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**COLOURED BANDS,
COVERABLE BADGES,
AND SEXUAL SELECTION
IN
RED-WINGED BLACKBIRDS**

by
Karen Jennifer Metz

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

Master's of Science

**Department of Biology
Carleton University
Ottawa, Ontario**

January, 1991

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Studies and Research acceptance of this thesis**

**"COLOURED BANDS, COVERABLE BADGES, AND
SEXUAL SELECTION IN RED-WINGED BLACKBIRDS"**

**submitted by Karen Jennifer Metz, B.Sc.
in partial fulfillment of the requirements for
the degree of Master of Science**

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1991

Abstract

A banding study on male red-winged blackbirds (*Agelaius phoeniceus*) demonstrated that red coloured bands (the same colour as males' epaulettes) affect male behaviour. Males given red bands suffered increased aggression from other males (particularly neighbours) and had more difficulty maintaining their territories than black-banded males. Red leg bands appeared to function similarly to male epaulettes which are displayed to signal threat and territory ownership. However, males could not cover their coloured leg bands as they could their epaulettes. Uncoverable red bands caused males to signal aggression during inappropriate situations (e.g. while trespassing on other males territories and while foraging) and to signal at an escalated intensity that did not reflect their true competitive ability. Ornithologists should take into account the potential effects of coloured bands when investigating bird behaviour, particularly when studying aspects of sexual selection. In addition, coloured bands may provide a useful tool for investigating sexual selection in the field.

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General Introduction

Many animal species are sexually dimorphic. In most cases the male is the more conspicuous sex, possessing secondary sexual characters such as antlers, combs and wattles, and bright plumage which appear to be indirectly related to reproduction. These traits are often used in courtship displays and aggressive interactions between males and can signal the dominance status of an individual. Darwin (1871) developed the theory of sexual selection to explain the evolution of these secondary sexual traits. Sexual selection according to Darwin (1871:568) "depends on the advantage which certain individuals have over others of the same sex and species, solely in respect of reproduction". Darwin made the distinction between sexual selection and natural selection because sexual selection favours the evolution of characters that may be detrimental to survival. However, the ability of an animal to survive is only one aspect of its fitness. The more important consideration is that an animal is able to pass as many of its genes as possible to future generations (Endler 1986:12). Therefore, sexual selection can be considered a subset of natural selection.

Sexual selection can be subdivided into two processes; female choice and competition among males (Trivers 1972). Females are usually viewed as the "choosing" sex because they normally invest more in reproduction and have more to lose by choosing an inappropriate mate. In most cases, the more copulations a male has, the greater his reproductive success

(Trivers 1972). Therefore, males have greater variation in reproductive success than females.

The presence of either or both female choice or male-male competition may give rise to secondary sexual traits (Butcher and Rohwer 1988). Darwin (1871) argued that the bright plumage of males in many bird species is a result of sexual selection, particularly female choice. Studies have shown that females do "choose" males on the basis of male secondary sexual characteristics (Andersson 1982; Burley et al. 1982; Burley 1986b; Møller 1988). Females may have evolved a preference for males with species-specific colours to avoid mating with a member of another species (Partridge and Harvey 1986). Another explanation is that females "choose" mates on the basis of secondary sexual characters, such as bright plumage, because these characters signal male quality. Male quality may include several aspects such as survival ability, parental ability, aggressive ability, overall health, etc. Females selecting males with reliable signals of "high" quality benefit because the "good" genes of their mates are passed on to their offspring (Weatherhead and Robertson 1979; 1981; Kirkpatrick 1987). Males possessing reliable signals should be able to attract more mates and/or select females of higher quality, enhancing their own reproduction success (Howlett 1988).

Secondary sexual characters can also arise from male-male competition. In many species males compete among themselves for possession of females directly, or to establish

ownership of resources which are attractive to females. Dominant males, which win fights, often have greater access to females and as a result greater reproductive success than subordinate males (Clutton-Brock 1988). Intrasexual selection has favoured the evolution of male characters, such as large size and weaponry, that enhance fighting ability. However, escalated fights are costly (Clutton-Brock et al. 1979). Fights between males can be minimized if males could determine the social status of their opponents without actually fighting them (Rohwer 1985). Reliable badges of social status may have evolved to serve this function.

Bright male plumage in many birds may be an example of a reliable badge. Conspicuous colouration can function as a signal of threat (Rohwer 1982). On the surface, conspicuous colouration does not appear to be energetically costly to produce or carry. Therefore, it should be easy to mimic by subordinate males, and lose its function of signalling male status. Reliable badges (e.g. patches of colour) of dominance status can only be maintained if there is a cost involved in cheating. Cheating should be costly if only males of high quality can survive with the handicap of being conspicuous to predators and/or competitors (Zahavi 1975), or if only males of high quality can advertise badges in energetically costly displays (Baker and Parker 1979), or if only healthy males that are free of ectoparasites and disease can produce bright feathers (Hamilton and Zuk 1982).

The aim of this study is to test the assumption that there is a cost to unreliably signalling competitive status in an eastern Ontario population of red-winged blackbirds (*Agelaius phoeniceus*).

In Chapter One, I assess the effects of increasing the intensity of territorial red-winged blackbirds signal of competitive ability by giving owners red-coloured leg-bands the same colour as their coverable badges (i.e. their red epaulettes). Male red-winged blackbirds display their epaulettes to signal threat (Røskft and Rohwer 1987) and territory ownership (Peek 1972; Smith 1972). If coloured bands function as epaulettes, owners given red bands should be perceived by rivals to be signalling at a higher and more aggressive intensity. There are two possible outcomes for red-banded males that signal at higher intensities. Red-banded males may signal inappropriately and unreliably, leading to increased harassment by other males. Alternatively, red-banded males may be more threatening to other males. If red-banded males are better at repelling intruders, the notion of reliable badges must be seriously reconsidered.

In Chapter Two, I examine certain aspects of the coverability of some badges. Many badges are continually displayed by their bearers. However, some badges are coverable (e.g. red-winged blackbird epaulettes). Hansen and Rohwer (1986) developed the "coverable badge hypothesis" to explain the evolution of coverable badges. The hypothesis states that coverable badges should be exposed when

appropriate and concealed when it is inappropriate to display the signal. This suggests that there should be costs involved for males that continuously display their coverable badges. In this chapter I ask what the costs and/or benefits involved in continually displaying a coverable badge are for territorial red-winged blackbirds.

In Chapter Three, I further test the effects of coloured bands on male red-winged blackbird behaviour. Two different experiments are outlined to test whether red bands serve a similar function as male red-winged blackbird epaulettes. More specifically they address the question of whether red bands signal aggression during contests. The first experiment deals with contests between males over territory ownership. In the second experiment, I test whether red bands affect the outcome of contests that involve food rather than resources directly related to reproduction.

CHAPTER ONE

**Colour bands function as secondary sexual traits in
male red-winged blackbirds.**

Introduction

Male secondary sexual traits are thought to have evolved because of the mating advantage they provide their bearers (Darwin 1871). Male birds with bright plumage may be either more attractive to females or better at competing with other males (Darwin 1871; Butcher and Rohwer 1988). Several studies have shown that colour bands used to recognize individual birds in ornithological research may affect reproductive behaviour and/or reproductive success (Burley 1981; 1985; 1986a; 1986b; Burley et al. 1982), particularly when those colours match those of secondary sexual traits (Brodsky 1988; Hagan and Reed 1988). If such effects are widespread, the implications for ornithology are potentially profound.

The red-winged blackbird is ideally suited to test band colour effects experimentally in a natural population. The red-winged blackbird is a territorial, polygynous, sexually-dimorphic passerine. Adult males are entirely black except for their brilliant red epaulettes (upper wing coverts or shoulder patches) that are fringed by a pale yellow border. Approximately half of all males fail to acquire territories during the breeding season (Searcy 1979a). Territory owners do not differ from males unable to establish territories (floaters) in body size or epaulette size (Eckert and Weatherhead 1987a). However, when on territories, owners fully expose their epaulettes during territorial and sexual displays (Nero 1956a,b), while floaters largely conceal their

epaulettes when trespassing on an owner's territory (Hansen and Rohwer 1986). Thus, the epaulettes function as signals of threat (Røskoft and Rohwer 1988) but are "coverable badges" (secondary sexual characters indicating social status, which are readily concealed) (Hansen and Rohwer 1986).

Recently, Beletsky and Orians (1989) examined the effect of red colour bands (which match males' epaulettes) on male mortality and reproductive success in a population of red-winged blackbirds *a posteriori*. Anodized aluminum bands of various colours were used in their study for all but the first year when plastic bands were used. Beletsky and Orians (1989) found no difference in harem size, number of young fledged, or number of breeding years for males that had and did not have red bands in their colour combinations. They concluded that it was "unnecessary to avoid using combinations of coloured leg bands that include red in studies of redwings under 'natural' conditions" (Beletsky and Orians 1989:994). However, despite these results red bands may still have subtle effects on red-winged blackbirds behaviour that cannot be demonstrated without experimental manipulations. These subtle effects may be exaggerated by magnifying the stimulus (i.e. number and brightness of red bands given to males). By studying these behavioural effects we may gain important insights into how sexual selection operates. In this chapter I present the first experiment to assess band colour effects in a natural population.

Methods

I conducted this study in an extensive cattail marsh (*Typha* sp.) near Seeley's Bay, Ontario during the 1989 breeding season. Male red-winged blackbird territory owners were captured using decoy traps (Smith 1976) and mist nets, measured, colour banded and released onto their territories in April and early May. Body size and epaulette size have been shown to be important in aggressive interactions between captive male red-winged blackbirds (Searcy 1979b; Eckert and Weatherhead 1987b). Therefore, I recorded these morphological measures as estimates of male competitive ability. Body size was indexed by wing length, measured (to the nearest mm) from the bend of the wing to the tip of the longest primary (Searcy 1979b), body weight (to the nearest g), and tarsus length (to the nearest 0.1 mm). Epaulette size was indexed by the length of a male's epaulette measured as the distance from the bend of the wing to the furthest extent of yellow plumage (Searcy 1979b).

