vocalizations. Female song-spread displays are similar to males although less pronounced.

The female perches upright with tail spread and head raised. The wings are held out from the body often exposing the feathers on the upper wing coverts (Nero 1956 a). The bill-tilt is also exhibited by both sexes. In this display the beak is pointed upward with the neck outstretched (Nero 1956 a). Females also have two distinct calls which are given in response to intruding females. The chit call is a short, sharp vocalization often given in series. The teer vocalization is a longer, unmelodious call often given with the song-spread display (Hurly and Robertson 1984). These correspond to the type I and type II songs described by Beletsky (1983).

Males often interact with females on their territories. Courtship involves various visual and vocal displays including exaggerated song-spreads given by the male in conjunction with the characteristic "oak-a-lee" song (Nero 1956 a). The male also performs a "crouch" display when approaching a female. When new females arrive on a territory, the resident female often attempts to drive the intruding female away. However, the male may intervene, chase his female away and begin courting the new female (Weatherrhead and Robertson 1977 b, Hurly and Robertson 1984). Often in these chases, both the resident female and the male fly off the territory. Chases may even be initiated by the resident female when she exhibits the precopulatory display. In this display the female leans

leans forward, holds her tail up and vibrates her wings will making a "whimpering" sound (Nero 1956 ~~a~~). This display signals sexual readiness and hence the pursuits that follow may be referred to as sexual chases (Nero 1956 a).

METHODS

On a daily basis, I monitored female settlement on the roadside territories beginning on April 1. I made all my observations from a truck parked along the road using binoculars and a spotting scope. Females were not individually marked until after they were established on territories so I did not influence settlement patterns. Therefore, females were considered to be settled on a territory on the date subsequent to which a female was always observed at that site (Teather et al. in press). Once females were settled I caught them either by decoy trapping or with mist nets. All birds were banded with a unique combination of 3 coloured (red, blue, gold, green, silver) aluminum bands and a U. S. Fish and Wildlife Service band. Body mass was measured to the nearest 0.5 g and wing length was measured to the nearest mm. Epaulet length was defined as the distance from the bend in wing to the furthest extent of the colouration in mm. The length of the colour patches found on chins (hereafter referred to as chin length) was measured by holding the bird in a

natural position with the neck at a right angle to the body and measuring the extent of colouration from the base of the bill to the breast. I classified epaulet and chin colour into scores based on colour swatches from the Naturalist's Color Guide (Smithe 1975). Swatches representing the range in colour variation of chins and epaulets were ranked according to brightness. I then compared the Munsell (1961) colour scores of value and chroma to my scoring scheme. Value measures the lightness of a colour with dark colours given scores of 1, 2, and 3 while light colours are scored between 8 and 9.5. Chroma refers to the intensity or purity of a colour. Low scores on this scale indicate a weak, gray colour while high scores indicate an intense, saturated colour. Swatches that I ranked bright generally had low value scores and high scores on the chroma scale (i.e. dark and saturated). I chose nine categories for epaulet colours ranging from vivid orange to pale yellow and eight categories of chin colours ranging from strong yellowish pink to light gray (Table 1-1). Epaulets and chins were held next to colour swatches for comparison and were assigned the scores of the colour they most closely resembled.

In order to assess plumage variation in the population and to obtain birds for the aviary (see Chapter 2), I caught birds in a spring roost 25 km south of the biological station. Mist nets were set up in the roost

Table 1-1. Ranking scheme for epaulet and chin colours using colour swatches from the Naturalist's Color Guide (Smithe 1979) and Munsell (1961) colour notation. Hue refers to the quality of colour (red, yellow, blue, green), value is the lightness (dark = 1, 2, 3 and light = 8, 9, 9.5) and chroma is the purity or intensity of colour (low # = weak gray and high # = intense, saturated).

Score	Colour Name (from Smithe 1979)	Munsell Notation		
		Hue	Value	Chroma
EPAULETS:				
1	vivid orange	2.2 YR	5.90	16.0
2	strong reddish orange	0.1 YR	5.37	12.3
3	moderate reddish brown	0.7 YR	4.00	5.3
4	brownish orange	1.2 YR	4.30	9.0
5	brownish orange	3.6 YR	4.50	6.7
6	dark orange yellow	5.0 YR	6.90	6.0
7	dark orange yellow	0.7 Y	5.98	7.4
8	pale orange yellow	0.9 Y	7.77	5.5
9	pale yellow	2.5 Y	8.08	3.5
CHINS:				
1	strong yellowish pink	1.9 YR	6.84	8.9
2	moderate yellowish pink	5.0 YR	6.90	6.0
3	moderate orange yellow	9.0 YR	7.97	7.5
4	pale orange yellow	0.9 Y	7.77	5.5
5	pale orange yellow	8.8 YR	7.55	4.3
6	moderate yellow	2.6 Y	7.89	6.1
7	light yellow	1.5 Y	8.30	5.5
8	pale yellow	2.5 Y	8.08	3.5

before dusk to catch females as they entered. Plumage was scored for each female as outlined above.

I also obtained data on female nesting dates in local marsh populations. Marshes were searched and all nests were marked by placing flagging tape on the vegetation within 1 m of the nest. Nests were visited every other day to determine the onset of egg laying. Females associated with the nests were caught using mist nets, banded and their plumage was scored in conjunction with another study being conducted by PJW.

To determine if males in the population were contributing to feeding nestlings, I watched nests on the day the nestlings were five days old. Nest watches lasted one hour and were conducted between 0800 and 1500 from a truck parked 20 meters away with the aid of binoculars. I recorded all feeding trips of females and males during this time.

Model presentations to Females

One method of catching females was a decoy trap (Smith 1976, Picman 1979). With this method, females responded to a taxidermic mount of a female red-winged blackbird placed inside a wire cage. A tape recording of aggressive calls was presented along with the decoy. Females had reduced visual contact with the decoy due to the cage. However, the call was a constant stimulus. I recorded the

responses of females to the decoy trap to determine if bright females were more aggressive than dull females. The strongest response a female could exhibit was diving at and landing directly on the cage (and hence setting off the trigger mechanism and being caught) which I will refer to as an attack. The same decoy model was used in all trials enabling comparison of the intensity of aggression with the brightness of plumage of the responding female.

In 1986 I presented decoy traps to 19 females after they had settled but before they began egg laying. Trials were conducted within 4 hours of sunrise. The trap was placed on 1 m aluminum poles within 2 m of the fence and near where the female had been seen perching. Once again, the decoy bird was a taxidermic mount of a female red-winged blackbird in an upright posture. A tape recorder playing a female "teer" call was suspended below the trap. Observations were made from a truck parked approximately 20 m away using binoculars and a tape recorder. Once the resident female responded by coming within 10 m of and facing the model, I recorded her behaviour every five sec with the aid of an electronic metronome for 10 min (Wiens et al. 1970). I recorded the female's distance from the model, whether she was in or out of view, vocalizations (chit and teer), displays (song spread, bill tilt), attacks, and interactions with the resident male. The presentation was terminated when the female was caught or

ten minutes had elapsed.

Since I wanted to determine if females discriminate between females of various plumages, I made taxidermic mounts of bright (chin score = 2, epaulet score = 3) and dull females (chin and epaulet score = 8) to be used in model presentations (see Table 1). Mounts were of females of comparable size, in upright positions with epaulets exposed.

