

## Colour bands, combs and coverable badges in willow ptarmigan

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**Abstract.** Willow ptarmigan, *Lagopus lagopus*, possess red supra-orbital combs. If this secondary sexual structure is important in attracting mates or in male–male competition, then colour banding males with red or orange bands (RO) could influence their pairing and reproductive success, survival and the amount of aggression directed towards them. Males with RO bands did not have more mates than those without RO bands, nor did males unbanded in year  $x$  improve their pairing success in year  $x+1$  when they were given RO bands. In a female removal experiment, males with RO bands did not have more females settling on their territories than males with other band colours. Number of chicks fledged from successful nests and annual survival did not differ for RO and non-RO males. Monogamous and polygynous males had similar comb areas, which were larger than the combs of unmated males. When pairing status was controlled, comb area was not related to annual survival or number of chicks fledged. Males with RO bands did not have larger combs than non-RO males. Area of comb was correlated with territory size in years of high breeding density, but not in years of low breeding density. Radiotagged non-territorial males did not preferentially intrude upon the territories of males with RO bands and song rates, number of border disputes, mean length of border disputes, and territorial intrusion rates did not differ significantly for RO and non-RO males. These results suggest that colour-banding willow ptarmigan with red colour bands does not have a negative or positive effect on reproductive success or survival, and thus the data do not support the coverable badge hypothesis.

Since the results of Burley (1981, 1985, 1986) and Burley et al. (1982) on the effects of colour bands on mate choice, reproductive success, and survival in zebra finches, *Taeniopygia guttata*, there have been a number of studies on birds both in captivity and the wild attempting to evaluate the impact of colour bands. Results have varied, some showing no effects of colour bands (e.g. Watt 1982; Ratcliffe & Boag 1987; Beletsky & Orians 1989) and others demonstrating effects (Brodsky 1988; Hagan & Reed 1988; Metz & Weatherhead 1991). The colour of the bands that influence mate choice, for example, are similar to the colour of secondary sexual characters (ornaments) used in mate choice in the species. Most studies, however, have examined the influence of red colour bands. Red colour bands are hypothesized to have three major effects on birds that have red ornaments. First, red colour bands are thought to emphasize red ornaments used by females to assess male quality, thus enhancing male attractiveness (e.g.

Burley et al. 1982; Brodsky 1988). Second, females mated to males with red colour bands are thought to increase their parental investment, thus increasing the fledging success of males with red bands (Burley 1986). Third, in species that have 'coverable badges', males with red bands cannot completely cover their badges and accordingly may be subject to increased aggression from conspecifics (coverable badge hypothesis). For example, in the red-cockaded woodpecker, *Picoides borealis*, red bands mimic the red cockade that is erected during intraspecific aggressive interactions. Red bands cannot be hidden and thus their bearers suffer more aggressive attacks, resulting in a decline in parental care and fledging success (Hagan & Reed 1988). In red-winged blackbirds, *Agelaius phoeniceus*, increased attacks on red-banded territorial males may lead to a loss of territory (Metz & Weatherhead 1991).

Male grouse (Tetraoninae) possess supra-orbital combs that are erected during male–male competition and courtship. The comb can be retracted and mostly hidden from view and thus could be a coverable badge. In some gallinaceous

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birds, comb size is thought to be a character used by females in mate choice (e.g. Brodsky 1988; Zuk et al. 1990). Comb size is controlled by testosterone level in the plasma (Gjesdal 1977; Stokkan & Sharp 1980; Hannon & Wingfield 1990) and thus may be an 'honest signal' of male aggression. Hence, banding males with red colour bands could enhance their ability to attract females or increase the amount of aggression directed towards them by conspecifics.