Because of the singular importance of red to red-winged blackbird displays I banded 38 territory owners with either red bands (the colour of epaulettes), or black bands (the same colour as their legs). Each day during the capture period I entered the marsh and randomly selected an area to trap territorial males. Males were alternately assigned red and black bands as they were captured. Thus, males were randomly assigned coloured bands with respect to all of their other attributes. The resulting spatial pattern of banded males

was such that all banded individuals shared at least part of their territory boundary with unbanded males. Of the 19 "red" males, seven also shared part of their territory boundary with both red- and black-banded males, two shared with red-banded males, seven shared with black-banded males, and three had neither red- nor black-banded neighbours. Of the 19 "black" males, six had both red and black neighbours, eight shared territory boundaries with red males, two shared with black males, and three had neither red nor black neighbours.

Red males received five plastic red bands and a numbered aluminum band (three bands per leg) and black males received five plastic black bands and one aluminum band. The colour of the red bands matched the colour of the epaulettes. Males' epaulette colour scores ranged from 34 to 40 on the Inter-Society Colour Council - National Bureau of Standards (ISCC-NBS) colour chart. Most males' epaulettes scored either as ISCC-NBS number 34 (Munsell notation 9.8R 5.4/14.5, $N = 17$) or ISCC-NBS number 36 (Munsell notation 9.2R 3.9/12.1, $N = 18$). The colour of the red bands was scored as ISCC-NBS number 36.

I recognized individuals by the position of the aluminum band and the bird's location in the marsh. Males that shared identical band combinations were separated on average by more than seven territories. Therefore, unless males with the same band combination switched territories (a highly improbable scenario), I was confident that I was able to distinguish individuals.

I estimated territory boundaries by marking the perches of displaying owners with flagging tape and plotting them on a map. I determined the fate of all nests in territories of banded males. Nineteen unbanded males' territories near red or black males' territories were similarly monitored by observing the perch positions of displaying unbanded owners for approximately 30 min every few days. I observed each banded male for 15 min intervals an average of 10 times through the breeding season to quantify the frequency and duration of aggressive displays and interactions with other males. Opportunistic observations of chases were also recorded.

I also recorded the intensity and rate of male song displays on their territories. I considered a display not to be a song spread when a singing male exposed little of his epaulettes and kept his wings at his side. A low intensity song spread involved exposure of half of the epaulette and slight arching of wings. A medium intensity song spread exposed three quarters of the epaulette with the wings arched out and down and the tail slightly fanned. In a high intensity song spread, epaulettes were fully exposed and ruffled, wings were fully arched out and down and the tail was completely fanned.

I returned to the marsh during the 1990 breeding season and checked the study area once a week from April to the middle of May to examine whether red and black males had returned to their territories.

Results

Although red and black males had similar body and epaulette sizes (Table 1-1), red males had greater difficulty maintaining territories than black males. Eleven of the 19 red males lost their territories to other males, four to black-banded neighbouring owners (neighbours), and seven to unbanded males. Floaters were suspected to have taken over red males territories in three of the seven cases involving unbanded males since the banded and unbanded neighbours' territory boundaries did not appear to change as a result of the takeover. All 19 black males were able to maintain their territories ($\chi^2 = 14.48$, $P < 0.001$). After losing their territories, red males were not seen in the marsh until after the second brood on their former territory was almost ready to fledge. About this time, five of the usurped red males were occasionally observed on or near their former territories.

The ability of some red males to hold their territories may be a function of superior competitive ability relative to those that lost territories (Parker 1974). Although losers were neither smaller (as indexed by wing and tarsus length) nor weighed less than winners (Table 1-2), the time from banding to territory loss decreased with decreasing mass ($r = 0.569$, $F = 3.82$ $N = 10$, $P = 0.043$, Figure 1-1). Competitive ability may also be signalled by the size of badges such as epaulettes (Rohwer 1982; Eckert and Weatherhead 1987b; Røskoft and Rohwer 1988). Surprisingly, however, red males that lost territories had larger epaulettes than those that kept their

Table 1-1 **Morphological, behavioural, and fitness comparisons between red and black males**

	Red males			Black males				
	$\bar{X}$	SE	N	$\bar{X}$	SE	N	<i>t</i>	<i>P</i>
Morphological Measures								
Mass	68.1	1.0	19	69.2	0.8	18	-0.87	0.40
Wing length (cm)	12.5	0.1	19	12.5	0.1	19	0.51	0.61
Tarsus length (mm)	27.1	0.4	17	27.8	0.3	18	-1.35	0.19
Epaulette length (mm)	40.8	0.7	19	41.6	1.0	18	-0.57	0.57
Behavioural Measures								
Duration of chases (sec)	38.8	9.6	12	17.6	2.7	12	-2.13	0.045
Time between song displays (sec)	27.1	3.6	11	21.0	4.5	7	-1.05	0.31
Fitness Measures								
Harem size	1.2	0.1	12	1.8	0.2	18	2.71	0.01
Fledglings per territory	1.0	0.3	13	1.5	0.5	18	0.79	0.44

Morphological and fitness values are means for red and black males, respectively. Behavioural measures are the means of individual means for red and black males, respectively. All *P*'s are based on 2-tailed *t* -tests; *N* = number of males.

Table 1-2 **Morphological and behavioural comparisons**
between red males that lost and red males that
retained territories

	Lost			Maintained			<i>t</i>	<i>P</i>
	$\bar{X}$	<i>SE</i>	<i>N</i>	$\bar{X}$	<i>SE</i>	<i>N</i>		
Morphological Measures								
Mass	67.0	1.1	10	69.4	1.8	8	-1.16	0.26
Wing length (cm)	12.6	0.1	11	12.5	0.1	8	0.70	0.49
Tarsus length (mm)	22.3	3.3	9	26.9	0.8	8	-1.16	0.26
Epaulette length (mm)	42.3	0.9	11	38.8	0.8	8	2.68	0.02
Behavioural Measures								
Duration of chases (sec)	52.2	16.8	6	25.5	7.3	6	-1.45	0.18
Time between song displays (sec)	28.3	5.6	7	25.0	3.2	4	-0.42	0.69

Morphological values are means for red males that lost and maintained their territories, respectively. Behavioural measures are the means of individual means for red males that lost and maintained their territories, respectively.

All *P*'s are based on 2-tailed *t*-tests; *N* = number of males.

Figure 1-1 The time (days) between banding and
territory loss relative to mass for red males
that lost territories.

territories (Table 1-2). Combining both factors, red males that lost territories had larger epaulettes relative to their mass than red males that retained territories (ANCOVA, $F = 8.82$, $N = 18$, $P = 0.01$).

Territory loss was associated with increased harassment of red males, particularly by their neighbours. Of the 93 observations of red males chasing intruders of known status from their territories, 36 (39 %) involved neighbours, whereas only 22 of 89 (25 %) chases by black males involved neighbours ($\chi^2 = 4.10$, $P = 0.043$). Most of the chases by red and black males involving neighbours were with either unbanded or black-banded neighbours (I observed only four cases where a red-banded neighbour was chased from an experimental male's territory). Chases by red males lasted longer than chases by black males (Table 1-1). Thus, red males had to contend with increased intrusion by their neighbours and had to work harder to repel those intrusions. This increased cost of territory maintenance is consistent with the least heavy red males being the quickest to lose their territories.

Because epaulettes are coverable, male red-winged blackbirds can vary the intensity of their displays. Red males tended to give fewer high intensity song spread displays per minute relative to black males (Table 1-3), even though their display rates remained the same (Table 1-1). This result suggests that red males reduced the intensity of their displays in the face of increased aggression by neighbours.

Table 1-3 **Song spread intensity differences between males**

	All Males				Red-banded males			
	Black Male		Red Male		Lost		Maintain	
	<i>N</i> = 12		<i>N</i> = 12		<i>N</i> = 12		<i>N</i> = 12	
Display intensity	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
SS1 ¹	0.41	0.17	0.83	0.32	0.65	0.33	0.90	0.42
SS2 ²	1.06	0.31	0.69	0.22	0.14	0.09	0.87	0.27
SS3 ³	0.75	0.23	0.99	0.39	0.61	0.55	1.12	0.49
SS4 ⁴	1.41	0.51	0.38	0.12	0.27	0.27	0.41	0.14
Treatment	F = 0.71, df = 1, P = 0.40				F = 1.52, df = 1, P = 0.23			
Display	F = 0.35, df = 3, P = 0.79				F = 0.84, df = 3, P = 0.48			
Treatment X Display	F = 2.31, df = 3, P = 0.08				F = 0.16, df = 3, P = 0.92			

¹SS1 = Number of calls without song spread display per 60 sec

²SS2 = Number of low intensity song spread displays per
60 sec

³SS3 = Number of medium intensity song spread displays per
60 sec

⁴SS4 = Number of high intensity song spread displays per
60 sec

The importance of red colouration to intersexual interactions in red-winged blackbirds is less clear than its role between males. Male red-winged blackbirds with blackened epaulettes that maintained territories are able to attract females (Peek 1972; Smith 1972; Morris 1975). I found that red males who maintained territories for at least one breeding attempt attracted significantly fewer females than black males (Table 1-1). This does not necessarily mean that females were less attracted to red males. Red males may have had smaller harem sizes because they had to devote more time to defending their territories than to courting females. In spite of their smaller harems, red males that maintained their territories did not fledge significantly fewer young (Table 1-1). Black bands were a suitable control since black males and unbanded males did not differ from each other in the number of females they attracted ($t = 1.83$, $P = 0.35$). It is important to note that these results for male reproductive success must be interpreted cautiously since DNA fingerprinting in this population has shown that neither harem size nor the number of young fledged on a male's territory are good predictors of a male's true reproductive success (Gibbs et al. in press).

In 1990 I observed 10 of 19 black males and 10 of 19 red males on their territories of the previous summer. Four of the 10 red males that returned had lost their territories in the previous summer. One of those red males lost his territory again during the 1990 breeding season. An unexpected result observed in 1990 was that significantly more returning red

males than black males had lost at least one of their bands. Nine of ten red males were missing at least one of the five coloured bands (mean number of bands lost = 2.3, $N = 9$) compared to only three of ten black males (mean number of bands lost = 2.0, $N = 3$; Fisher Exact Test, $P = 0.01$). Birds often peck at their bands and are sometimes successful in removing them. This result may indicate that red males were more persistent and/or aggressive in their attempts to remove their bands than black males. Alternatively, it is possible that red bands were lost more readily because they are more brittle than black bands and thus easier to remove.