In order to standardize when models were presented I monitored the nesting cycle of females. When a nest was found I marked a piece of vegetation 1 m away with flagging tape. The nest was then visited every two days to determine the onset of egg laying. I presented a model on the second day after a full clutch was laid. All model presentations took place between sunrise and 1000 on days when it was not raining and winds were not excessive. If model presentations were scheduled for days when it rained they were postponed until the next clear day. I randomly assigned which model (dull or bright) was to be presented first by a coin toss. Each model was placed on a 1 m high aluminum pole 5 m from the nest, and 1 m from the fence. As with the decoy trapping, observations were made from a truck parked 20 m away along the side of the road using binoculars and a spotting scope. At 5 second intervals I recorded the females position in relation to the model, vocalizations, displays, attacks, and interference by the

male. The model presentation was terminated when either ten min had elapsed or the female attacked the model. Two days later the other model was presented to the female.

Model Presentations to Males

Since male red-winged blackbirds exhibited varying degrees of courtship behaviour I wanted to determine if they discriminated between dull and bright females. Therefore, bright and dull models were placed on a male's territory simultaneously. I conducted these presentations in April just as males were establishing territories. If a male was present for several days and gave song spreads, I assumed he was the territory holder, and models were presented. Some males had been banded in previous years and since these males remained resident on the territories they defended early in the season this assumption of territory ownership appears valid. Models were placed on or near fenceposts positioned 5 m apart and located centrally on the territory. I made observations from a truck parked 20 m away and used the same methods as for the model presentations to females. Presentations began when the male came within 5 m of the models. Every 5 secs I recorded which model the male was closer to. I continuously recorded all song spreads and to which model they were directed. Trials continued for 10 minutes or until the male attempted copulation with one of the models.

Analysis of Model Presentations:

Male interaction with the resident female affected the amount of time the female spent responding to the model. Therefore I removed the time the female was chased by the male from the total observation time. From this, I estimated the proportion of time that each female spent (i) at the nest, (ii) less than one meter from the model, (iii) one to five meters from the model, (iv) greater than five meters from the model, and (v) out of sight at these distances. I calculated the proportion of the total time that the female was chased by the male. Vocalizations (chit, chit series, teer) per minute were recorded when the female was in sight during the entire presentation. I also recorded whether or not the female attacked the model or solicited the male.

The most aggressive response was for the female to attack the model. Other variables also indicated the level of aggression. An aggressive female would be one that remained within 1 m of the model and gave numerous teer calls and displays. If the female returned to the nest without interacting with the model then it was considered a non-aggressive response. Females that remained in clear view indicated a more aggressive response than females that remained in the undergrowth. The amount of vegetation on the territory would affect this variable and therefore this must be interpreted with caution.

To test if females responded more to dull or bright models, I performed an analysis of covariance on each of eight response variables (time at nest, time less than one meter from the model, time one to five meters, time out of sight, time chased by male, number of chit calls, number of chit series, number of teer calls). I controlled for female body size and also tested the effects of the order of model presentation. However, describing a female's behaviour using each of these variables separately is difficult because some of the variables are likely to be correlated. Therefore, I performed a principal component analysis (PCA) to account for the variation in the original variables. The PCA reduces the original variables into several factors that are linear combinations of those variables (see Aspey and Blankenship 1977 for overview). This statistical technique has been applied in similar behavioural studies (Eckert and Weatherhead 1987 c, Yasukawa 1978, Rohwer 1978). The first factor that is extracted represents the maximum amount of total variation in the variables. It consists of weighted values of the original variables. The subsequent factors account for the maximum amount of remaining variation and are mutually uncorrelated. Each factor can be interpreted by examining the relative loadings of each variable on that factor. I performed the analysis separately on the decoy trap presentations (N = 19) and on the dull and bright model

presentations ($N = 38$). Scores for each female were calculated by multiplying the factor loadings by the standardized value of the female's response on each variable and then summing them for each factor. It was necessary to use standard values (calculated by subtracting the mean of the variable and dividing by the standard deviation) since all variables were not measured in the same units.

Variables that represented proportions (time at nest, time less than 1 m from model, time 1 to 5 m from model, time greater than 5 m from model) were transformed using an arcsine squareroot transformation (Zar 1976). A 2 X 2 contingency table was used to compare the number of attacks on bright versus dull models (Steel and Torrie 1960).

Statistical analyses were conducted using the Honeywell CP6 system at Carleton University and BMDP (April 1985) and SPSS-X (1984, Release 2.1) packages. Statistical significance was taken at the 0.05 probability level.

RESULTS

Plumage patterns

I caught 157 female red-winged blackbirds on roadside territories and in the spring roost in 1986 and 1987. In order to assess plumage characteristics of the population I recorded epaulet and chin rank for each female. Female epaulet colour was positively correlated with chin colour although there was a lot of variation (Figure 1-1, Spearman $r = 0.253$, $p < 0.05$). Therefore, females with bright epaulets did not necessarily have bright chins.

Between 1986 and 1987, four roadside and nine marsh females were recaptured (Figure 1-2). Of these, nine had brighter epaulets in the second season while only three had brighter chins. Three remained the same in epaulet score and seven had equivalent chin scores between the two years.

Settlement patterns

Females with bright chins or epaulets did not always settle first on roadside territories (Figure 1-3). I do not have settlement data for marsh females. However, I do know the dates of clutch initiation. Since settlement date is positively correlated with first egg date for this population, the date of clutch initiation can approximate settlement date (Teather *et al.*, in press). Chin score and epaulet score were not significantly correlated with clutch initiation in the marsh population (Figure 1-4).

Figure 1-1. Epaulet colour versus chin colour,
for 157 female red-winged blackbirds.
Individual cases are represented by X's
while numbers indicate multiple cases.

Figure 1-2. Epaulet and chin colour for 13 females that were captured in both 1986 and 1987.

Figure 1-3. Epaulet and chin colour in relation to
settlement date for upland females.

SETTLEMENT DATE

Figure 1-4. Epaulet and chin colour in relation to clutch initiation date for marsh females.

Male feeding

I observed nests to determine if males in the population were contributing to the care of nestlings and hence if females may benefit from inhibiting the settlement of other females. In 1986, eight out of 13 males fed nestlings while in 1987, seven out of 12 males were seen feeding young. I compared plumage scores of females that were assisted by their mate in feeding nestlings to females that were unassisted. Females that were assisted in feeding nestlings were not brighter than unassisted females (Table 1-2).

Model presentations to females

Twelve females were given decoy trap presentations. Since these models were accompanied by a tape recording, the response of females tended to be greater than for the dull and bright models which did not have a playback. To compare the plumage of the responding female to the magnitude of her response to the decoy traps I first obtained an index of response by calculating the principal component factors (Table 1-3). The first principal component accounted for 36.5 percent of the variation and had high loadings for the number of vocalizations (chit, calls and teers). This factor was interpreted as an agitation response since chit calls are given mainly in female-male interactions. The second factor had a high loading for the time spent less than one meter from the

Table 1-2. Mean epaulet and chin scores of females whose mate fed nestlings and females whose mate did not. Standard deviations are indicated in brackets (for both $T < 1.2$, $p > 0.10$).