Currently the information available regarding effects of colour bands in grouse is confusing. Two previous papers on the influence of red colour bands on pairing success in ptarmigan (*Lagopus*) came to opposite conclusions. In the first, Brodsky (1988) reported that in rock ptarmigan, *L. mutus*, comb size of males was positively correlated with potential mating success in 1 of 2 years and that in 1 year males with red/orange colour bands had more mates than males that did not have red/orange bands. In addition, males with red/orange bands increased their pairing success from one year to the next. Tomlinson (1988) interpreted this paper as showing that females used 'non-fussy preferences' for female choice generalizing from combs to colour bands. More recently, Holder & Montgomerie (1993), working on the same population as Brodsky did, discounted her findings. They found no relationship between red/orange colour bands and pairing success. However, they claimed that males with red/orange bands received more aggressive intrusions on their territories than males without red/orange bands, a result consistent with the coverable badge hypothesis.

Hannon has been conducting long-term studies on population dynamics, life-history traits and mating system on a colour-banded population of willow ptarmigan since 1979 (e.g. Hannon 1983, 1984; Martin et al. 1989; Hannon & Martin 1992). The results from the rock ptarmigan studies prompted us to examine whether red/orange colour bands and comb size influenced pairing success, reproductive success, survival and number of territorial intrusions in the willow ptarmigan. In this paper we report relationships between red/orange bands and comb size and pairing status (polygynous, monogamous, unmated), fledging success and survival of males. We also removed females as they settled on the territories of an array of males on contiguous territories to determine whether band colour affects the number

of females that settle on a male's territory. Finally we report results from time-budget analysis of territorial males and radiotelemetry studies of non-territorial males that examine whether males banded with red/orange colour bands receive more territorial intrusions than males banded with other colours.

## METHODS

### Study Area, Capture, Banding and Territory Plotting

We conducted the study in the Chilkat Pass area of northwestern British Columbia (59°50'N, 136°30'W) in subalpine tundra and data for this paper were collected from 1980 to 1981 and 1984 to 1992. The study area is described in detail in Weeden (1960) and Mossop (1988). We captured most unbanded males in ground nets or nooses (Hannon 1983) soon after their arrival on the study area in April and May and prior to the settlement of females on territories. We categorized males that were captured after females had chosen mates as unbanded for the purposes of this paper. We captured and colour banded females soon after their arrival on the area, and from 1985 to 1988 fitted most with radio transmitters to facilitate location of nests and broods (see Schieck 1988 for details of radiotelemetry).

We gave birds individual combinations of three coloured plastic and one aluminium (silver) leg bands, two per leg. The plastic was 0.09 mm thick C-Darvic (King's Plastic Ltd, Bristol, U.K.), which we cut and rolled into bands. Bands were 7.5 mm high and appeared 14 mm wide when viewed from the front of the bird. The colours were (with numbers from the Naturalist's colour guide (Smithe 1975) in parentheses): red (12), orange (17), yellow (18), dark green (62), light green (162D), blue (69), and black (89). Similar to Brodsky (1988), we categorized any bird having red or orange bands as being a 'red' bird (hereafter called an RO bird) and those with other colour combinations as being 'non-red' birds (hereafter called non-RO). Field workers chose band combinations from a list of all possible unused combinations prior to going into the field each week. They attempted to pick colour combinations that were quite variable (i.e. avoided choosing a group of similar combinations). Combinations were then assigned to birds as they were

captured by working down the field list. Although we avoided banding neighbouring birds with similar combinations to prevent confusion during censuses, the colours received by each male were likely close to being randomly assigned.

At capture we measured the length and height of the comb to the closest mm and we multiplied length and height to give an index of comb area. Combs were scarlet (No. 14, Smithe 1975). Comb measurements were only used for birds captured before the beginning of incubation (approximately 15 June) as comb area decreased after that (Hannon & Wingfield 1990). We classified birds as adults or yearlings (hatched the previous summer) based on the pigmentation of their primaries (Bergerud et al. 1963).

We plotted territories of males in late April and May by marking on scale maps of the area sightings of males, locations of all territorial calling, boundary disputes and locations where males turned back when walking away from an observer (Hannon 1984). Plotting was facilitated by a permanent grid of stakes on the ground spaced 100 m apart throughout the study area.