Discussion

Collectively, my results indicate that red bands somehow interacted with a male's epaulettes to cause increased aggression toward that male. That aggression appears to have been greater to males displaying the most red (epaulettes + bands), with those males least able to bear the cost of increased aggression against them (i.e. least heavy males) being the first to lose their territories.

There are several possible explanations why red males suffered increased aggression from other males. First, red males may have signalled at an intensity inconsistent with their competitive ability which caused them to be challenged by other males. However, experiments using model birds had suggested that increasing the size of an owner's epaulettes (i.e. increasing the intensity of the signal) should decrease his cost of territoriality due to lower rates of intrusion by floaters. Røskaft and Rohwer (1988) placed mounts of red-winged blackbirds with enhanced, and normal sized epaulettes on territories from which the resident had been removed. They found that nonterritorial (floater) males intruded more and landed closer to mounts with normal-sized epaulettes than with enlarged epaulettes. Thus, enhanced epaulettes on "resident" males deterred challenges by floaters. However, in my study the increased intrusion pressure on red-banded males came from neighbours rather than floaters. Neighbours may be more familiar than floaters with the competitive ability of nearby owners from regularly interacting with them and

from watching contests between neighbouring territory owners and intruders. Freeman (1987) presented eastern kingbird (*Tyrannus tyrannus*) and red-winged blackbird mounts to territorial male red-winged blackbirds and found that subsequently, neighbours intruded upon owners that had failed to vigorously attack the red-winged blackbird mounts. Thus, owners who were perceived to have "poor" competitive ability suffered increased aggression from their neighbours. If neighbours know one another's competitive ability, they may challenge a neighbour that starts signalling at an intensity inconsistent with their competitive ability. Red bands may have simulated such an escalation in signal intensity. My results suggest that male red-winged blackbirds continue to test one another's competitive ability relative to the size of their epaulettes, thereby maintaining the reliability of the epaulette as a signal of competitive ability.

A second possible explanation for the high aggression against red males is that red males were attacked more when they trespassed on other males' territories. Because red males were unable to cover their red bands as they can their epaulettes, they may have inadvertently and inappropriately signalled aggressiveness when trespassing. In turn, neighbouring males may have attacked red males more vigorously than black males to protect their territories. Hansen and Rohwer (1986) presented red-winged blackbird mounts with blackened, reduced, enhanced, and normal-sized epaulettes to territorial male red-winged blackbirds. Owners

were less aggressive toward mounts with smaller epaulettes than toward those with enlarged epaulettes. Thus, floaters that cover their epaulettes when trespassing are able to avoid provoking strong aggression, but they are immediately able to display their epaulettes if they become owners. My observation that red males began displaying less of their epaulettes is consistent with them attempting to reduce the intensity of their aggressive badges. The differential loss of red and black bands in the year following my experiment may also be consistent with red males trying to reduce their aggressive badges. If this explanation is correct, then I would predict that males that were unable to cover their epaulettes should be affected in the same way as the males I gave red bands.

A third possibility is that the aggression against red males may simply have been due to them having an unnatural marking. Red males may not have been recognized by other males or females as red-winged blackbirds. This species recognition hypothesis seems unlikely, however, because other males responded more aggressively rather than less aggressively toward red males than black males. Territorial male red-winged blackbirds are less aggressive toward conspecific Brewer's blackbird (*Euphagus cyanocephalus*) males, even when the conspecific males have their epaulettes blackened (Hansen and Rohwer 1986). Therefore, I will not discuss this hypothesis further in my thesis.

A final possibility that I cannot discount is that any colour contrasting with the black of the legs may cause males to signal inappropriately or be perceived as unhealthy. However, it is not obvious that colours other than red should interact with the red epaulette in the manner I observed.

My results for red-winged blackbirds are consistent with the results of an *a posteriori* examination of banding effects on red-cockaded woodpeckers (*Picoides borealis*) (Hagan and Reed 1988). Males of both species that were unable to signal status correctly by continually and inappropriately displaying an aggressive signal (i.e. coloured leg band similar in colour to coverable badges) suffered increased aggression from other males. Both red-cockaded woodpeckers and red-winged blackbird males given red bands (similar in colour to male cockades and epaulettes, respectively) ultimately suffered reduced reproductive success. However, male red-cockaded woodpeckers given red leg bands fledged fewer young than males without red bands (Hagan and Reed 1988), whereas red-banded red-winged blackbird males had greater difficulty maintaining their territories. In the woodpecker study, red was the only colour that produced this negative effect of colour banding.

The contrast in the effect of red bands on male red-winged behaviour between Beletsky and Orians' (1989) study and my study is most likely a result of the difference in the number and type of bands used. Beletsky and Orians (1989) conceivably found no colour band effect because red males in

their population only had one to three red bands rather than the five in my study. Also, they predominantly used red anodized aluminum bands that may not have been as similar in colour to male red-winged blackbird epaulettes as were the bands I used. Thus, the number and colour of the red bands that Beletsky and Orians used may not have altered a male's status signal enough to change the behaviour of neighbours. In an *a posteriori* analysis of band colour effects from eight years of research on red-winged blackbirds, involving both plastic and anodized aluminum bands, Weatherhead et al. (in preparation) also failed to find any negative effect of red bands (or any other colour). Since this analysis was based on studies conducted in the same area as the results I report here, the difference between my observations here and the results of Beletsky and Orians (1989) is clearly not a consequence of red-winged blackbirds behaving differently in different parts of their range. The different outcomes of my experimental study and the two correlational studies of band colour effects suggest that the effects may be sufficiently subtle that they can only be detected by an experimental approach in which the colours are exaggerated over normal banding practices. What remains to be determined is whether smaller, but still detrimental effects of colour banding occur under those normal practices.

Whatever its cause, the strong influence colour bands have on red-winged blackbird reproductive behaviour in my study makes it imperative that we investigate this phenomenon in other species. Without taking band colour into

account, misleading results may be obtained, particularly when investigating sexual selection questions. In addition, a novel technique for investigating sexual selection in the field may be missed.

CHAPTER TWO

The need to conceal coverable badges

Introduction

Red bands given to territorial red-winged blackbirds (owners) in the experiment described in chapter one somehow interacted with males' epaulettes and caused red-banded owners to lose their territories. Territory loss was associated with increased harassment of red-banded males. Red-banded males had more intrusions on their territories by their neighbours and had to work harder to repel those intrusions. I proposed three hypotheses that may explain why red-banded owners suffered increased aggression and lost their territories. First, red bands could have increased the size of males' signal of competitive ability so that red-banded males were displaying too aggressively for their competitive ability. Second, red-banded males may have been inappropriately signalling aggression and territory ownership when they trespassed on other males' territories. Third, red bands may have made red-banded males appear abnormal or unhealthy to conspecifics. In this chapter I will focus on the first two hypotheses.

The foundation of the first two hypotheses explaining why red-banded males suffered increased aggression is that red bands functioned similarly to male epaulettes. Epaulettes appear to reliably signal social status (Peek 1972; Smith 1972; Morris 1975; Hansen and Rohwer 1986; Eckert and Weatherhead 1987b; Røskoft and Rohwer 1987). Badges that reliably signal social status should be beneficial to males if,

during interactions with other males, conflicts are resolved passively rather than by actually fighting (Rohwer 1982).

The reliability of badges of social status can only be maintained if there is a cost involved in cheating. According to the first hypothesis proposed above, red bands caused owners to signal at an intensity inconsistent with their competitive ability. As a result, other males tested red-banded owners whose true competitive ability was less than the competitiveness that they were displaying. Neighbours, which are familiar with the competitive ability of nearby owners from regularly interacting with them and from watching contests between neighbouring territory owners and intruders (Freeman 1987), should challenge males that they know are signalling at an escalated intensity inconsistent with their competitive ability. Not only could red bands have increased the size of the aggressive signal, red bands may also have increased the frequency that an aggressive signal was displayed by males. Owners could not conceal their red bands as they could their epaulettes. Assuming red bands functioned similarly to male epaulettes, red-banded males were continually giving an aggressive display and they may have appeared to have been signalling unreliably. Territorial male red-winged blackbirds do not continually display their epaulettes while on their territories (Nero 1956a,b). Thus, according to this hypothesis owners that are unable to cover their epaulettes and continually display an aggressive signal

should also be signalling unreliably similar to the red-banded males of chapter one.

Another result of continually signalling aggression is that males would appear to be aggressive in inappropriate situations (e.g. while trespassing on other males' territories). The second hypothesis I proposed to explain why red-banded males suffered increased aggression, suggests that red bands may have caused males to inappropriately signal aggression when they trespassed on neighbours' territories. Territorial male red-winged blackbirds frequently trespass on neighbours' territories. Owners may have to pass over the territories of neighbours when flying to nearby fields to feed, during female chases, or when chasing intruders from their own territories. Owners may also actively trespass to feed on neighbours' territories, to intrude and possibly take over the territories of neighbours, or to gain access to females that have settled on neighbours' territories. Male red-winged blackbirds normally conceal their epaulettes while foraging and when trespassing on other males' territories (Nero 1956a,b) by covering the badge with feathers the same colour as their body plumage. Owners expose their epaulettes during territorial and courtship displays (Nero 1956a,b). The proposed advantage of coverable badges comes from being able to conceal the badge when it is inappropriate to display the signal and to expose it when appropriate (Hansen and Rohwer 1986). The first and second hypotheses I proposed above, suggest that red bands were

detrimental to male red-winged blackbirds because males could not cover their red bands as they could their epaulettes.

The 'coverable badge hypothesis' (Hansen and Rohwer 1986) states that coverable badges should evolved when conspicuous badges function as signals of threat and territory ownership. Intruders (floaters) benefit from being able to switch easily from signalling submissiveness to signalling territory ownership when they acquire a territory. By contrast, badges that cannot be covered should evolve in species that normally flock in large numbers or if the composition of membership in the flock is unstable (Rohwer 1982). A key requirement is that the social status of individuals is stable within seasons, such that subordinates are rarely if ever capable of becoming dominant during one season (Hansen and Rohwer 1986). Under these conditions continual exposure of badges should be favoured because dominant individuals are recognized by subordinates even if they have not had prior contact with the dominant individuals, and subordinates avoid fighting with dominant individuals to gain access to resources (e.g. food) (Rohwer 1982).