Characteristics of Female	Mean Chin Score	Mean Epaulet Score
Male fed nestlings	4.5 (1.6)	5.3 (2.2)
Male did not feed nestlings	3.5 (1.5)	4.0 (1.9)

Table 1-3. Unrotated factor loadings from a principal components analysis on decoy trap presentations to 19 female red-winged blackbirds. See text for definition of variables.

Variable	Factor 1	Factor 2	Factor 3
Time < 1 m from model	0.361	0.747	-0.068
Time 1 - 5 m	-0.288	0.067	0.836
Time chased by male	0.345	0.329	-0.377
Time out of sight	-0.491	-0.406	-0.535
Number of chits	0.820	-0.506	0.089
Number of series	0.875	-0.430	-0.098
Number of teers	0.736	0.311	-0.037
Cumulative proportion of variance explained	0.365	0.561	0.726
Interpretation	Agitation	Aggression	

model. This was interpreted as an aggressive response since this represented a female-female interaction. Females with bright chins or epaulets did not respond more to the decoy traps than those with dull chins or epaulets as indicated by their "agitation" score (from the first factor in the analysis, Figure 1-5).

Thirty eight females were presented with both dull and bright models during early incubation. The response to these models was quite variable. Ten birds gave a maximum aggressive response by attacking the models. However, the number of attacks did not differ significantly between the two models (Table 1-4). Solicitations to the male could not be considered an act of aggression but would serve to distract the male from the new female. Four females solicited the resident male during the bright model trial, one female solicited during both bright and dull trials, and no females solicited only during the dull model presentation.

The bill-tilt display was given during aggressive interactions. However it was difficult to observe since it was often given in dense vegetation. In 1987 I concentrated on recording bill tilts given by responding females. Out of 24 model presentations, eight females gave bill tilt displays to both bright and dull models while three displayed to only the bright model and three others

Figure 1-5. Agitation response in relation to epaulet and chin colour for 19 females reacting to the decoy trap.

Table 1-4. The number of times 38 females that were given both dull and bright model presentations attacked or did not attack ($\chi^2 = 1.286$, $p > 0.05$).

		BRIGHT MODEL	
		Attack	No Attack
DULL MODEL	Attack	3	2
	No Attack	5	28

displayed to only the dull model. Results of the analysis of covariance indicated that overall, females did not respond differently to dull and bright models (ANCOVA all F values < 3.70 , $p > 0.05$). For example, there was no difference in the amount of time that responding females spent close to the models (Figure 1-6). I also found that there was no effect of the order of presentation so, females were not habituating to the models.

Since there was no difference between the response to dull and bright models, the female's average response to both models was used in the subsequent analyses. To obtain an index of the female's response to the intruding females, I calculated the principal components factors for the response variables (Table 1-5). The first factor had high loadings on the number of vocalizations (chits and series) and also on the time spent greater than five meters from the model and accounted for 34.4 percent of the variation between females. Since chit calls are given mainly in female-male interactions this is interpreted as an agitation response. The second factor had high loadings for teer vocalizations and the time spent less than one m from the model. Since teer calls are given mainly in female-female aggressive interactions, this factor represents the level of aggression. This factor accounted for an additional 25.8 percent of the variation. The third factor in this case had the highest loading for the time

Figure 1-6. Proportion of time 38 females spent at various distances from the dull and bright models.

Table 1-5. Unrotated factor loadings from a principal components analysis for dull and bright female model presentations to 38 female red-winged blackbirds. Factor loadings were calculated by taking the average score for the bright and dull models.

Variable	Factor 1	Factor 2	Factor 3
Time at nest	-0.652	-0.215	0.661
Time < 1m from model	-0.006	0.776	-0.497
Time > 5 m from model	0.662	-0.576	0.007
Time chased by male	0.534	-0.351	-0.136
Time out of sight	0.571	-0.367	-0.542
Number of chits	0.801	0.266	0.499
Number of series	0.775	0.365	0.493
Number of teers	0.186	0.788	-0.048
Cumulative proportion of variance explained	0.344	0.602	0.780
Interpretation	Agitation	Aggression	

the female spent at the nest. If the female returned directly to the nest it was considered a non aggressive response. This factor represents the propensity for females to continue incubation and not respond to the intruding female. Bright females did not respond more than dull females as indicated by the scores on the first (agitation) and second (aggression) factors (Figures 1-7 a, b).

Model presentations to males

I presented models to 18 male red-winged blackbirds in 1987 in order to test if males discriminated between dull and bright females. There was no significant trend in the amount of time spent close to either model (Figure 8 a). Males tended to direct more song spreads toward the bright model but this was highly variable between males and not significantly different (Figure 8 b). There was also no difference in the mating response of the males to either model. Five males attempted copulation with the bright model while four males attempted to copulate with the dull model.

Figure 1-7. a) Agitation scores in relation to epaulet
and chin colour for 38 females.

b) Aggression scores in relation to
epaulet and chin colour for 38 females.

Figure 1-8. Male response to dull and bright female models.

a) Proportion of time spent less than 1 m from the model.

b) Number of song-spreads directed toward each model.

A

B

DISCUSSION

Female competition

Results of this study have confirmed the assumption that female red-winged blackbirds are aggressive. The possible role of this aggression is to deter settlement of other females to help ensure male assistance in feeding young (Yasukawa and Searcy 1982). Since in some populations males rarely feed young (Orians 1961, Yasukawa and Searcy 1981), it was essential to establish that males in the population were contributing to nestlings. In the present study, over fifty percent of the males fed young. Therefore, females that settled first on a territory could have an advantage.

Plumage patterns

Delayed plumage maturation in males has been well documented (Selander 1965, Greenwood 1985). If sexual selection is acting directly on females, younger females could retain dull plumage as is the case with males. I predicted that females should become brighter with age. From the recapture data I found that female epaulets tended to become brighter with age. In a 3.5 year study of captive females, Miskimen (1980 a, b) found that 84 percent of the birds had dilute orange, or rust coloured epaulets after their first moult, and all birds acquired bright epaulets after the second moult. This is also consistent

with the indirect selection hypothesis. Since males delay plumage maturation, females could simply be reflecting male traits due to genetic correlation.

The expression of genetically based traits may be affected by both internal (physiological) and external (social, physical activity) environments (Eisen and Legates 1966). The interaction between genetic and physiological factors is likely the mechanism leading to plumage variation in some species (Vardy 1971). The plumage colouration that a female red-winged blackbird attains after moulting may be related to her condition (Johnsen et al. 1986). Johnsen et al. (1986) proposed that older females are more efficient at acquiring resources than are younger individuals and therefore can moult into brighter plumage. The acquisition of adequate food is especially important since carotenoid pigments that are responsible for the yellow, orange and red colours of birds cannot be synthesized metabolically and therefore must be obtained in the diet (Brush and Power 1976). In feeding experiments with House Finches (Carpodacus mexicanus) Brush and Power (1976) found that without proper amounts of carotenoids in the diet the birds moulted into abnormal dull yellowish feathers rather than the characteristic red plumage.

Even though the epaulets became brighter with age, the chins of females did not change consistently between years and were not strongly correlated with epaulet colour.