### Pairing Status, Reproductive Success and Survival

We classified the pairing status of males as monogamous, polygynous (usually two females, but occasionally three), or unpaired territorial. We determined the pairing status of males by searching their territories for hens using pointing dogs (1980, 1981) or a combination of dogs and radiotelemetry (1985–1988). Searches were made at least once every fourth day and usually every second day. A male was classified as monogamous if he was consistently observed prior to laying with the same single hen and/or that hen nested on his territory. A polygynous male was consistently seen with two or more of the same hens prior to laying and/or these hens nested on his territory. Unmated males were not consistently seen with the same hen and no hens nested on their territories. Occasionally a female was depredated prior to nesting but she was classed as being paired to a male if she was seen with him at least three times prior to her death.

We investigated several different possible effects of band colour on pairing status. First, we examined whether RO males were likely to have more mates than were non-RO males, and we considered whether RO males were more likely

than were non-RO males to increase the number of females they attracted from one year to the next. Finally, we considered the effect of RO bands on the number of females that settled in a removal experiment (see below).

We used the number of chicks fledged/male from successful nests (i.e. those that hatched at least one young) as our measure of reproductive success. Clutch predation can be very high in this population and appears to be stochastic (Schieck 1988), thus, depredated clutches were not included. The number of chicks fledged was the number of flying chicks observed 15–20 days after hatching. We located broods with the help of pointing dogs and/or radiotelemetry and made a thorough search of a 50 m radius around the hen to count all flying chicks. Males were said to have survived the breeding season and winter if they returned to the study area in a subsequent year. Only 3.5% of males switch more than one territory away between years (Schieck & Hannon 1989), and thus return rates are a good estimate of survival.

### Removal of Hens from Territories of Males

If red colour bands are attractive to females, males with RO bands should have more females settle on their territories. This was tested by removing females sequentially every 2–3 days as they settled on the territories of 15 males from 12 May to 4 June 1980 on one part of the study area. We counted the number of females that settled with each male. We assumed that a female had settled with a male if she was accompanied by the male and did not fly off his territory when approached. This experiment was originally conducted to determine whether surplus females were present in the area (Hannon 1983), however, the design is appropriate for testing whether RO males are more attractive to females than are non-RO males.

### Test of the Coverable Badge Hypothesis

The coverable badge hypothesis states that males with RO bands cannot cover their badges completely, and thus incur higher intrusion rates from other males. We used focal-animal sampling to observe 34 territorial males (five in 1988 and 29 in 1991) between 20 April and 17 May, a period of high territorial activity. Each male was observed

for four to seven periods, with each period lasting about 45–60 min. The time that a bird was out of sight during an observation period was subtracted from the time watched. We recorded the number of rattles ('song on the ground'; Watson & Jenkins 1964) and aerial beks ('song in flight'; Watson & Jenkins 1964), the number and length of border disputes, and the number of intruders onto the territory for each observation period. Aerial beks and rattles are territorial advertisement calls (Watson & Jenkins 1964). Rattles given during border disputes were not included in the total number of rattles. Chases were not frequent enough to analyse. If the coverable badge hypothesis is true we would expect RO males to have higher numbers of intruders, more border disputes and longer border disputes than non-RO males. We first had to test whether the calling rates of RO and non-RO males were similar because the amount of advertisement could influence intrusion rates, irrespective of the colour of bands.

From 1984 to 1991 we radio-tagged 21 unpaired males and followed their movements throughout May and June (four in 1984, four in 1988, two in 1989, 11 in 1991). We attempted to locate each male at least twice per week. For each sighting, we recorded the position of the male and the identity of the owner of the territory upon which the unpaired male was intruding. When unpaired males were within 10 m of the territorial boundary, we classified them as being on the boundary and did not assign a territory owner. If males with RO colour bands were more likely to be intruded upon, we expected that sightings of unpaired males would occur more frequently on the territories of RO males than would be expected based on the ratio of RO males to non-RO males on the study area in that year.