To test whether the inability to conceal a naturally occurring coverable badge (i.e. epaulettes) negatively affects territorial male red-winged blackbirds, I clipped the feathers that cover owners' epaulettes. The first hypothesis predicts that males that are unable to cover their epaulettes should display aggression at an increased intensity that they cannot back-up during competitive interactions with other males. As

a result, other males (particularly neighbours) should initially be threatened by males that are continually displaying aggression. However, other males should eventually become familiar with the true competitive ability of the clipped males that are signalling unreliably by regularly interacting with them and from watching contests between clipped territory owners and intruders (Freeman 1987). Thus, other males should ultimately intrude more frequently on the territories belonging to clipped males and should be extremely persistent during competitive interactions with clipped males that are signalling unreliably. If signalling inappropriately was the reason for the detrimental effect of red bands in chapter one, then at least some males with their epaulette covers clipped should lose their territories.

The second hypothesis predicts that clipped males would be displaying an aggressive signal during inappropriate situations (e.g. while trespassing on neighbours' territories). Territorial males should vigorously attack clipped males that trespass on their territories. Thus, clipped males should be restricted in their ability to travel on or over neighbours' territories when foraging, chasing females, or defending their territories. According to this hypothesis, clipped males would be appropriately signalling aggression and territory ownership while on their own territories. Therefore, clipped males should not suffer increased aggression from other males while defending their territories.

Methods

I conducted this study in three cattail marshes (*Typha* sp.) near Portland, Ontario during the 1990 breeding season. Two of these marshes (Harlem and Mathews marshes) had never been used previously for research. Therefore, all males in these marshes were unbanded at the outset of the experiment. McTaggart marsh had been used the previous year in a banding study of male red-winged blackbirds (Chapter one). However, I conducted the experiment in a new area of McTaggart marsh where no males had been captured in the previous year.

Thirty, six, and four males were captured from Harlem, Mathews, and McTaggart marshes, respectively, between 31 March and 25 April, before females had settled on their territories. Captured territorial males were measured, given a unique colour band combination, assigned to a clipping treatment and released onto their territories. I used orange, yellow, green, blue, and white plastic bands for the band colour combinations. Red bands were not used because of the strong effect they had on male red-winged blackbird reproductive behaviour (Chapter one). I measured aspects of body and epaulette size as estimates of male competitive ability (Searcy 1979b; Eckert and Weatherhead 1987b). Body size was indexed by wing length measured (to the nearest mm) from the bend of the wing to the tip of the longest primary (Searcy 1979b), body weight (to the nearest g), and tarsus length (to the nearest 0.1 mm). Epaulette size was indexed by the length

of a male's epaulette measured as the distance from the bend of the wing to the furthest extent of yellow plumage (Searcy 1979b), and by the maximum width (perpendicular to the length) of the red plumage of the epaulette.

To test whether continually and/or inappropriately signalling aggression entails a cost to owners, I clipped the scapular feathers used by males to cover their epaulettes so that the epaulettes were continually exposed, on 20 experimental males. Clipping the scapular feathers caused approximately 3/4 of the area of the epaulettes to be continually exposed. On 20 control males I clipped an equivalent number of contour feathers from near the epaulette but not used to cover it. The control treatment did not produce any visible change in the appearance of control males. Each day during the capture period I entered one of the three marshes and randomly selected an area to trap territorial males. Males were alternately assigned a clipping treatment as they were captured. Thus, males were randomly assigned a clipping treatment with respect to all their other attributes. Both experimental and control males from the three marshes could interact with similar numbers of unbanded, clipped, and control neighbours immediately adjacent to their territories, as well as with floaters.

I estimated territory boundaries by noting the perches of displaying owners and locations of aggressive interactions between territorial males and plotting them on a map. I determined the fate of all first broods in territories of males of

both clipping treatments. Harem sizes were calculated as the minimum number of females needed to account for the nesting activity on a male's territory (Weatherhead and Robertson 1977). Nestlings were assumed to have fledged if they were present in the nest on the tenth day after hatching but absent on any following date.

I observed experimental and control males for 15 min periods four times during the breeding season to quantify the frequency and duration of aggressive interactions with other males. I also recorded the intensity and rate of male song displays on their territories. I could not rank the intensity of song spread displays on the basis of the amount of epaulette exposed by singing males (as per chapter one), since clipped males continually exposed their epaulettes. Therefore, I classified the intensity of song spread displays only using the body postures of singing males. I considered a display not to be a song spread when singing males' wings remained at their sides and their tails were not fanned. A low intensity song spread involved males slightly arching their wings out from their sides, and holding their tails down but not fanned. In a medium song spread the wings were arched out and down and the tail was slightly fanned. In a high intensity song spread, the feathers of the epaulette were ruffled, the wings fully arched out and down and the tail completely fanned.

Results

Clipped and control males had similar-sized bodies and badges. A discriminant function analysis was able to classify only 62.5 % of males as clipped or control using morphological measures (Discriminant Function Wilks' Lambda $\chi^2 = 2.41$, $P = 0.30$, Table 2-1). Thus, my method of assigning a clipping treatment to captured males resulted in there being no morphological differences between clipped and control males. Three clipped males lost their territories during the breeding season and five control males were unable to maintain their territories. Thus, clipping the feathers that cover epaulettes did not effect whether or not males lost their territories. Territories were taken over by a control neighbour in two of the eight cases of territory loss, shared by two clipped males once, shared by a clipped and a control male once, once taken over by a floater, and by males of unknown status in the other three cases. Thus, there was no obvious pattern to the status or treatment of males that took over owners' territories.

Intrusions by other males on experimental males' territories

Clipped and control males also did not differ in the frequency of intrusions on their territories. I observed 78 intrusions on clipped males' territories in 18 hrs 14 min of observation, and 82 intrusions on control males territories in 18 hrs 26 min of observation (χ^2 Goodness of fit = 0.10, $P = 0.75$). Neighbours intruded 14 times on clipped males' territories, and 24 times upon control males territories during my observations. Floaters intruded upon clipped males

Table 2-1 Discriminant function analysis of morphological differences between clipped and control males

Variables	Clipped		Control		Wilks' λ P		Entered at Step
	$N = 20$		$N = 20$				
	$\bar{X}$	SE	$\bar{X}$	SE			
Mass (g)	68.7	0.8	69.6	1.0			
Wing length (cm)	12.5	0.1	12.4	0.1			
Tarsus length (mm)	28.1	0.2	28.4	0.2			
Bill length (mm)	24.8	0.3	24.7	0.2			
Epaulette length (mm)	39.2	0.6	39.9	0.6	0.962	0.24	1
Epaulette width (mm)	42.0	0.4	41.2	0.7	0.935	0.30	2

Discriminant Function Wilks' Lambda $\chi^2 = 2.41$, DF = 2, $P = 0.30$

territories 28 times, and 25 times upon control males' territories. Thus, there was also no significant difference in the status of males that intruded upon clipped and control males territories ($\chi^2 = 2.88$, $P = 0.10$).

Although clipped and control males had similar numbers of intruders upon their territories, clipped males had to work harder to repel the intruders. Chases by males increased in duration as the season progressed ($r = 0.257$, $N = 182$, $P = 0.0003$). Controlling for the date on which the chase occurred by performing an ANCOVA with date as the covariate, clipped males were involved in significantly longer chases than control males or unbanded males (Table 2-2). The status of the intruder also affected the duration of chases on clipped and control males territories. Chases involving neighbours were significantly longer in duration on clipped males territories than on control males territories (Table 2-2). However, there was no significant difference in the duration of chases involving floaters on clipped and control males' territories (Table 2-2).

Since clipped males were involved in lengthier chases than control males, clipped males probably used more energy during chases and may have had less energy available to chase future intruders from their territories. Clipped and control males chased 68 and 77 intruders from their territories, respectively. There were only 10 occasions in which clipped males did not chase intruders from their territories, and 5 cases where control males did not chase intruders. Thus,

Table 2-2 Duration of chases with intruders of different status and females on clipped, control, and unbanded males territories.

ANCOVA Duration of chase (sec) with date (covariate)

	Unbanded			Clipped			Control		
	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N
All intruders	16.5	2.8	15	49.1	9.6	70	21.1	1.6	97

Date (Covariate) $F = 14.11$, $P < 0.001$

Treatment $F = 5.34$, $P = 0.006$

Explained $F = 8.26$, $P < 0.001$

ANOVA Duration of chase (sec) with females and intruders

	Unbanded			Clipped			Control			F	P
	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N		
Female chase	40.0	15.0	7	25.0	3.0	47	35.7	7.3	45	1.18	0.31

Status of Intruder	Clipped			Control			t	P
	$\bar{X}$	SE	N	$\bar{X}$	SE	N		
Neighbour	49.5	19.0	15	19.8	2.3	26	2.02	0.050
Floater	39.5	12.1	26	24.3	3.3	24	1.17	0.25
Unknown	59.9	19.6	27	20.7	2.8	43	2.47	0.02

clipped and control males were also just as likely to chase intruders from their territories ($\chi^2 = 2.13$, $P = 0.15$). Together these results suggest that clipped male were not signalling reliably. Consequently, intruders (particularly neighbours) were more persistent during chases with clipped males than during chases on control males territories. However, clipped males were able to cope with the increased aggression from intruders and were able to successfully defend their territories.

Experimental males trespassing on neighbours' territories

Clipped males that continually displayed an aggressive signal may have been signalling inappropriately when trespassing on neighbours' territories. Consequently, clipped males may have suffered increased aggression from their neighbours and have been restricted in their ability to trespass on or over territories of other males while foraging, defending their own territory, or chasing females. There were only three occasions when clipped males were observed on territories belonging to other males. In comparison, control males were observed 16 times on other males' territories. Thus, there was a significant difference between clipped and control males in the number of times they were seen trespassing (χ^2 Goodness of fit = 8.89, $P = 0.003$).

Clipped males did not spend all of their time defending territories. Clipped and control males frequently flew off their territories to feed in fields that surrounded the marshes. I used discriminant function analysis to see if I could reliably predict whether males belonged to clipped or control treatment

groups from behavioural measures. Discriminant function analysis showed that clipped males spent more time off their territories and gave medium song spread displays at a higher rate than control males (Table 2-3). Discriminant function analysis was able to correctly classify clipped and control males with 60.5 % accuracy using song rates and the time males spent foraging off their territories (Discriminant Function Wilks' Lambda $\chi^2 = 9.09$, $P = 0.028$, Figure 2-1).