Meanley and Bond (1970) noted that young females had little salmon colouration of the chin and head when compared to older individuals. Nero (1954) documented that male red-winged blackbirds occasionally exhibit a pinkish tinge to the chin, throat and breast. He suggested that this colouration is in fact present in all males but is masked by black pigments. Though he drew no conclusions as to the significance of the concealed colours in males, Nero (1954) pointed out that closely related tropical species (Agelaius icterocephalus and A. ruficapillus) have red and yellow feathers in the head region. Arrival and settlement

If sexual selection was acting on female plumage brightness directly, I expected to find bright females arriving on territories first in spring. Brighter females did not begin nesting first on upland territories. In an upland population, Dolbeer (1976) found that the same percentage of females with bright epaulets nested during the first and second half of the breeding season. In contrast, Crawford (1977) and Blank and Nolan (1983) studied marsh populations and noted that dull females began nesting later than did the bright females. Furthermore, bright females did not settle with males that fed nestlings more frequently than dull females. Eckert and Weatherhead (1987 b) suggested that male provisioning of young and male nest defense behaviour may be predictable but do not covary and hence female mate choice does not rely on a single

factor.

Overall, Crawford (1977) found that dull individuals had lower nesting success and he suggested that these individuals may be forced to nest in poorer habitats. Upland habitats may not be optimal but the mean number of young fledged per successful nest is about the same as in marsh habitats (Robertson 1972). In my study area many bright females nested in upland habitat and this does not support the idea that young, dull birds are those that are forced to nest in uplands. Females exhibit habitat fidelity (Albers 1978, Picman 1981) and this may be a partial explanation for bright females occupying upland territories. Four of the females in my study showed not only habitat fidelity but also returned to the same territory in consecutive years.

I found that the females with bright epaulets or a bright chin did not respond more to the decoy trap than did dull females. The PCA indicated that most of the variation was accounted for by the factor emphasizing the number of chit calls and series of calls given toward the model. The chit call is given at all times during the nesting season and its probable function is in communication with the male (Yasukawa et al. 1987). Therefore, this call is given more as an agitation response than in an aggressive context. I predicted that bright females would be more aggressive than dull females and this would have been reflected in the

second factor extracted by the principal component analysis. This factor had high loadings for number of teer calls. This call is used in female-female interactions during attempts to delay breeding of later arriving individuals (Yasukawa et al. 1987). However, the scores of females on the aggression factor did not differ significantly between dull and bright individuals.

I also expected a relationship between the brightness of the responding female and the frequency of displays and hence the ability of females to deter intruding females. However, birds with dull chins performed as many bill-tilts and song-spreads as birds with bright chins. Female aggression may not result in the intruder being driven away because males may intervene and begin courtship displays directed toward the new female (Searcy 1986). Males may actively inhibit female aggression since an increase in harem size would be advantageous for males (Weatherhead and Robertson 1981, Searcy 1986). In order for plumage brightness to be selected for it must confer a reproductive advantage. If females are unable to control settlement of other females due to male aggression, then there would not be an advantage to signal dominance.

If bright females were dominant, they could have been perceived as more of a threat to settled females but there were no significant differences between the responses to the bright and dull models. Females attacked both models

equally and spent an equivalent amount of time close to both models. Therefore, females did not distinguish between bright and dull models in their aggressive responses. Females did solicit males more often during bright model presentations. However, since only five individuals were involved it is difficult to draw any conclusions. Any female can be seen as a threat when it comes to the non-shareable portion of male parental assistance (feeding of nestlings). If the primary female's first nest is destroyed and she is forced to renest after another female has settled, she may forfeit male assistance since males are more likely to aid the first or second females (Yasukawa and Searcy 1982, Muldal *et al.* 1986). Furthermore, nesting success decreases with increasing female density (Weatherhead and Robertson 1977 a). It is not surprising then that both models elicited the same aggressive response.

Model presentations to males

An advantage may also be gained by the males if they can influence which females settled on their territories (Searcy and Yasukawa 1983). Older, more experienced females may have better breeding success than younger individuals (Crawford 1977). I predicted males could use plumage brightness to discriminate between experienced and inexperienced breeders. However, males did not concentrate their courtship displays or copulation attempts toward

bright females. Even though males do not discriminate, they probably rely on behavioural cues from the female that indicate her receptiveness. It would not be advantageous for a male to discourage any female that appeared on his territory since male reproductive success increases with increasing harem size (Hurly and Robertson 1985).

The evidence presented here is overwhelmingly against the hypothesis that epaulet brightness in female red-winged blackbirds is involved in competitive interactions between females during the breeding season. Although epaulets brighten with age there is no indication that they have evolved in the context of a signal to indicate competitive ability. Males and females did not discriminate between dull and bright female models. Epaulet plumage of females did brighten with age and this result seems to parallel the delayed plumage maturation found in males. Lande (1980) stressed that males and females do not evolve independently, and therefore, a change in a male character may result in a similar response in the homologous character in females. If epaulet colouration in females is due to a genetic correlation with male epaulets it may be indirectly selected for by strong sexual selection acting on males. However, variation in epaulet colouration does not appear to be adaptive with respect to female-female competition. Chin colouration also appears to have no signalling

function but cannot be accounted for by the genetic correlation hypothesis since it is only expressed in females.

Chapter 2. Plumage variation in relation
to dominance

INTRODUCTION

There are two hypotheses that might explain why females of some species exhibit brightly coloured plumage. Direct selection could act on the female due to intrasexual competition for resources or mates. This process of selection is thought to have led to the development of exaggerated characters in males (Darwin 1871). For example, selection could result in conspicuous plumage badges that reflect fighting ability (Rohwer 1977). The second possibility is that male characters could be expressed in females due to genetic correlation (Lande 1980). In this case, the characters need not confer an advantage for the female. In fact, natural selection may oppose the expression of male traits in females through increased predation due to conspicuous females (Baker and Parker 1979).

An ideal species for the study of plumage variation in relation to competition is the red-winged blackbird. Red-winged blackbirds are gregarious in the winter and form large feeding flocks (Weatherhead 1985). In the spring both males and females become intolerant of other individuals of the same sex. At this time, both sexes have characteristic behaviour patterns which involve displaying patches of colour found on the epaulets (Nero 1956 a b, Orrians 1961). Chins are also displayed even though only

females have coloured feathers in this region. In contrast to the adult males which are uniformly black with immaculate red and yellow epaulets, females are brown with dark brown streaking on the breast and back. Females have epaulets that are much duller and smaller than those found in the males and vary in colour from pale yellow to orange. Females also have chin plumage which varies from pale yellow to yellowish pink.

All studies addressing the function of epaulets have dealt with males and most have involved free-living birds (Peek 1972, Smith 1972, Morris 1975, Røskoft and Rohwer 1987). However, the ease of keeping these birds in captivity has led to a number of aviary studies. For example, Searcy (1979) found that male red-winged blackbirds form "peck-dominance" hierarchies when kept in an aviary. This meant that dominant individuals won the majority of encounters but the outcome of any particular interaction could not be predicted with certainty. Aggressive interactions occurred around food, water and preferred perches and dominance in groups was highly correlated with body size. In another aviary study of males, Eckert and Weatherhead (1987 a) found that dominance was correlated not only with body size but also to the size of the red epaulets. This finding suggests that epaulets may play a role in hierarchy formation.