### Statistical Analysis

Most contingency analyses were done using a *G*-test with William's correction; however, where cell sizes were less than 5, we used the *G*-randomization test ( $G_{\text{ran}}$ ) (Sokal & Rohlf 1981). Multiway contingency tables were analysed using the log-linear hierarchical model from the 'Number Cruncher Statistical System' package. Our null hypothesis was that band colour and comb size had no effect on life-history variables or behaviour; our alternative hypothesis was that RO colour bands and larger combs increased

**Table 1.** Number of adult and yearling willow ptarmigan assigned band combinations with red/orange (RO) and no red/orange (non-RO) over 6 years\*

	Age	RO	Non-RO
1980	Adult	5	4
	Yearling	8	1
1981	Adult	13	3
	Yearling	9	2
1985	Adult	28	12
	Yearling	26	8
1986	Adult	54	20
	Yearling	16	8
1987	Adult	34	17
	Yearling	11	4
1988	Adult	28	11
	Yearling	1	2

\*1984 was excluded from the analysis because a low proportion of birds was banded prior to females settling.

pairing and reproductive success and survival, and increased intruder pressure. Thus, statistical tests were one-way, where applicable. We used power analysis (Cohen 1977) on all parametric and contingency analyses to determine the power of our tests to detect the observed effect size and a range of effect sizes from small to large. We used the definitions of small, medium and large effect sizes given in Cohen (1977). We increased the power of our tests by setting the probability of rejecting a null hypothesis to  $\alpha=0.10$  (Cohen 1977).

## RESULTS

### Distribution of RO Colour Bands over Years and Age Classes

The proportion of males that become polygynous varies over years (Hannon & Martin 1992) and adult males are more likely than yearlings to become polygynous (S. J. Hannon, unpublished data). Thus, we classified adults and yearlings as having RO or non-RO bands for each year (Table 1) and ran a hierarchical log-linear model to look for interactions between band colour and age or year. There was a significant age  $\times$  year interaction; but no interaction of colour bands with year or age. Thus, no year had a disproportionate amount of RO bands in an age class, so we combined data from different years in the analyses.

Table II. Percentage of polygynous, monogamous and unpaired males that had red/orange (RO) bands

	% RO	N
<b>All banded males</b>		
Polygynous	65.9	41
Monogamous	71.9	239
Unpaired	75.6	45
<b>Available males*</b>		
Polygynous	62.5	16
Monogamous	73.1	134
Unpaired	75.5	45
<b>Males on large territories†</b>		
Polygynous	78.2	23
Monogamous	74.4	94

\*Males available to be mated (males whose previous partner did not return or new males).

†Males on territories larger than 4.5 ha (1985–1988 only).

### RO Colour Bands and Pairing Status

If males with RO bands are more attractive to females, then a higher proportion of polygynous males should have RO bands, and unmated males should have the lowest proportion of RO bands. When all males were included in the analysis, the proportion of males with RO bands did not differ among the three groups (Table II;  $G=0.99$ , effect size  $w=0.06$ , power=0.28  $df=2$ ,  $N=325$ ,  $P=0.61$ ). Although this test had fairly low power to detect this very low effect size, it has very high power to detect medium and large effect sizes (power=0.99). Some of these males, however, were paired with the same females they had paired with the previous year. Females have a strong tendency to return to their former mate in subsequent springs (Schieck & Hannon 1989). This could confound the analysis because males may have paired the previous year while unbanded, or their experienced mate of the present year could prevent other females from settling. Therefore, we restricted the analysis to only those males whose mates of the previous year did not return or males that were new to the area. Again, there was no difference in the distribution of colour bands among the three groups of males (Table II;  $G=0.96$ , effect size  $w=0.07$ , power=0.23,  $df=2$ ,  $N=195$ ,  $P=0.62$ ). As above, this test had very high power to detect medium and large effect sizes (power=0.99). Finally, Hannon (1984) has shown that only males on the largest territories become

Table III. Number of male willow ptarmigan unbanded in year  $x$  that increased, decreased or had the same pairing status in year  $x+1$  after receiving either RO or non-RO bands

	Increase	Decrease	Same	N
RO	10	3	18	31
Non-RO	2	0	8	10

polygynous. Therefore, we restricted the next analysis to only males that defended territories equal to or larger than 4.5 ha (90% of all polygynous males had territories larger than this; S. J. Hannon, unpublished data). We only included data from 1985 to 1988 because breeding density did not vary over these years (densities were higher in 1980 and 1981) and because sample sizes for territories were too low for 1980 and 1981. Unmated territorial males were excluded from this analysis as only five had territories larger than 4.5 ha. There was no significant difference in the proportion of polygynous and monogamous males that had RO colour bands (Table II;  $G=0.14$ , effect size  $w=0.04$ , power=0.12,  $df=1$ ,  $N=117$ ,  $P=0.71$ ). Again this test had high power to detect medium and large effect sizes (power=0.94 and 0.99, respectively).