The inability to cover epaulettes did affect males' behaviour when interacting with other males. However, the inability to cover badges did not seem to affect female choice or male behaviour when interacting with females. Unbanded, clipped, and control males were all seen chasing females during the breeding season. These chases were of similar length regardless of whether the male had been an unbanded, clipped, or control male (Table 2-2). Clipped and control males also attracted similar numbers of females to their territories at the same time in the breeding season, and fledged similar number of young (Table 2-4). Thus, clipped and control males appeared to have similar reproductive success.

Table 2-3 Discriminant function analysis of behavioural differences between clipped and control males

Variables	Clipped	Control			
	$N = 74$	$N = 73$	Entered		
	$\bar{X}$	$\bar{X}$	Wilks' λ	P	at Step
No song spread (#/900 s)	2.97	3.33			
Low intensity song					
spread (#/900 s)	4.86	5.11			
Medium intensity song					
spread (#/900 s)	9.56	6.59	0.939	0.028	1
High intensity song					
spread (#/900 s)	9.82	7.89			
Total call per 900 s	36.46	31.24	0.983	0.112	2
Off territory (s)	95.52	65.78	0.955	0.036	3

Discriminant Function Wilks' Lambda $\chi^2 = 9.09$, $DF = 3$, $P = 0.028$

Figure 2-1 Discriminant function scores for the behaviour of clipped (unshaded bars) and control males (solid bars) ($N = 147$). The groups were not significantly different in discriminant function scores ($\chi^2 = 9.09$, $DF = 3$, $P = 0.028$)

Table 2-4 **Fitness comparisons between clipped and control males.**

Variables	Clipped			Control			<i>t</i>	<i>P</i>
	$\bar{X}$	<i>SE</i>	<i>N</i>	$\bar{X}$	<i>SE</i>	<i>N</i>		
Harem size	2.3	0.5	17	2.6	0.4	15	-0.52	0.61
Fledglings								
per territory	3.7	1.0	20	4.0	0.8	20	-0.20	0.84
Date first								
egg laid	122.4	5.0	15	124.5	4.2	20	-1.40	0.17

Discussion

Although epaulettes function as signals of threat (Røskoft and Rohwer 1987) and territory ownership (Peek 1972; Smith 1972), territorial male red-winged blackbirds do not continually display their epaulettes (Nero 1956a,b). This suggests that there are costs involved for owners in inappropriately displaying their coverable epaulettes. My results support this hypothesis. Clipped males, being unable to cover their epaulettes, had to devote more time chasing intruders from their territories and were more restricted in their movements within the marshes than control males. Clipped males also spent more time off their territories, possibly feeding to replenish energy reserves used in lengthy chases, and they also increased the intensity of their displays compared to control males.

The major cost involved in continually exposing a coverable badge appears to be increased aggression from neighbouring males when owners, inappropriately displaying an aggressive signal, trespass on neighbours' territories. Hansen and Rohwer (1986) demonstrated that owners respond more aggressively toward intruders that signal aggressively while trespassing. Hansen and Rohwer (1986) presented mounted specimens with blackened, reduced, normal, and enlarged epaulettes to owner red-winged blackbirds. Owners responded more aggressively towards models with larger epaulettes than with smaller epaulettes. Clipped males in my study probably elicited similar aggressive responses from

owners as mounts with larger epaulettes did in Hansen and Rohwer's (1986) study. Most likely as a result of this increased aggression, clipped males avoided trespassing and were rarely seen on other males territories. Thus, clipped males were restricted in their ability to intrude upon and possibly usurp neighbours' territories, secretly gain access to neighbours' females, and/or resources (e.g. food), or just to fly over neighbours' territories on the way to and from feeding.

Unlike the results from the banding experiment of chapter one, the inability to conceal a coverable badge did not affect territorial male red-winged blackbirds' ability to maintain their territories in my clipping experiment. In chapter one I hypothesized that red bands functioned as epaulettes. However, unlike epaulettes, red bands were uncoverable. I suggested that red-banded males were inappropriately signalling competitive status by continually exposing an aggressive signal (i.e. red bands). As a result, red-banded males suffered increased aggression from other males which ultimately caused them to lose their territories. If this hypothesis is correct why did clipped males (which could not cover their epaulettes in this experiment) also not lose their territories?

The reliable badge hypothesis (Rohwer 1982) states that males should signal as aggressively as they can, provided that they can backup their signal of competitive ability during actual fights with other males. Males with too large a badge may signal too aggressively, such that other males continue to

test the reliability of their badges. Therefore, males that unreliably signal status should be attacked more by other males. This should happen most frequently in situations where neighbours, which are more familiar with nearby owners' competitive ability than floaters, test the honesty of owners signalling more aggression than they are capable backing up in fights (Freeman 1987).

Red-banded males with large epaulettes in my banding study of chapter one were probably signalling at an escalated intensity that was too aggressive, which caused them to be tested by neighbours and lose their territories. Although clipped males in my study were continually signalling aggressiveness, the size of their signal was unchanged. Thus, clipped males were displaying within their normal range of intensities while on their territories, albeit at the more aggressive end. As a result, neighbours did not intrude upon the territories of clipped males more frequently than upon control males' territories. However, during chases intruders (particularly intruding neighbours) were more persistent and aggressive in chases on clipped males' than control males' territories. Intruders should have a better estimate of an owner's true competitive ability when engaged in contests with that owner than by assessing the owner's competitive ability based solely on his badges. The initial aggressive signal of clipped owners (i.e. continual exposure of their red epaulettes) may not have matched their aggressiveness after being

invaded. Thus, intruders may have been more willing to fight an owner that had been signalling inappropriately.

The evidence I have presented here suggests that owners as well as floaters benefit by concealing their coverable badges when appropriate. Inappropriately displaying social status or aggressiveness can result in increased aggression from other males, particularly neighbours, when trespassing on their territories. These results may explain why red-banded males in the previous experiment suffered higher levels of aggression and suggest why those males lost their territories.

CHAPTER THREE

**The effects of coloured bands on
red-winged blackbird behaviour**

Introduction

In chapter one I showed that red bands (the same colour as male red-winged blackbird epaulettes) severely affected the ability of male red-winged blackbirds to maintain their territories, unlike black bands which had no noticeable effect on male behaviour. Coinciding with territory loss by red-banded males was increased aggression toward them, particularly by neighbouring males. I proposed three hypotheses that may explain why red-banded males suffered increased aggression. First, males given red bands may have been signalling at an escalated intensity that did not reliably reflect their competitive status. Second, red-banded males were unable to cover their bands and may have been signalling aggression during inappropriate situations (e.g. when trespassing on neighbours' territories). Third, red bands may have made males appear abnormal or unhealthy.

In chapter two I performed a clipping experiment to address the first two hypotheses explaining why red-banded males suffered increased aggression. An important component to both of these hypotheses is that red bands functioned similarly to epaulettes, but unlike epaulettes were uncoverable. Thus, I tested whether the inability to conceal coverable badges (i.e. epaulettes) negatively affected territory owners. Males that had their cover feathers clipped, and thus could not conceal their epaulettes, were restricted in their ability to trespass on territories of other males while foraging, defending their territories, or chasing females. Clipped males also

appeared to be signalling unreliably. As a result, intruders (particularly intruding neighbours) were more persistent during chases on clipped males' territories than on territories of control males. These results support the hypothesis that red-banded males in the first experiment were also inappropriately signalling aggression. Red-banded males probably suffered increased aggression when they trespassed on other males' territories.

Chapters one and two addressed whether the continual exposure of red bands or red epaulettes, respectively, was detrimental to male red-winged blackbirds. The presence of colours other than red on male red-winged blackbird bodies may also affect male reproductive behaviour. In this chapter I will test whether red and blue leg bands (colours that contrast with males' naturally black legs) cause males to appear abnormal and/or unhealthy to conspecifics. I will also extend the study to consider if the continual exposure of a red badge is detrimental in situations that are not directly related to reproduction (e.g. roosting and foraging).

Although males that had their feathers clipped in chapter two suffered increased aggression from other males, they were still able to maintain their territories. This contrasts with the result from chapter one in which red-banded males had great difficulty maintaining their territories. Factors other than the inability to conceal an aggressive signal may also have contributed to red-banded males suffering increased aggression from other males and eventually causing them to

lose their territories. For example, the presence of an unnatural marking may have affected the ability of red-banded males to defend their territories. Leg bands that contrast with the males' natural leg colour (black) could make male red-winged blackbirds appear abnormal or unhealthy to conspecifics. As a result, males could suffer increased aggression from other males and eventually cause them to lose their territories. This hypothesis predicts that territorial male red-winged blackbirds should respond equally aggressively to intruders with blue bands (not a naturally occurring colour on male red-winged blackbirds) or intruders with red bands (the same colour as males' epaulettes) and the response to intruders with red or blue bands should be more aggressive than to intruders with black bands. In this chapter I test the response of territorial male red-winged blackbirds to intruders given different coloured bands.

In this chapter I also test whether red bands are detrimental to male red-winged blackbirds when they forage together in groups. Red-winged blackbirds become gregarious by mid-July (after the breeding season is complete) and begin feeding in large flocks and roosting together at night (Weatherhead and Bider 1979). Male red-winged blackbirds normally conceal their epaulettes while feeding (Nero 1956a,b). However, observations of roosting red-winged blackbirds (Weatherhead and Hoysak 1984) indicated that males also display aggression in nonbreeding situations. Assuming that red bands function similarly to epaulettes, males given

uncoverable red bands would be continually displaying aggression at an intensity that they could not back-up during competitive interactions. According to this hypothesis, red bands should be detrimental to males when they forage in flocks. Red-banded males should suffer increased aggression from other males with which they are foraging. Alternatively, red bands may cause males to appear more threatening to other males. Thus, red-banded males may provide an advantage in that other males initially perceive red-banded males as dominant and avoid fighting with them in contests over food.