In some species, formation of hierarchies may be facilitated by differences in plumage which serve as badges of social status (Rohwer 1977). The status-signalling hypothesis was developed to explain conspicuous plumage in winter flocking birds. Much research has been conducted on sparrows (Zonotrichia sp.) and juncos (Junco sp.) that compete for access to food through the establishment of dominance hierarchies. The advantage of a signalling system is that subordinates will recognize and avoid dominants without having to fight and risk injury. Similarly, unique plumage patterns could be used for individual recognition (Shields 1977).

In the previous chapter I outlined reactions of male and female red-winged blackbirds in the field to mounts of conspecific females of varying plumage intensity. In this chapter I examine interactions between females kept in small groups in an aviary. In the field study, females were potentially competing for mates and nesting areas whereas in the present chapter females established dominance relationships centered around a food source. If female plumage is selected for due to female-female competition, I predicted that females with bright plumage would be dominant over females with dull plumage. I also expected that birds dyed to resemble bright individuals would rise in status while birds that had their plumage

dulled would fall in status.

If epaulet colour in females is due to genetic correlation for this trait with males, then I predicted that there would not be a correlation between brightness and status. I also did not expect a consistent rise or fall in status if the epaulets of individuals were brightened.

Since individual recognition may be important in the maintenance of stable hierarchies, chin and epaulet colours could be involved. Therefore, if I alter plumage I predicted that hierarchy relationships would change because recognition cues would have been altered. Birds dyed brighter could either rise or fall in status.

METHODS

Female red-winged blackbirds were caught in late April or early May of 1986 and 1987 in a spring roost near Inverary, Ontario. This site was approximately 25 km south of the Queen's University Biological Station and was composed mainly of cattail (Typha latifolia) and willow (Salix sp). We entered the roost before dusk and set up mist nets to catch incoming birds. Females were transported directly to an outdoor, covered aviary located at the biological station.

On the day following their capture, all birds were banded with a single, aluminum Fish and Wildlife band. Mass was measured to the nearest 0.5 g and wing length (from the bend in the wing to the tip of the longest primary) to the nearest mm. Epaulet length was measured using Vernier calipers as the furthest extent of colouration from the bend in the wing. I measured chin length from the bill to the furthest extent of coloration on the breast with the bird held with its beak pointing perpendicular to its body. I classified chin and epaulet colours using the Munsell (1961) system (see Table 1 and Methods from field study). For the purpose of comparison, epaulet and chin scores of 1 to 4 were classified as bright while scores of greater than 5 were considered dull.

Females were divided into groups of 6 - 11 individuals and were placed in separate compartments (measuring 3 X 2 X

1.5 m). The design of the aviary and procedures for the care of the birds were established by Eckert (1985). The outside of the aviary was covered with chicken wire mesh screen while the inside was lined with aluminum screen to help prevent injury of the birds. An electric fence was placed around the aviary to deter predators from harassing the birds. I hung numerous perches in each compartment to minimize competition for perch sites and to simulate a roost. Birds were fed a mixture of 3 parts cracked corn to 2 parts millet and 1 part Purina # 3 trout chow placed in small plastic dishes on the floor on the aviary. I placed more dishes than there were females in each compartment to ensure that all individuals would be able to feed. Two water containers were kept in each compartment and were cleaned and refilled daily.

Each female was given a unique mark on her wings and/or tail feathers using Clairol* Basic White powdered hair bleach (White et al. 1980). The powdered bleach was mixed with 20 percent by volume peroxide until a paste was formed. This was applied directly to the feathers. Birds were released into the aviary and left for approximately half an hour at which time I recaptured them, rinsed the feathers in warm water and released them into their respective compartments. Some of the birds attempted to preen the bleach off their feathers. These individuals may have ingested small quantities of bleach but did not appear

to suffer any ill effects.

Videotapes were made of the interactions around a single food dish placed in the aviary. On the evening before a trial all food was removed from the aviary and the floor was swept clean. Videotapes were made on the following morning between 0900 and noon using a video camera mounted on a tripod positioned above the food dish. The food dish was covered except for a 2 cm square hole in the center of the lid that allowed only one bird to feed at any given time. A taping session lasted approximately 70 min. After each session uncovered food dishes were returned to the compartment and birds were allowed to feed undisturbed for the remainder of the day.

Aviary Group Composition and Experimental Manipulations:

In 1986 I caught 41 females and divided them into 5 groups. Four groups were allowed to establish dominance hierarchies without any manipulations of plumage. In a fifth group, the epaulets were dyed before individuals were allowed to establish a hierarchy. This was accomplished by first bleaching all the epaulets to a buff colour using Clairol* Basic White powdered hair bleach and then brightening the epaulets of 4 birds in the group using a red permanent magic marker. The colour produced was equivalent to a bright red of a male epaulet (brighter than a score of 1, see Table 1-1) although the colour tended to

fade slightly upon drying. I paired birds with similar epaulet ranks and coloured one individual of the pair. I also bleached the epaulets of the other individual but this time I coloured the epaulet with a brown magic marker to match the rest of the body feathers. Brightened individuals represented a range of epaulet colours. For all groups videotapes were made to obtain ten interactions per pair or for 5 hours of interaction for each group.

In 1987 I caught females in the spring roost between May 2 and May 4. These birds were first scored by plumage colour before being placed into four groups in the aviary. The control group (9 birds) had a range in chin ranks from 1 to 8 and epaulets ranging from 2 to 9. The first chin manipulation group (9 birds) had uniformly dull chins while the second chin manipulation (11 birds) had bright chins. The epaulet manipulation group (9 birds) had dull epaulets. During the first two weeks videotapes were made to determine dominance hierarchies.

On May 17 I bleached chins of all birds in the first chin group and then coloured the chins of four birds bright orange (chin score brighter than 1, Table 1-1) using a permanent magic marker. First, I scanned the videotapes made during the period prior to manipulation to ensure that some of the individuals dyed were subordinate birds. A subordinate bird was one that either lost many interactions or avoided interactions with dominants. The remaining

birds in the aviary were left with bleached chins that did not contrast with the buff streaking found on the breast. On May 21 the chins of five birds in the second chin manipulation group were brightened in the same manner and the remaining birds had chins bleached. At the same time, the epaulets of birds in the epaulet manipulation group were bleached and four were brightened (epaulet score brighter than 1). The remaining birds had epaulets coloured brown to match the body feathers. Birds were videotaped until June 3 to obtain approximately 5 hours of interactions per group.

Video Analysis

I recorded supplants, threats and attacks made by birds at the dish and recorded them in a winner-loser matrix until ten interactions per pair were noted. Dominance matrices were constructed using the method of Brown (1975). This method keeps the number of interactions below the diagonal of a winner-loser matrix to a minimum. I also calculated the percent of encounters won for each female.

Statistical Analysis

I computed Spearman rank correlation coefficients between the rank in the hierarchy and morphological characteristics of the female (Steel and Torrie 1960).

Each aviary group was analysed separately. All analyses were performed using BMDP (BMDP April 1985) and SPSS-X (release 2.1, 1984) computer packages on the Carleton University Honeywell CP-6 computer system. Statistical significance was taken at the 0.05 probability level.