### Change in Pairing Status of Unbanded Males that Received RO Bands

There were 38 males that were unbanded in year  $x$  when females settled but were banded prior to females settling in year  $x+1$ . We classified them as increasing, decreasing or remaining at the same status (i.e. an increase in status represented a change from unmated to mated or from monogamous to polygynous). If RO bands are attractive to females we would predict that males receiving RO bands should increase their status more frequently than males having no RO bands. This was not the case (Table III; 1000 iterations,  $G_{\text{ran}}=2.64$ , effect size  $w=0.22$ , power=0.33,  $df=2$ ,  $N=41$ ,  $P=0.34$ ). This test had moderate power to detect medium effect sizes (power=0.50) and high power to detect large effect sizes (power=0.89).

### RO Bands, Comb Size and the Number of Females Settling in a Removal Experiment

The age structure of RO and non-RO males in the removal experiment was similar (comparing %

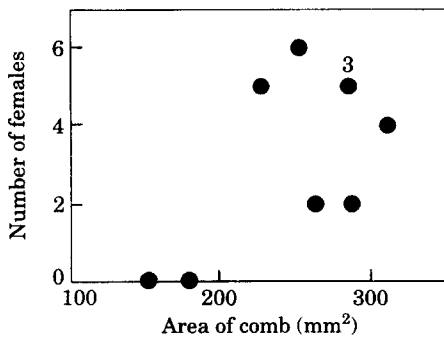


Figure 1. Number of females settling on the territories of males with different comb areas.

yearlings between groups,  $G_{\text{ran}}=0.54$ ,  $P=0.61$ ), and thus female selection of males based on age should not influence the experiment. RO and non-RO males also did not differ in the size of their territories (Mann-Whitney  $U$ -test,  $z=-0.12$ ,  $P=0.91$ ). Males with RO colour bands did not attract more females than those without RO bands (RO:  $\bar{X} \pm \text{SE}=3.75 \pm 0.96$  females,  $N=8$ ; non-RO:  $3.71 \pm 0.68$  females,  $N=7$ ;  $z=-0.18$ ,  $P=0.86$ ).

The area of comb was not correlated with the number of females settling for yearling males (Spearman rank correlation  $r=0.27$ ,  $N=10$ ,  $P=0.42$ ; Fig. 1). Combs of adults were not measured in this experiment. Two yearling males did not have any females settle on their territories and these males had significantly smaller combs than the other yearling males ( $z=-1.98$ ,  $P=0.05$ ).

#### RO Bands and Fledging Success and Survival of Males

We combined adults and yearlings in this analysis as there was no difference in fledging success ( $F=0.005$ ,  $P=0.94$ ) and used only monogamous males to control for effects of status. Males receiving RO bands fledged a mean of 5.3 chicks ( $\text{SE}=0.27$ ,  $N=50$ ) from successful nests, similar to the number fledged by males with no RO bands ( $5.6 \pm 0.43$  chicks; effect size  $d=0.15$ , power=0.25,  $F=0.49$ ,  $N=23$ ,  $P=0.49$ ). The effect size was small, but the test had good power to detect medium (power=0.76) and large (power=0.97) effect sizes.

Return of males from one spring to the next was not related to pairing status ( $G=1.47$ ,

Table IV. Adjusted\* mean area of comb ( $\text{mm}^2$ ) for polygynous, monogamous and unpaired male willow ptarmigan

Status	$\bar{X}$	SE	N
Polygynous	321.9	14.3	17
Monogamous	303.7	4.7	162
Unpaired	274.2	9.4	44

\*Adjusted with two-way ANCOVA with pairing status and male age as factors and date of measuring comb as covariate.