Methods

Model presentations

I conducted this experiment in three cattail marshes (*Typha* sp.), McTaggart, Mathews, and Harlem marshes, near Portland, Ontario from 26 April to 22 May, 1990. In this experiment I presented a male red-winged blackbird model given red, blue, or black leg bands to territorial male red-winged blackbirds and recorded how aggressively owners responded to the model. Blue bands were chosen because blue is not a naturally occurring color on male or female red-winged blackbirds and the blue bands did not match any of the colours of the vegetation in the marshes. It was assumed red-winged blackbirds could discern the blue bands from black and red bands. Approximately half of the owners ("naive" males) had never been previously exposed to a model red-winged blackbird and were not used in any of the other experiments I conducted during the 1989 or 1990 breeding season. The other half were males that I used in my clipping experiment of chapter two ("experienced" males). Experienced owners had previously been captured by presenting them unbanded, taxidermy models of red-winged blackbirds in decoy traps (Smith 1976) or near mist nets in conjunction with a play-back of male red-winged blackbird song. Since male red-winged blackbirds may respond less aggressively to models after their initial exposure (Hansen and Rohwer 1986), I compared the reaction of naive and experienced males to the red-, black-, and blue-banded model. I also compared the reaction of

clipped and control males to the red-, black-, and blue-banded model.

Aggressive territory owners can destroy taxidermy models in a matter of minutes (Rohwer 1978; pers. obser.). This can cause serious problems in keeping the stimulus the same when presenting the model to several males in succession. Therefore, I designed a model that was virtually attack proof. The model's body was made from black cotton material stuffed with cotton balls. Using velcro, I fastened a male red-winged blackbird wing with the epaulette fully exposed to either side of the cotton body. A male red-winged blackbird head covered with the same black cotton cloth as on the body so that only the bill was exposed was fastened with velcro to the body. Pairs of male red-winged blackbird legs given six blue, black, or red plastic leg bands could also be fastened with velcro to the body. Thus, the only feature of the model that varied when presented to owners was the colour of the models' leg bands.

Model presentations were conducted between 0600 to 0900 hours DST, the time when males were most active. I placed the model approximately in the centre of a male red-winged blackbird's territory while the owner was present, then moved 30-50 m away to observe the response. Five-minute time budgets were recorded immediately after placing the model on the territory. Male red-winged blackbird songs were not played during the model presentations since intruders

normally do not sing when trespassing on other males' territories (Hansen and Rohwer 1986).

I measured the following aspects of the owners' behaviour during the model presentations (after Rohwer 1978):

1) T 1st - the latency in seconds to the first time an owner reacted to the model (up to 300 sec). Reactions included flying closer to the model, or directing a song spread display at the model;

2) T HIT - the latency in seconds to the first time an owner struck the model (up to 300 sec);

3) N HITS - the number of times the owner struck the model;

4) 0-2 m - the amount of time in seconds an owner spent within two metres of the model;

5) >10 m - the amount of time in seconds an owner spent greater than 10 metres from the model;

6) Total SS - the total number of song spread displays directed by the owner towards the model;

7) The intensity of song spread displays given by the owner that were directed toward the model. I classified the intensity of song spread displays using the method described in chapter two. I totalled the number of high (SS4), medium (SS3), low (SS2), and non (SS1) song spread displays.

I only presented the model once to an owner. This minimized the possibility that owners would become familiar with the model and respond differently upon subsequent presentations. I randomly assigned whether an owner was

presented with the red-, blue-, or black-banded model. I usually performed 5-12 model presentations per morning. This normally resulted in all three band colours being presented each morning. Thus, potential variation in behavioural responses caused by weather or other factors were randomized.

Aviary Contests over food

To test whether red bands caused male red-winged blackbirds to unreliably signal social status while foraging in groups, I recorded the outcome of contests between captive red- and black-banded males over food. Altogether, 27 adult male red-winged blackbirds were captured from roosts or from their territories and placed in five groups. Fourteen of the males were caught from a roost located near Inverary, Ontario, approximately 25 km south of Queen's University Biological Station, on 25 April and 8 May, 1990. Males were caught from the roost by placing mist nets in the marsh before dusk and capturing birds as they flew into the roost at dusk. The remaining 13 males were caught from their territories in two marshes near Westport, Ontario using mist nets and decoy traps (Smith 1976), on 15 May and 5 June, 1990. All males were transported directly to an outdoor aviary constructed of wood and wire mesh at the biology station.

Males that were captured on the same day and from the same area or roost were placed together in an aviary compartment. Groups size ranged from 4 to 9 males per compartment. All the compartments were of equal size (3 x 2 x

1.5 m) in the aviary. Each compartment had several perches, two sources of fresh water, and a long tray filled with food (consisting of approximately 3 parts cracked corn, 2 parts millet, and 1 part Purina chick starter). Eckert and Weatherhead (1987b) established the design of the aviary and the procedure for the care of the birds.

The day after being captured, each male was given a unique colour band combination, a unique bleach marking and was measured. Males were given one blue, green, yellow, white, or orange plastic leg band and either five additional red plastic leg bands (the same colour as used in chapter one) or five additional black plastic leg bands. Males were alternately assigned red or black bands, so that every second male received red bands. This ensured that there was a similar proportion of red- and black-banded males in each compartment.

To facilitate in the identification of individuals on videotape (see below), I bleached approximately five cm of the end of three or four feathers on their tail and/or wing in unique combinations. Bleaching was done by rubbing a commercial hair dye and 30 % peroxide into the feathers until most of the feather pigment was removed. Bleached feathers were then thoroughly rinsed with water.

Body size and epaulette size are important in aggressive interactions between captive male red-winged blackbirds (Searcy 1979b; Eckert and Weatherhead 1987b). Therefore, I measured aspects of male morphology as estimates of their

competitive ability. Body size, body weight, and tarsus length were measured as described in chapter one. I also recorded bill length (to the nearest 0.1 mm) as a measure of the size of male weaponry and calculated body condition as weight divided by wing length cubed. Epaulette size was indexed by the length of a male's epaulette measured as the distance from the bend of the wing to the furthest extent of yellow plumage (Searcy 1979b), and by the maximum width (perpendicular to the length) of the red plumage of the epaulette.

Males were allowed to adjust to captivity for four days after being captured. After this four day adjustment period, videotapes were made of competitive interactions around a single food dish placed in each aviary compartment. The night before males were videotaped all food was removed from the aviary and the floor swept clean. The next morning (between 0800 and 0930 hours DST) a single food dish that was only accessible to one male at a time was placed in the center of the aviary compartment. The videotaping sessions lasted for approximately 70 min, after which time the large food tray was returned to the compartments.

Videotapes were made every second day until 10 interactions were recorded for each pair of males (dyads) in a single compartment. Competitive interactions at the food dish ranged from threats to all out attacks. I could usually determine the winner and loser of an interaction. I excluded any interaction where it was unclear whether a bird left the food dish voluntarily or in response to the approach of another

male. After videotaping was complete I totalled the number of wins and losses within dyads. The ratio of wins to losses for each dyad was tested if it significantly differed from random using Binomial tests. I calculated the relative size differences (body and epaulette size) between dominant and subordinate males by subtracting the morphological values of the male that lost the encounter from the morphological values of the male that were won in the contests over food. I then used these relative size differences to test whether there were any morphological differences between red-banded winners and red-banded losers from "mixed" dyads (i.e. red-banded male winning significantly more encounters than a black-banded male and red-banded male losing significantly more encounters than a black-banded rival, respectively).

The relative dominance of an individual was estimated by calculating the percentage of contests a male won. Dominant status was assigned to the male that won the highest percent of contest in each aviary compartment. I also recorded the time each male spent on the food dish. Males that spent the greatest amount of time feeding at the food dish in each compartment were assigned dominant status using this method. The relationships between aspects of the males' morphology and their dominance status were assessed using Spearman rank correlations of male characteristics with the percentage of encounters won and with the relative amount of time spent on the dish.

After videotaping was complete I reweighed the males to determine their rate of weight loss while in captivity and released them from the aviary. I had one male escape from Group IV on May 21 (after being in captivity for six days), and therefore could not calculate his weight loss. If I had videotaped a minimum of 10 interactions for dyads in which one member of the pair was the male that escaped, I included these dyads in analyses comparing win/loss ratios and morphological differences between red- and black-banded winners. The male that escaped was excluded from the Spearman rank correlations between dominance status of males (using proportion of time on dish and percent of encounters won) and aspects of male morphology. Three males also died in Group IV while in captivity (two on May 23 and one on May 27; after eight and 12 days of captivity, respectively). The males that died are presented but not included in the behavioural analyses.

Results

Model presentations

Prior experience did not effect the response of males to the model. Eighteen of 31 experienced males did not strike the model. Naive males failed to attack the model on 22 of 42 occasions ($\chi^2 = 0.23$, $P = 0.63$). There was also no significant difference between naive and experience males in how vigorously they responded to the model (Table 3-1). Clipped and control males used in the study described in chapter two were also just as likely to attack the model. Five of 15 clipped males failed to hit the model, and 8 of 16 control males did not attack the model ($\chi^2 = 0.88$, $P = 0.35$). The behaviour of clipped and control males was also similar when reacting the to model (Table 3-2). Since naive and experienced, and clipped and control males all behaved similarly when presented the model, I grouped all owners and compared their response to the red-, black-, or blue-banded model. Sixteen of 23 owners failed to strike the model given red bands, 11 of 25 owners did not hit the black model, and 13 of 25 owners did not strike the model given blue bands. Thus, territory owners were just as likely to attack the model when it was given red, black, or blue bands ($\chi^2 = 3.28$, $P = 0.20$).