RESULTS

Correlates of Dominance

Dominance hierarchies for control groups were based on between 528 and 922 interactions in 1986 and 996 in 1987.

In experimental groups I scored 528 to 996 interactions per group before and 859 to 2054 after manipulations.

While dominance hierarchies were generally linear, some non-linear relationships were observed (see Appendix).

Females involved in intransitive relationships were placed in the hierarchy in a position that minimized the number of times a bird was placed in the hierarchy above an individual to which it was really subordinate. When no interactions were recorded for a pair, hierarchies were constructed by placing the bird that won a greater percentage of encounters with other birds in the dominant position.

To see if bright females were generally dominant over dull females, I compared dyads in which females differed in plumage scores. There were no significant trends involving epaulet or chin colour, length of the epaulet or chin patch or overall body size (Table 2-1). Females in better condition won significantly more encounters.

Four of the aviary groups in 1986 and one group in 1987 were control groups as they contained individuals of a range of plumage scores. Dominance was not directly related to either epaulet or chin score (Table 2-2).

Table 2-1 . Relationship between morphological variables and within-dyad dominance for those dyads in which females differed with respect to the variable. "N" represents the number of asymmetric dyads.

Female with	N	Percent of dyads in which female dominant	χ^2	P
Longer epaulets	228	47.8	0.356	> 0.05
Brighter epaulets	201	47.8	0.318	> 0.05
Longer chin	227	48.0	0.282	> 0.05
Brighter chin	171	53.2	0.584	> 0.05
Longer wings	206	51.9	0.238	> 0.05
Better condition index	224	59.4	7.504	< 0.05

condition=weight/wing length

Table 2-2 . Dominance in relation to epaulet or chin brightness for each control group. The most dominant individual is "1". Bright (B) birds had an epaulet or chin score of 1 to 4 while dull (D) birds had scores of 5 or greater.

A. Epaulet score

Group	Rank order of females								
	1	2	3	4	5	6	7	8	9
1	B	B	B	D	B	D	D	-	-
2	B	B	D	B	D	B	-	-	-
3	D	B	B	D	B	B	-	-	-
4	D	D	B	D	B	B	-	-	-
5	D	D	B	D	D	D	B	B	D

B. Chin score

Group	Rank order of females								
	1	2	3	4	5	6	7	8	9
1	B	D	B	D	D	B	D	-	-
2	B	B	B	B	D	D	-	-	-
3	B	B	D	B	B	D	-	-	-
4	B	D	B	D	D	B	-	-	-
5	D	B	B	D	D	B	D	B	B

For each control group I calculated Spearman rank correlations between rank in hierarchy and female plumage score (Table 2-3). There were no consistent correlations between any of the plumage characters and the position in the hierarchy. Body weight was also not a good indication of hierarchy position (Table 2-4). Correlations between wing length and position were significant in three groups. However, these were not consistent as two were positive and the other was negative.

To see if dominant individuals were brighter than subordinates, I compared the mean epaulet and chin scores for the top two females in each group to the average for the bottom two females (Table 2-5). Mean values did not differ consistently between groups.

Plumage manipulation experiments

Chin colour

In the first of two chin manipulation groups, three of the birds that were brightened increased in rank while one bird decreased in rank (Figure 2-1). Of the individuals that were dulled, two stayed in the same hierarchy position, one rose in rank and one decreased in rank. In the second chin group two of the five birds that had chins brightened rose in dominance. However, the other three decreased dramatically.

Table 2-3 . Spearman rank correlation coefficients between rank in hierarchy and plumage characteristics. Coefficients were calculated separately for each group (* $p < 0.05$).

	Epaulet		Chin	
	Rank	length	Rank	length
Group 1 (n = 7)	0.441	0.179	0.243	0.393
Group 2 (n = 6)	-0.116	0.143	0.714	-0.600
Group 3 (n = 6)	-0.841*	0.771	0.353	0.029
Group 4 (n = 6)	-0.371	0.371	0.340	-0.086
Group 5 (n = 9)	0.051	0.100	-0.281	0.117
Chin I (n = 9)	-0.085	-0.433	-0.173	0.017
Chin II (n = 11)	0.197	0.309	0.071	0.155
Epaulet (n = 9)	0.431	-0.433	-0.009	0.034

Table 2-4. Spearman rank correlation coefficients between rank in hierarchy and size measurements (* $p < 0.05$).

	Wing length	Body weight
Group 1 (n = 7)	-0.288	-0.342
Group 2 (n = 6)	-0.754	-0.086
Group 3 (n = 6)	0.886*	0.083
Group 4 (n = 6)	0.928*	0.029
Group 5 (n = 9)	-0.759*	-0.051
Chin I (n = 9)	-0.244	0.084
Chin II (n = 11)	-0.351	-0.552
Epaulet (n = 9)	0.621	-0.458

Table 2-5. Mean epaulet and chin scores for top and bottom two females in each control group. The brightest score is 1 and the dullest is 9 for epaulets and 8 for chins.

A. Epaulet scores

	Group				
	1	2	3	4	5
Two highest ranking females	3	3	6.5	7.5	6
Two lowest ranking females	5	5	2.5	3	5.5

B. Chin scores

	Group				
	1	2	3	4	5
Two highest ranking females	5	2.5	3.5	5	5
Two lowest ranking females	5	6	3.5	5.5	1

Figure 2-1. Effect of manipulating chin or epaulet colour on the position of females in the dominance hierarchy. Letters refer to individuals as identified in hierarchies (see Appendix). Circles indicate that the female had her chin or epaulets brightened. An upward pointing arrow indicates that the female rose in rank after being coloured.

Epaulet colour

In one group in 1986 I coloured the epaulets of four individuals. A hierarchy was established that was not related to whether individuals had their epaulets brightened or dulled (see Appendix, Table 6). In the 1987 epaulet manipulation group, of the four birds brightened, two remained at the same rank, one rose in rank and one decreased in rank (Figure 2-1).

Interaction type and frequency

For control group 5, chin I and II and the epaulet manipulation groups, I examined the number of threats and attacks resulting in a takeover at the food dish before and after manipulations (Table 2-6). For the control group I scored the videotapes made before I manipulated the other groups and analyzed these for the number of threats and attacks before manipulations even though no alterations of the plumage were made in this group. The number of attacks or threats either increased or decreased for the experimental groups but remained the same for the control group.

Table 2-6. Total threats and attacks (per min) that resulted in a takeover at the food dish before and after plumage manipulations in four aviary groups. Significance values were calculated using Wilcoxon matched-pairs signed-ranks test considering totals for each individual (* $p < 0.05$).

GROUP	Attacks		Threats	
	BEFORE	AFTER	BEFORE	AFTER
Control	0.27	0.10	0.50	0.49
Chin I	0.36	0.09*	0.52	0.49
Chin II	0.39	0.39	0.30	0.90*
Epaulet	0.27	0.22	0.47	1.26*

DISCUSSION

Correlates of Dominance

Most of the hierarchies established between female red-winged blackbirds consisted of linear, "peck-dominance" relationships. Linear hierarchies have also been observed for captive male red-winged blackbirds (Searcy 1979, Eckert and Weatherhead 1987 a). Rowell (1974) argued that due to abnormally high densities of animals in captive studies, caution must be observed when extrapolating to natural situations. However, red-winged blackbirds are gregarious during the non-breeding season and roost in large flocks (Weatherhead 1985). Even though captivity places stress on individuals there was no evidence that birds behaved abnormally and behaviours observed in the aviary were similar to those recorded in the field. Interactions around the food dish involved direct pecking or threats and these actions were also noted during model presentations. Some females guarded the dish by spreading their wings and crouching over the dish. This posture was similar to the song-spread display given in territorial interactions.