$P=0.48$ ), so all males were combined to examine the effects of RO bands on survival. The return rate of males with RO bands did not differ from that of males with no RO bands (RO: 60.30%,  $N=204$ ; non-RO: 61.5%,  $N=78$ ;  $G=0.04$ , effect size  $w=0.01$ , power=0.06,  $df=1$ ,  $N=282$ ,  $P=0.85$ ). This test had very high power to detect medium and large effect sizes (power=0.99).

#### Area of Comb, Pairing Status, Survival, Fledging Success and Territory Size

In an analysis of covariance with male age and year as factors and date of measuring comb as covariate, area of comb varied with year ( $F=5.23$ ,  $P=0.0001$ ) and with male age ( $F=9.49$ ,  $P=0.002$ ). Thus, we used the residuals from this analysis in subsequent analyses. The means presented in the tables are adjusted means of actual comb sizes. Polygynous and monogamous males had larger combs than unmated males, but monogamous and polygynous males did not differ (ANOVA,  $F=7.34$ ,  $P=0.0008$ ; Duncan's multiple range test; Table IV). Males that returned to breed from one spring to the next ( $N=111$ ) did not have larger combs than those that did not return ( $N=78$ ; effect size  $d=0.05$ , power=0.27,  $t=0.22$ ,  $P=0.83$ ; power to detect medium and large effect sizes was very high; power=0.98 and 0.99, respectively). Comb area was not significantly correlated with the number of chicks fledged from successful nests (power=0.38,  $r=0.09$ ,  $N=97$ ,  $P=0.37$ ; power to detect medium (power=0.96) and large (power=0.99) effect sizes was high).

We next examined whether males with RO bands had larger combs than males with other band colours using a multiple-way analysis of variance with band colour, male age and pairing

**Table V.** Adjusted\* mean area of comb (mm<sup>2</sup>) for male willow ptarmigan that had either RO or non-RO colour

	$\bar{X}$	SE	N
RO	274.3	6.4	104
Non-RO	286.7	8.8	41

\*Adjusted with three-way ANCOVA with date of measuring as covariate; band colour, male age and status as factors.

status as factors and date of measuring the comb as a covariate. Males with RO bands did not have larger combs (Table V; effect size  $d=0.20$ , power=0.42,  $F=1.75$ ,  $P=0.19$ ; the test had high power to detect medium (power=0.93) and large (power=0.99) effect sizes).

Area of comb was positively correlated with territory size in 1980 and 1981 when breeding density was high ( $r=0.46$ ,  $N=35$ ,  $P=0.006$ ), but not in 1985–1988 when breeding density was about half the 1980/1981 level (power=0.37,  $r=0.03$ ,  $N=104$ ,  $P=0.73$ ; power to detect medium (power=0.93) and large effect sizes (0.99) was very high; residuals used in the analysis).

### Song Rates, Border Disputes and Territorial Intrusions of RO and Non-RO Males

Territorial males were observed for a total of 113.4 h ( $\bar{X} \pm \text{SE} = 200 \pm 6.7$  min/male). We first tested whether male age (adult or yearling) or status (polygynous, monogamous, unpaired) influenced any of the behavioural variables and found that they did not (Kruskal–Wallis one-way ANOVA, all  $P_s > 0.05$ ). Thus, we combined data for all males in subsequent analyses. Song rates (aerial beks and rattles), number of border disputes, average length of border disputes, and intrusion rates did not differ significantly between RO and non-RO males (Table VI).

Radio-tagged unpaired males intruded on the same proportion of territories held by RO males as were present in the study area as a whole (Table VII). The power of these tests was low (1984:  $w=0.14$ , power=0.25; 1988:  $w=0.03$ , power=0.10; 1989:  $w=0.04$ , power=0.10; 1991:  $w=0.04$ , power=0.11), however the power to detect medium to large effect sizes was high (power > 0.93) in all cases except for 1984 for medium effect size (power=0.68). Thus, non-territorial males did not appear to preferentially intrude on RO male's territories.