Although the proportion of males that attacked the model with red, black, or blue bands was similar, there was a difference in how vigorously males responded to the red-, black- and blue-banded model. I used discriminant function analysis to see if I could predict whether males had been

Table 3-1 Comparison of the responses of naive and experienced owners to a model presentation (regardless of the colour of bands given to the model)

Variable	Naive (<i>N</i> = 42)		Experienced (<i>N</i> = 31)		<i>t</i>	<i>P</i>
	$\bar{X} \pm SE$		$\bar{X} \pm SE$			
N HITS	2.2 ± 0.6		2.9 ± 1.3		-0.57	0.57
T 1ST	35.0 ± 8.0		60.0 ± 10.7		-1.91	0.060
T HIT	227.7 ± 18.7		270.4 ± 22.3		-1.47	0.15
0-2 m	132.5 ± 19.3		126.8 ± 24.0		0.19	0.85
>10 m	51.4 ± 13.4		32.9 ± 11.6		1.00	0.32
Total SS	14.9 ± 1.5		16.4 ± 1.0		-0.79	0.43
SS1	0.4 ± 0.3		0.1 ± 0.05		0.93	0.36
SS2	0.4 ± 0.3		0.3 ± 0.1		0.20	0.84
SS3	1.1 ± 0.3		1.2 ± 0.3		-0.16	0.87
SS4	9.2 ± 1.3		10.7 ± 1.2		-0.81	0.42

Table 3-2 Comparison of the responses of clipped and control owners to a model presentation (regardless of the colour of bands given to the model)

Variable	Control (<i>N</i> = 16)	Clipped (<i>N</i> = 15)	<i>t</i>	<i>P</i>
	$\bar{X} \pm SE$	$\bar{X} \pm SE$		
N HITS	4.5 ± 2.4	1.2 ± 0.5	1.27	0.21
T 1ST	63.3 ± 16.1	56.5 ± 14.5	0.32	0.76
T HIT	258.8 ± 32.1	282.7 ± 31.6	-0.53	0.60
0-2 m	146.8 ± 34.7	105.5 ± 33.4	0.85	0.40
>10 m	11.5 ± 4.9	55.7 ± 22.3	-1.99	0.056
Total SS	16.9 ± 1.4	15.8 ± 1.6	0.51	0.61
SS1	0.0 ± 0.0	0.1 ± 0.1		
SS2	0.1 ± 0.1	0.5 ± 0.3	-1.63	0.11
SS3	1.1 ± 0.4	1.3 ± 0.5	-0.40	0.69
SS4	11.6 ± 1.7	9.7 ± 1.8	0.79	0.44

presented the red-, black-, or blue-banded model from their response to the model. A discriminant function analysis was able to correctly classify the response of owners to red, black, and blue bands with 53.4 % accuracy using song rates, location from the model, time to first response, time to first hit, and number of hits (Wilks' Lambda Function 1: $\chi^2 = 22.35$, $P = 0.03$ Figure 3-1a; Function 2 $\chi^2 = 8.67$, $P = 0.12$ Figure 3-1b). An important variable in the discriminant function was the time owners spent at various distances from the model with red, black, or blue bands. Owners spent more time at distances greater than 10 m when the model was given red bands than when the blue- or black-banded model was presented to the owners (Table 3-3). Thus, territory owners appeared to be more threatened by the model when it was given red leg bands than when the model had blue or black leg bands. Owners also gave more low intensity song spread displays, and took longer to strike the red-banded model than when the model had black or blue bands (Table 3-3). The model with black bands appeared to be the least threatening to owners. Owners spent more time within zero to two metres of the black-banded model, than when the model had red or blue bands (Table 3-3).

Contests over food

Red- and black-banded males had similar-sized bodies and badges. A discriminant function analysis was able to classify only 51.9 % of males as red or black using morphological measures ($\chi^2 = 1.102$, $P = 0.29$, Table 3-4).

Figure 3-1a Discriminant function scores for the response of owners to the red- (unshaded bars), black- (hatched bars), and blue-banded (solid bars) model ($N = 73$). The groups were significantly different ($\chi^2 = 22.35$, $P = 0.03$).

PERCENTAGES

DISCRIMINANT FUNCTION SCORES

Figure 3-1b Discriminant function scores for the response of owners to the red- (unshaded bars), black- (hatched bars), and blue-banded (solid bars) model ($N = 73$). The groups were not significantly different ($\chi^2 = 8.67$, $P = 0.12$).

PERCENTAGES

Table 3-3 Discriminant function analysis of behavioural differences of owners to a conspecific model that had red, black, and blue coloured bands during five minute activity budget recordings.

	Red	Black	Blue			
	<i>N</i> = 23	<i>N</i> = 25	<i>N</i> = 25			
Variable	$\bar{X}$	$\bar{X}$	$\bar{X}$	Wilks' λ	<i>P</i>	Entered at step
T 1st	42.57	56.16	37.84			
T HIT	274.61	230.52	234.60	0.718	0.034	6
N HITS	1.87	3.92	1.68			
0-2 m	105.43	172.32	110.56	0.814	0.028	3
>10 m	77.43	26.08	29.84	0.912	0.039	1
Total SS	14.83	14.32	17.16	0.740	0.026	5
SS1	0.70	0.00	0.08			
SS2	0.87	0.12	0.04	0.859	0.032	2
SS3	1.57	1.16	0.76	0.781	0.031	4
SS4	7.78	10.16	11.40			

Function 1 Wilks' Lambda $\chi^2 = 22.35$, *P* = 0.034

Function 2 Wilks' Lambda $\chi^2 = 8.67$, *P* = 0.12

Table 3-4 Morphological comparison between red- and black-banded males

	Red-banded	Black-banded
	(<i>N</i> = 14)	(<i>N</i> = 13)
	$\bar{X} \pm SE$	$\bar{X} \pm SE$
Tarsus length (mm)	28.36 $\pm$ 0.23	28.18 $\pm$ 0.24
Bill length (mm)	24.34 $\pm$ 0.23	24.28 $\pm$ 0.29
Wing length (cm)	12.29 $\pm$ 0.07	12.35 $\pm$ 0.08
Epaulette length (mm)	37.78 $\pm$ 0.42	38.09 $\pm$ 0.76
Epaulette width (mm)	39.42 $\pm$ 0.51	40.21 $\pm$ 0.75
Weight (g)	70.21 $\pm$ 1.17	68.58 $\pm$ 0.96

Thus, my method of assigning band colours to males resulted in there being no morphological differences between red- and black-banded males.

I recorded 2283 interactions between males around the food dish where a winner and loser could be identified (Group I: 547, Group II: 137, Group III: 274, Group IV: 963, Group V: 362). The data are summarized in Table 3-5 (a,b,c,d,e). If red-banded males were more threatening to black-banded males, red-banded males should have been dominant over black-banded males during interactions around the food dish. Alternatively, if red bands caused males to signal unreliably or inappropriately, red-banded males should have suffered increased aggression and been subordinate to black-banded males. I tested whether red-banded males were dominant or subordinate to black-banded males by restricting the analysis to the dyads in which a red-banded male interacted with a black-banded male (29 of the 48 total dyads). Red-banded males won over black-banded males 10 times and black-banded males won over red-banded males 9 times. In the remaining dyads neither male won significantly more interactions. Thus, it does not appear that the colour of bands a male was wearing greatly influenced his performance in contests over food.

Searcy (1979b) and Eckert and Weatherhead (1987b) demonstrated that male epaulette and body size are positively correlated with dominance status among captive male red-winged blackbirds. I was unable to perform rank correlation

Table 3-5 Winner-loser matrices for five groups of captive male red-winged blackbirds.

Table 3-5a Group I

		LOSER					
band colour ¹ :		B	B	R	B	R	R
male ² :		A	B	C	D	E	F
W	A	-	15	28	29	14	20
I	B	3	-	21	34	17	19
N	C	14	15	-	21	29	65
N	D	16	18	29	-	13	27
E	E	7	12	9	26	-	9
R	F	6	5	7	14	5	-

¹ Band colour: B = black-banded male; R = red-banded males

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

Table 3-5b Group II

		LOSER			
band colour:		R	B	B	R
male:		G	H	I	J

W					
I	G	-	50	12	11
N	H	1	-	9	18
N	I	3	9	-	14
E	J	1	10	0	-
R					

Table 3-5c Group III

		LOSER			
band colour:		B	R	R	B
male:		K	L	M	N

W					
I	K	-	41	59	69
N	L	2	-	25	24
N	M	3	5	-	24
E	N	4	1	17	-
R					

Table 3-5d **Group IV**

LOSER									
band colour:	B	R	R	R	B	R	R	B	B
male ¹ :	O	P	Q	R	S	T	U	V	W
fate ² :	R	R	R	R	R	E	D	D	D

	O	-	23	66	177	6	88	122	10	27
W	P	12	-	51	122	37	41	102	19	11
I	Q	10	25	-	50	15	19	37	4	6
N	R	18	47	33	-	26	31	69	4	9
N	S	4	21	13	6	-	7	11	0	1
E	T	1	1	5	8	2	-	4	0	0
R	U	10	28	32	68	16	27	-	30	3
	V	4	1	10	16	0	4	6	-	1
	W	1	2	3	3	0	2	3	1	-

¹ Males are ranked as described in Table 2-2a, except for those males that died in the aviary

² Fate: R = released from aviary; E = escaped from aviary;
D = died in aviary (not used in analyses)

Table 3-5e Group V

		LOSER			
band colour:		R	B	R	B
male:		X	Y	Z	AA

W					
I	X	-	50	149	20
N	Y	1	-	52	11
N	Z	21	37	-	14
E	AA	0	2	11	-
R					

analysis on each group separately due to the low number of males within groups. Using the data for all of the males together I tested whether the percent of encounters males won was correlated with aspects of the males' body or epaulette size and the proportion of time males spent on the dish (actual time male was on dish / total time the group to which the male belonged was videotaped). The proportion of time males spent on the dish was significantly correlated with the percent of encounters a male won (Spearman rank correlation $r = 0.395$, $P = 0.03$). Therefore, dominant males won a greater percent of encounters and spent more time on the dish foraging. Dominance status was not correlated with any morphological characters of the males. Spearman rank correlation coefficients were weak and non-significant for all aspects of the males' morphology (Table 3-6).