From the direct sexual selection hypothesis I predicted that females with large, bright epaulets and chins would be dominant. However, results from the control aviary groups indicated that asymmetries in epaulet and chin colour or length were not related to dominance. Searcy (1979) found that dominance in a captive group of adult male red-winged

blackbirds was not related to epaulet size or colour. He stressed that body size would reflect age and experience and therefore would be a better signal of dominance. Eckert and Weatherhead (1987 a) found that dominant males were larger and had longer epaulets than subordinate individuals. However, when female body size differed between individuals the smaller female won in just as many instances as did the larger.

Similarly, Weatherhead and Teather (1987) found that body size and weight were not related to dominance in captive groups of brown-headed cowbirds (Molothrus ater). In free-ranging black-capped chickadees (Parus atricapillus), Smith (1976) found that weight did not influence dominance. Instead, males were dominant over females and older, more experienced individuals were dominant overall. In contrast, many studies have found that dominant individuals in stable hierarchies were larger or had larger fat reserves (Fretwell 1969, Baker and Fox 1978, Searcy 1979, Ketterson 1979, Eckert and Weatherhead 1987a).

I also examined the colouration of chins in relation to dominance in females. Because chin colours are only expressed in females, selection would have to affect females directly if chin colours have evolved as a signal of status. Bill-tilt displays are used in aggressive encounters and the bright colouration would accentuate the

chin (Hurly and Robertson 1984). Older females tend to have brighter chins (Payne 1969) and also will have had more experience in defending resources. If females were signalling status by chin brightness I would have expected a significant relationship between status and chin colour. Full bill-tilt displays (with the female holding the rigid bill-up position) did not occur in the aviary probably because females were defending a small, discrete resource. If females had given bill-tilts other females could have easily approached and fed from the unguarded dish. Since the variation in colouration of female chins cannot be explained by either direct or indirect sexual selection its significance is not known.

A further test of the sexual selection hypothesis was to examine overall hierarchy positions in relation to plumage. There was no consistent relationship between rank in the dominance hierarchy and the colour of either chins or epaulets in the control groups. Therefore, plumage colour did not signal status. Fugle *et al.* (1984) demonstrated that crown brightness was a status signal in white-crowned sparrows but only operated as such when differences were extreme (i.e. differences between immature brown-crowns and adult white-crowns). Since the control groups in my study contained individuals with a full range in plumage colours I should have been able to detect status-signalling if it were occurring.

Plumage manipulation experiments

If chins or epaulets function as signals for individual recognition, alteration of these characters could lead to changes in dominance relationships due to "mistaken identities". All but two of the females that had chins or epaulets brightened changed their position in the hierarchy. From the status-signalling hypothesis I predicted that when females were brightened they would rise in status. However, there was no consistent tendency to either increase or decrease in rank. This supports the hypothesis that female plumage variation is due to genetic correlations with male variation and could also indicate that plumage affects individual recognition. Disguising birds by brightening them may not result in an increase in status if they are recognized upon being reintroduced to the group. Parsons and Baptista (1980) showed that disguising juvenile white-crowned sparrows (originally having brown crowns) as high-ranking adults (with white crowns) did not result in an increase in social status when they were released back into their former flocks. They concluded that individual recognition is more important than crown colour in determining dominance relationships.

After females were dyed in the second chin manipulation group and the epaulet manipulation group there were increases in the number of threats or attacks involving takeovers of the food dish. Threats and attacks increased

2 of/de 2

against both bright and dull birds and therefore there was no evidence of persecution of brightened individuals. In Harris' sparrows, individuals bleached to resemble subordinate birds became highly aggressive probably due to the loss of signalled status (Rohwer 1977). Rohwer and Rohwer (1978) suggested that deceptively brightened sparrows were persecuted by other birds because they still behaved subordinately. This illustrates the importance of behaviour in determining status. If a bird is changed to look like a dominant bird but does not act like one it is not likely to rise in status. The internal state of the bird and in particular the levels of hormones will greatly affect its aggressive behaviour. Rohwer and Rohwer (1978) showed that when subordinate sparrows were dyed and given testosterone, they increased in social rank.

However, my study indicates that plumage brightness is not related to dominance in female red-winged blackbirds. Females formed stable hierarchies which indicates that some mechanism of dominance signalling or individual recognition is occurring. Plumage variation may aid in individual recognition but it does not function as a signal of social status. Since females are not signalling competitive ability by variation in plumage, is there any adaptive significance to plumage variation? Evidence from this study supports the hypothesis that female epaulet colouration may simply be the result of genetic correlation

with male plumage. This explanation does not account for variation in chin colours.

Gould and Lewontin (1979) suggested that the failure to explain a trait on the grounds of adaptive significance should lead to the consideration that perhaps each trait has not evolved for a specific purpose. Hence the non-adaptationist approach is to distinguish between the reasons for the origin of a particular trait and its present significance. The present study is the first to illustrate that plumage brightness in female red-winged blackbirds does not signal competitive ability but may simply have originated due to the genetic correlation with male characters.

SUMMARY

The evidence presented is consistent with the hypothesis that variation in the colouration of epaulets of female red-winged blackbirds is not maintained due to direct sexual selection acting on the female but is instead due to genetic correlation with male plumage.

1) Female epaulets brightened with age and chin colours did not change consistently. Delayed plumage maturation is a characteristic of males.

2) Females with bright epaulets and chins were not the first to settle on upland territories. Bright females did not initiate clutches first in marsh populations.

3) Males and females failed to distinguish between dull and bright female models. The aggressive response of females to intruding females was quite variable and was not related to plumage colouration of the intruder or the responding female.

4) Females established dominance hierarchies in captive groups but dominance status was unrelated to epaulet or chin colour.

5) When plumage was altered, interactions between individuals tended to increase and therefore plumage colouration may aid in individual recognition.

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Appendix:

- A) Tables 1 to 9. Winner-loser matrices for eight captive groups of female red-winged blackbirds. Hierarchies were constructed by placing individuals in a position that minimized the number of losses below the diagonal (Brown 1975).

Table 1. Dominance matrix for control group 1.

		LOSER						
Female	A	B	C	D	E	F	G	
WINNER	A	-	9	21	10	11	21	12
	B	4	-	47	21	30	55	15
	C	15	31	-	63	53	128	52
	D	2	15	44	-	20	61	27
	E	0	14	18	8	-	22	6
	F	1	10	12	3	6	-	23
	G	1	3	8	0	4	16	-

Table 2. Dominance matrix for control group 2.

	Female	LOSER					
		H	I	J	K	L	M
WINNER	H	-	36	36	13	14	28
	I	3	-	55	28	37	29
	J	33	48	-	89	78	65
	K	1	6	40	-	15	42
	L	3	5	9	8	-	43
	M	0	0	1	0	0	-

Table 3. Dominance matrix for control group 3.