**Table VI.** Mean ( $\pm$  SE) song rates (aerial beks and rattles), intrusion rates, number of border disputes (all per hour), and average length of border disputes (min) for male willow ptarmigan with RO and non-RO colour bands

	RO ( $N=24$ )	Non-RO ( $N=10$ )	$P^*$
Aerial beks	2.7 $\pm$ 0.36	2.6 $\pm$ 0.36	0.89
Rattles	14.8 $\pm$ 1.38	14.4 $\pm$ 1.66	0.73
Intrusions	0.22 $\pm$ 0.11	0.13 $\pm$ 0.47	0.86
Border disputes	0.87 $\pm$ 0.12	0.67 $\pm$ 0.23	0.26
Length of border disputes	2.93 $\pm$ 0.47	2.67 $\pm$ 0.48	0.81

\* $P$ -values from Kruskal–Wallis one-way ANOVA.

**Table VII.** Percentage of males (that were banded with RO bands) that had their territories intruded upon by non-territorial males and percentage of RO males in the study area

Year	Males intruded on		Males on study area		$G$	$P$
	% RO	$N$	% RO	$N$		
1984	75.0	8	56.4	39	1.00	0.36
1988	77.8	9	73.3	131	0.09	0.78
1989	55.5	9	61.5	78	0.12	0.74
1991	71.8	39	68.1	72	0.16	0.68

## DISCUSSION

### **RO Bands and Pairing Success, Fledging Success and Survival of Males**

We found no evidence that red/orange colour bands on male willow ptarmigan influenced pairing success or the number of females attracted to a male's territory. Results from other studies appear to be mixed: some support an effect of red colour bands and others do not. Burley (1985, 1986) reported that captive male zebra finches with red bands were more attractive to females, lived longer, and produced more young than males banded with other colours. Ratcliffe & Boag (1987), on the other hand, found that red-banded male zebra finches were not superior to green-banded males in nestbox acquisition or mate acquisition. These opposite results suggest that the conditions under which the experiments were done might influence the outcome.

More pertinent to field biologists are studies done on free-living birds. Unfortunately these studies have been rare (Brodsky 1988; Hagan & Reed 1988; Beletsky & Orrians 1989; Metz & Weatherhead 1991) and the results far from uniform. Our results are contrary to the study of Brodsky (1988), who claimed that male rock ptarmigan with RO bands had more mates than non-RO males and that RO males increased their pairing status from one year to the next. She suggested that comb-coloured bands enhance the attractiveness of males to females. However, because of small sample sizes, effects limited to 1 of 2 years, and the use of incomplete data on the actual pairing success of males (nests were not found), her results are questionable. Indeed, in a later analysis on the same population over 4 years, Holder & Montgomerie (1993) did not find an effect of red colour bands on pairing success. For red-cockaded woodpeckers, Hagan & Reed (1988) only found an effect of red colour bands on fledging success, but their study was criticized on methodological grounds by Hill & Carr (1989; but see Hagan & Reed 1989). Beletsky & Orrians (1989) found no effect of red colour bands on survival, harem size or fledging success in red-winged blackbirds.

Data from our study on 325 males over 6 years also do not support an association between red bands and fledging success or survival. We conducted power analyses for most of our statistical tests, and found effect sizes to be very low

throughout. Our power to detect these small effect sizes was low to moderate for most tests, however if the effect sizes had been medium or large (as defined by Cohen 1977) our tests had high power to detect these differences. We argue that low effect sizes suggest that any differences that might be present are not important biologically. Thus although we cannot categorically accept our null hypothesis, we argue that our results are consistent with it.

### **RO Bands and the Coverable Badge Hypothesis**

We found no support for the *coverable badge* hypothesis in willow ptarmigan. Territorial males with RO bands did not have more or longer border disputes nor did they have more territorial intrusions than non-RO males. In addition, radio-tagged unpaired males did not intrude preferentially on the territories of RO males. Support for the *coverable badge* hypothesis from other field studies of birds is equivocal.