These results suggest that the outcome of competitive interactions was not influenced by the relative size of the two contestants nor by the colour of their bands. Although body size and band colour separately could not explain why certain males were dominant over other individuals during contests at the food dish, an interaction between these two factors might account for differences in the competitive ability of males. For example, red-banded males with large epaulettes may be less successful during encounters with other males than black-banded males with large epaulettes, and red-banded males with small epaulettes may be more competitive than than black-banded males with small epaulettes. If this were the

Table 3-6 Spearman rank correlations¹ between aspects of male morphology and dominance status. Dominance status measured as percent encounter won (A), and measured by the proportion of time spent on the food dish (B). (one-tailed test), $N = 23$

Wing length	Epaulette length	Epaulette width	Weight	Body condition	Tarsus length	Bill length
(A) +0.258	+0.186	+0.169	+0.002	-0.163	+0.289	-0.136
(B) +0.144	+0.085	-0.027	+0.217	+0.126	+0.144	+0.027

¹ None of the coefficients are significant at $P = 0.05$; all P 's > 0.10

case then the correlation between epaulette size and dominance status would disappear if band colour is not taken into consideration, and overall, neither red- nor black-banded males should win a greater number of contests. I compared the morphology of dominant red-banded males (red-banded male won significantly more encounters than his red- and black-banded opponents) and dominant black-banded males (black-banded male won significantly more encounters than his red- and black-banded rivals). There was no significant difference in the relative body and epaulette size differences between dominant red-banded males and their opponents and dominant black-banded males and their rivals. A comparison between dyads where a red-banded male was dominant and dyads where a black-banded male was the victor revealed that red-banded males that won against black-banded males lost relatively more weight than their rivals, whereas red-banded males that won against other red-banded males and victorious black-banded males tended to lose relatively less weight than their opponents (Table 3-7).

Restricting this analysis to only mixed dyads (red-banded male versus black-banded male) showed that red-banded males that won against black-banded males tended to have relatively longer epaulettes and shorter bills than their opponents, whereas red-banded males that lost against black-banded males tended to have relatively shorter epaulettes and longer bills than their opponents (Table 3-8). However, the relative size differences between red-banded winners and

Table 3-7 A comparison of the relative size difference between red-banded males that were victorious over red- and black-banded rivals and black-banded males that won in contests against red- and black-banded opponents

Winner	Red-banded		Black-banded		F	P
Opponent	Red	Black	Red	Black		
	(N =10)	(N =10)	N = 9)	(N = 5)		
	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$		

Variables						
Epaulette length (mm)	+1.40±0.75	+0.62±0.65	+1.40±1.02	+1.06±1.40	0.20	0.90
Epaulette width (mm)	+0.02±0.97	-2.33±0.96	+0.19±1.13	+0.96±1.68	1.46	0.25
Wing length (cm)	-0.01±0.11	-0.10±0.16	+0.16±0.09	-0.18±0.21	0.95	0.43
Tarsus length (mm)	-0.37±0.40	-0.21±0.59	+0.02±0.25	-0.28±0.58	0.14	0.94
Bill length (mm)	-0.34±0.29	-0.49±0.30	-0.17±0.48	-0.78±0.53	0.36	0.79
Weight (g)	+2.10±1.45	+2.35±1.46	-0.44±1.61	-2.90±1.89	1.48	0.24
Condition (g/cm ³)	+0.01±0.10	+0.25±0.13	-0.08±0.09	-0.002±0.14	2.49	0.08
Weight loss (g/day)	-0.09±0.10	+0.24±0.09	-0.12±0.08	-0.08±0.19	2.89	0.054

Table 3-8 Comparison of the relative size difference between red-banded males that won and that lost in mixed dyads.

Variable	Red-banded winners		Red-banded losers		<i>t</i>	<i>P</i>
	<i>N</i>	$\bar{X} \pm SE$	<i>N</i>	$\bar{X} \pm SE$		
Epaulette length (mm)	10	+0.62 $\pm$ 0.65	9	-1.40 $\pm$ 1.02	1.71	0.11
Epaulette width (mm)	10	-2.33 $\pm$ 0.96	9	-0.19 $\pm$ 1.13	-1.46	0.16
Wing length (cm)	10	-0.10 $\pm$ 0.16	9	-0.16 $\pm$ 0.09	0.29	0.77
Tarsus length (mm)	10	-0.21 $\pm$ 0.59	9	-0.02 $\pm$ 0.25	-0.28	0.78
Bill length (mm)	10	-0.49 $\pm$ 0.30	9	+0.17 $\pm$ 0.48	-1.19	0.25
Condition ¹ (g/cm ³)	10	+0.25 $\pm$ 0.13	9	+0.08 $\pm$ 0.09	1.04	0.31
Weight (g)	10	+2.35 $\pm$ 1.46	9	+0.44 $\pm$ 1.61	0.88	0.39
Weight loss ² (g/day)	10	+0.24 $\pm$ 0.07	8	+0.12 $\pm$ 0.08	0.94	0.36

¹ Weight loss equals the weight of the male when first captured minus the weight of the male when released divided by the number of days held in captivity

² Condition equals the weight of the male divided by its wing length cubed

their black-banded opponents and red-banded losers and their black-banded rivals was not significantly different for any of the morphological variables (Table 3-8).

Discussion

The results from the model presentation do not support the third hypothesis proposed above (i.e. that coloured bands make males appear abnormal and/or unhealthy). Males did not respond the same to the model presentation when the model was given red and blue bands. Instead, owners appeared to be more threatened by the red-banded model than when the model was given blue or black bands. The results from both the model presentation experiment and the aviary study are consistent with the findings from the first two chapters. Uncoverable red bands given to male red-winged blackbirds seem to interact with the males' epaulettes causing males to signal more aggressively and signal combativeness during inappropriate situations (e.g. while trespassing on other males' territories). In the model presentation experiment, red bands appeared to make the model more threatening to territorial male red-winged blackbirds. Owners spent more time at distances greater than 10 m and displayed at lower intensities when the model was given red bands, than when the model had blue, or black bands. Red bands probably increased the intensity of the models' aggressive display (exposure of epaulettes and red bands combined) causing the red-banded model to be more threatening to owners than the black-, or blue-banded model.

If larger badges are more threatening to other males why do floaters not aggressively display when entering occupied territories? Hansen and Rohwer (1986) demonstrated that

models that had epaulettes that were double their normal size were attacked more vigorously by owners than models with normal-sized epaulettes. A difference between Hansen and Rohwer's (1986) study and my model presentation study that may possibly account for the disparity in responses of owners to models displaying an overly aggressive signal, is the duration that owners' aggressive behaviour was recorded. In my study, I only recorded owners' behaviour for the five minutes immediately following setting the model on males' territories. Hansen and Rohwer (1986) started their observations when they had moved to their observation post (40-60 m from the male's territory) or when the male first flew at the model and observed the male's behaviour for a total of 10 minutes. Owners may be initially threatened by intruders that signal aggressively upon entering the owner's territory. If owners are unfamiliar with intruders, owners would be wise to initially treat aggressive males with caution. However, after a brief time assessing intruders, owners should attack and chase intruders that are not signalling reliably from their territories. During my five minutes of observation per male, owners may have spent most of this time assessing the red-banded models competitive ability. If I had recorded owners' behaviour towards the model for another five minutes I might have had results similar to Hansen and Rohwer (1986), in that owners may have vigorously attacked the red-banded model that was signalling inappropriately and unreliably.

While in the aviary, victorious red-banded males lost relatively more weight than their black-banded rivals, whereas victorious black-banded males generally lost less weight than their red-banded opponents. Males with uncoverable red bands may have incited increased aggression from other males. Consequently, red-banded males may have been involved in more fights with other males and had to use more of their energy reserves than black-banded males. Red-banded males may have incited increased aggression from other males if they were unable to back up their signal of competitive ability during aggressive interactions. During the four day adjustment period, males in this aviary experiment were allowed to interact and assess one another's competitive ability. Both red- and black-banded males may have perceived red-banded males to be signalling at an increased intensity that did not reliably reflect the red-banded males actual competitive ability.

Red bands do appear to be costly to male red-winged blackbirds. Red bands most likely caused males to signal more aggressively than they could back-up during competitive interactions and caused males to signal aggression during inappropriate situations. Consequently, red-banded males suffered increased aggression from other males. By adjusting the number of red bands given to male red-winged blackbirds researchers can easily manipulate the size of male red-winged blackbird badges and the aggressiveness of their displays, thus

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providing a simple technique for studying sexual selection questions in red-winged blackbirds.

List of Conclusions

CHAPTER ONE

- 1) Over half the red-banded males lost their territories while black-banded males retained their territories. Among red-banded males those that lost their territories had larger epaulettes and were in poorer condition than those retaining territories.
- 2) Red-banded males suffered higher intrusion rates, particularly by neighbours, than black-banded males. Red-banded males also had to work harder than black-banded males to repel intruders.
- 3) Half of the red-banded males and half of the black-banded males returned to the marsh the following breeding season. Therefore, the colour of bands given to the males had no effect on their overwinter survival.

Interpretation

Three probable explanations for these results were that red leg bands (the same colour as epaulettes): 1) caused males to signal aggression during inappropriate situations (e.g. while trespassing on the territories of other males), 2) increased the intensity of males' aggressive signal to such an extent that red-banded males could no longer back-up their display during

competitive interactions, 3) caused males to appear abnormal or unhealthy and thus of lower competitive status.

CHAPTER TWO

- 1) Three clipped males lost their territories and five control males were unable to maintain their territories. Thus, clipping the feathers that cover males' epaulettes did not effect whether or not males lost their territories.
- 2) Clipped and control males did not differ in the frequency of intrusions on their territories. However, clipped males were involved in lengthier chases on their territories than control males.
- 3) Clipped males were rarely observed trespassing on neighbours' territories, unlike control males that frequently trespassed. This suggests that clipped males may have suffered increased aggression from their neighbours, and were less 'willing' to trespass than control males.
- 4) The inability to cover epaulettes did not effect male behaviour when interacting with females.

Interpretation

These results suggest owners benefit by being able to cover their epaulettes when it is inappropriate to display an

aggressive signal. Other males, particularly other territory owners, may vigorously attack owners that signal aggression during inappropriate situations.

Clipped males also appeared to be signalling unreliably. Thus, males that continually expose their epaulettes may not be able to back-up their overly aggressive display of combativeness during actual contests with other males. These results support both explanations (1) and (2) above.

CHAPTER THREE

- 1) Owners in the model presentation experiment responded equally aggressively to the black- and blue-banded models, but spent more time at distances greater than 10 m and displayed at lower intensities when the model was given red bands. Thus, red bands appeared to make the model initially more threatening to territorial male red-winged blackbirds.
- 2) Red-banded males lost relatively more weight than their opponents. This result indicates that red bands can also have effects on male behaviour in nonbreeding situations.

Interpretation

The results from the model presentation experiment do not support the hypotheses that red bands caused males in the first experiment to appear unhealthy or abnormal to conspecifics.

Red bands in the aviary experiment probably caused males to signal at an intensity that was too high for them to back up in competitive interactions with other males.

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