	Female	LOSER					
		N	O	P	Q	R	S
WINNER	N	-	67	27	0	15	39
	O	4	-	87	15	34	11
	P	7	85	-	15	39	7
	Q	15	2	4	-	13	11
	R	0	1	2	3	-	11
	S	3	4	4	1	2	-

Table 4. Dominance matrix for control group 4.

	Female	LOSER					
		T	U	V	W	X	Y
WINNER	T	-	41	54	15	58	75
	U	28	-	57	21	31	57
	V	3	2	-	12	26	45
	W	2	0	11	-	19	31
	X	25	1	17	4	-	13
	Y	3	0	10	1	5	-

Table 6. Dominance matrix for first group with epaulets
experimentally brightened (*) or dulled.
LOSER

Female	Ae	Be	Ce	De	Fe	Ee	Ge	He	Ie
*Ae	-	16	13	27	25	22	12	31	15
Be	12	-	26	31	24	14	29	48	23
Ce	1	2	-	94	10	8	4	41	6
*De	5	4	6	-	56	30	35	74	20
*Ee	3	5	25	0	-	21	28	58	13
Fe	1	2	4	0	4	-	17	43	18
Ge	6	2	23	0	11	6	-	32	17
*He	3	4	3	1	0	3	0	-	13
Ie	1	1	8	0	0	0	0	1	-

WINNER

Table 7. Dominance matrix for the first chin manipulation group.

I. Before:

LOSER

WINNER	Female	JJ	KK	LL	MM	NN	OO	PP	QQ
	JJ	-	9	20	22	26	37	23	30
	KK	10	-	1	8	6	2	5	15
	LL	1	5	-	6	15	20	11	27
	MM	2	3	1	-	4	1	7	1
	NN	0	15	6	3	-	9	8	17
	OO	0	1	8	2	7	-	2	8
	PP	0	1	4	4	1	2	-	11
	QQ	0	0	1	0	0	0	0	-

Birds that had chins brightened are marked with a *.

II. After

LOSER

WINNER	Female	JJ*	KK	MM*	NN*	PP	LL	OO*	QQ
	JJ*	-	38	25	107	27	95	110	91
	KK	3	-	1	7	9	0	6	4
	MM*	3	1	-	9	6	2	18	13
	NN*	33	4	3	-	13	7	36	42
	PP	16	1	4	2	-	0	10	19
	LL	4	1	1	5	0	-	3	7
	OO*	3	0	3	2	3	2	-	19
	QQ	12	3	8	3	0	2	13	-

Table 8. Dominance matrices for the second chin manipulation group.

I. Before:												
WINNER												
LOSER												
Female	RR	SS	TT	UU	VV	WW	XX	YY	ZZ	AAA	BBB	
RR	-	13	54	4	74	6	23	4	14	15	7	
SS	10	-	39	10	72	7	23	4	13	3	5	
TT	10	10	-	26	123	21	40	27	41	16	17	
UU	3	5	12	-	20	1	12	1	7	3	1	
VV	7	1	24	3	-	9	22	11	10	5	10	
WW	5	2	15	1	7	-	11	1	3	2	0	
XX	0	0	1	1	3	0	-	0	1	1	0	
YY	0	0	2	1	4	1	3	-	0	3	1	
ZZ	0	1	6	0	10	0	6	0	-	6	0	
AAA	0	0	0	0	0	0	0	0	0	-	0	
BBB	0	0	0	0	0	0	0	0	0	0	-	

WINNER

● Birds that had chins brightened are marked with a *.

II. After

LOSER

Female	RR	UU	TT	YY	VV	SS*	WW	AAA*	BBB*	ZZ*	XX*
RR	-	36	89	52	125	45	40	14	47	21	34
UU	21	-	53	43	100	17	24	6	28	9	25
TT	28	33	-	62	196	37	53	8	27	14	17
YY	4	5	18	-	85	10	9	11	26	16	11
VV	40	16	25	45	-	23	59	6	67	23	17
SS*	0	2	6	8	19	-	9	6	14	9	6
WW	14	7	10	26	21	5	-	7	19	6	4
AAA*	0	0	0	0	0	4	6	-	3	2	0
BBB*	0	2	6	1	5	3	0	1	-	6	0
ZZ*	0	1	0	0	0	0	0	1	1	-	0
XX*	0	0	0	0	0	0	0	0	0	0	-

WINNER

Table 9. Dominance matrices for the epaulet manipulation group.

I. Before:		LOSER								
WINNER	Female	CCC	DDD	EEE	FFF	GGG	HHH	III	JJJ	KKK
	CCC	-	26	31	25	36	13	57	19	67
	DDD	13	-	8	8	6	4	18	4	31
	EEE	4	1	-	4	5	2	18	0	7
	FFF	36	6	2	-	9	3	35	18	27
	GGG	14	2	0	8	-	2	14	5	5
	HHH	17	2	3	0	0	-	1	0	0
	III	5	1	7	12	11	0	-	6	34
	JJJ	2	0	0	0	1	0	0	-	1
	KKK	0	1	0	2	0	0	0	0	-

Birds that had epaulets brightened are marked by *.

II. After:		LOSER								
WINNER		DDD	CCC	GGG	III*	FFF	EEE	HHH*	JJJ*	KKK*
	DDD	-	57	30	24	10	52	44	36	17
	CCC	19	-	46	113	34	180	101	28	17
	GGG	3	35	-	21	19	29	14	7	9
	III*	7	9	12	-	57	102	32	61	20
	FFF	2	65	13	6	-	78	23	39	17
	EEE	16	26	39	44	33	-	52	41	32
	HHH*	2	10	2	20	14	8	-	8	10
	JJJ*	0	1	0	0	4	10	7	-	5
	KKK*	0	1	0	0	1	0	1	2	-

Appendix:

B) Detailed description of non-linear aviary interactions

1) Control Groups

Group 3: This group had non-linear interactions (Table 3). Bird "Q" was dominant over bird "N". However, it was subordinate to "O" and "P". "Q" was placed fourth in the hierarchy because this positioning minimized the number of intransitive relationships. Here a relationship between colour and dominance is not apparent. The dominant bird had a bright chin and dull epaulets while the subordinate bird had a dull chin and bright epaulets.

2) Chin patch Experimental Groups

Chin I: There was an ambiguous relationship between bird "OO" and bird "PP" before manipulation (Table 7). Both won two out of a total of four interactions. After chins were coloured, "JJ" lost to "LL" in the one interaction the pair was involved in. However, "JJ" was clearly dominant overall.

Chin II: In the final matrix before manipulations the relationships involving bird "AAA" and "BBB" were unclear as these individuals did not win any interactions and were never seen fighting each other. Once chins had been manipulated the hierarchy became non-linear. Bird "WW" was dominant to "YY" although was subordinate to "SS" and "VV". There were three dyads for which no interactions were recorded and therefore hierarchies had to be constructed taking into consideration the relationships between all individuals.

3) Epaulet Experimental Group

Here there was a non-linear relationship before epaulets were coloured. "HHH" won over "CCC" and "EEE" but only by several interactions (Table 9).

END

08-08-88

FIN