Hagan & Reed (1988) found that male red-cockaded woodpeckers banded with red bands fledged fewer young than males without red bands, but that red bands did not affect male attractiveness or survival. They interpreted their results as support for the *coverable badge* hypothesis. Unfortunately, they did not present any data to support the contention that males with red bands incited more aggression nor that they provided poorer parental care. Thus, their support of the hypothesis is indirect.

Metz & Weatherhead (1991) conducted an experimental test of the *coverable badge* hypothesis on red-winged blackbirds. They found that males banded with red bands received higher intrusion rates and lost their territories at a higher rate than males with black bands, even though their display rates were the same. Although their experimental approach is a stronger test of the *coverable badge* hypothesis than a posteriori studies, their results may not be highly relevant to field workers using normal banding procedure. Metz & Weatherhead (1991) banded birds with five red plastic bands; normally birds would have one to two, and rarely three red bands. In fact, an a posteriori analysis of data for normally banded birds in their population showed no negative effects of colour banding (Metz & Weatherhead 1991).

Holder & Montgomerie (1993) reported that male rock ptarmigan banded with RO bands



suffered more territorial intrusions than males without RO bands. They interpreted their data as support for the coverable badge hypothesis. Their measure of territorial intrusions, however, was whether a male received a territorial intrusion at any time after he had been colour banded. Information on how long each male was watched was not given; thus, it is possible that RO males were observed longer than non-RO males. In our study we systematically observed both territorial males and unpaired radio-tagged males and found no effect of band colour on intrusion rate, or border disputes. Therefore, we conclude that the coverable badge hypothesis is not relevant to willow ptarmigan, and more thorough study is necessary to assess its relevance to rock ptarmigan.

### Comb Size and Male Pairing Success

Combs are conspicuous secondary sexual characters in many male gallinaceous birds, and in ptarmigan they are erected during courtship and male-male competition. Female junglefowl, *Gallus gallus*, prefer males with larger combs (Zuk et al. 1990). We found that mated male willow ptarmigan had larger combs than unmated territorial males, but polygynous males did not have larger combs than monogamous males. In addition, in the removal experiment, males that had more females settle on their territories did not have the largest combs. Males with no females, however, had smaller combs than males that had at least one female settle on their territories. If combs are used by females in mate choice, our results suggest that there is a threshold comb size, and males with combs smaller than this are not chosen by females. Comb size does give an honest signal to females about some male characteristics such as age (S. J. Hannon, unpublished data), aggressiveness or dominance (Gjesdal 1977; Moss et al. 1979; Stokkan 1979), testosterone level (Hannon & Wingfield 1990), and territory size, at least in years of high density (this study). Comb size was not, however, related to other aspects of fitness that would be important to females, such as fledging success or survival.

### Interaction between Red Colour Bands and Combs

We question the interpretation of Brodsky's (1988) data set by Tomlinson (1988) suggesting

that females show non-fussy preferences, that is, they base their choices more on general characters than specific traits. This interpretation appears faulty primarily because Brodsky did not demonstrate that mate choice by females was occurring. A polygynous male was assumed to have been chosen by the females that were seen on the male's territory during the laying period. A male could in fact have become polygynous by random chance, because of territory quality, or because his territory was large enough to encompass the territories of more than one female (e.g. Hannon 1984; Wootton et al. 1986). If the process of mate choice is not observed directly, the number of females on a male's territory may not be a good indicator of what types of males are preferred or even if active choice based on male morphological characters has occurred. Monogamy appears to be the preferred mating status for female willow ptarmigan (Hannon & Martin 1992) and polygynous females have poorer body condition than monogamous females (Robb et al. 1992). This suggests that in many cases, males that become polygynous do so not by active choice by females, but because their territories are larger and thus secondary females are able to settle there after better quality females have settled.

In conclusion, we suggest that there are no studies on free-living birds that have red ornaments and that are banded in a conventional way (i.e. one or two red bands) that provide convincing support for any effect of red colour bands on pairing success, reproductive success or survival. Nor do any studies on birds banded in the conventional way provide convincing support for the coverable badge hypothesis.

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