RED COLOR BANDS REDUCE FLEDGING SUCCESS IN RED-COCKADED WOODPECKERS

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ABSTRACT.—An analysis of the effects of colored leg bands on Red-cockaded Woodpeckers, in a long-term field study, showed that males that wore red bands fledged significantly fewer young than males without red bands. Other colors were unrelated to fledging success. Band color had no detectable effect on the fledging success of adult females. The offspring sex ratio of breeding males wearing red bands was significantly female-biased. Offspring sex ratios were not related to the presence or absence of red bands on breeding females. Wearing a red band did not affect the probability of a male attracting a mate or the probability of switching mates. For both sexes, annual age-specific survival was independent of the presence or absence of a red band, but nestlings wearing red bands were less likely to be sighted as fledglings. Males with red bands fledged fewer young, consistent with both the species-recognition hypothesis and the coverable-badge hypothesis. The coverable-badge hypothesis, which predicts that the inability to conceal a voluntary social signal (the red cockade) can be detrimental, is the more parsimonious explanation of our results. *Received 25 August 1987, accepted 15 March 1988.*

UNDER laboratory conditions colored leg bands can affect mate selection (Burley 1981, 1986a; Burley et al. 1982), reproductive success, sex ratio of surviving offspring (Burley 1981, 1986b, c), and longevity (Burley 1985a). Female Zebra Finches (*Poephila guttata*), for example, preferred males with red plastic leg bands and avoided those banded with light-green, whereas males preferred females banded with black and avoided those with light-blue plastic leg bands (Burley et al. 1982). Birds with "attractive" leg bands produced disproportionately more young (Burley 1986b) and, in color-banded experimental populations, offspring sex ratios tended to be biased toward the sex of the more attractive parent. Red-banded males also lived longer than orange-banded or light-green-banded birds, and black-banded females outlived orange-banded or light-blue-banded females (Burley 1985a). Males with leg bands of preferred color had increased reproductive success, and Burley (1986a) hypothesized that this increase was due to females contributing greater parental investment to rearing the young of males wearing attractive colors.

Band-color preferences tended to coincide with colors that occur naturally in the plumage and beak of this species (Burley 1986b, Burley et al. 1982). Zebra finches preferred colors that were found on conspecifics but absent in congeners, while less attractive color bands coincided with colors present on congeners but absent on conspecifics (Burley 1986a). Such results are predicted if color preferences are related to the evolution of species recognition (Burley 1986a). However, preference for novel colors (those not occurring naturally on the species) was also demonstrated (Burley 1985b).

The effects of color bands have not been limited to the laboratory. A recent field study (Brodsky in press) showed that male Rock Ptarmigan with red or orange leg bands acquired more mates than those without, even after adjusting for variation in the size of the red supraorbital comb.

Color-band effects offer potential for studying behavioral processes in evolution (Burley 1981, 1986a, b, c), but they also pose a potential problem for laboratory and field studies of birds where color-banding is used to identify individuals. Color-banding is commonly used in field studies of demography and population dynamics, with an implicit assumption that bands do not affect these processes. We found an effect of color-banding on a natural population of Red-cockaded Woodpeckers (*Picoides borealis*). Our objectives were to determine whether band color was correlated with reproductive success, age-specific survival, or sex ratio of fledged offspring.

There is little sexual dimorphism in Red-cockaded Woodpeckers (Ridgway 1914, Ligon 1968, Mengel and Jackson 1977), and the only sexual dichromatism is the red cockades found on males, just above and behind the eyes. The cockades are small tufts of red feathers that are usually only visible when the bird is disturbed (such as during territorial conflicts or during intragroup conflicts) and raises the overlying feathers (Ligon 1970). The role of the cockade in courtship, if any, is not known. All other plumage on this species is either black or white. We predicted, in accord with Burley's hypothesis, that if color-band effects existed they would more likely be related to the presence or absence of red; but this does not preclude possible effects of novel colors (Burley 1985b).

We made no a priori assumptions as to the potential effect red would have on reproductive success or longevity. If the red cockade were a sexually selected feature associated with male competition or female choice, then addition of red to an individual would be predicted to increase fitness. However, congeners also bear red plumage on the head and, if the ability to cover the cockade were a feature to allow discrimination from congeners, the artificial addition of red might result in confusion and lower fitness. Another hypothesis consistent with a negative effect of red predicts that the inability to conceal an important intraspecific social signal at will (exposure of the cockade) may conflict with pairing or intraspecific competitive ability (Hansen and Rowher 1986).

Methods

We drew on data from a long-term study of the cooperative breeding system of the Red-cockaded Woodpecker in the Sandhills region of south-central North Carolina (for project description, see Carter et al. 1983, and Walters et al. in press). The study was initiated in 1978; the population was not extensively banded until 1980. Our analyses are restricted to data collected from 1980 to 1985. On average over this time there were 460 adults in the population at the beginning of the breeding season. Each year an average of 94.5% of the population was color-banded at the beginning of the breeding season, and the remainder was banded by the end of the season, including all nestlings. Most birds were color-banded as nestlings, although a small number were captured and banded as adults (see Walters et al. in press for methods). One leg was banded with 2 or 3 colored bands that identified the group to which the bird belonged at the time it was banded, while the other leg carried bands, one colored and one aluminum/USFWS band, to identify the individual within the group. The bands were red, hot pink, orange, purple, yellow, white, light-blue, dark-blue, light-green, and dark-green. Hot pink was not used after 1981 because of observer difficulty in distinguishing it from red, and was excluded from the analyses.

Each bird involved in these analyses was assigned to either the category of wearing a specific color of band, or *not* wearing that color of band. The associated presence or absence of other colors was ignored by necessity because the number of pairwise or 3-way color combinations was statistically intractable. Fledging success, defined as the number of young fledged per annual breeding attempt (there was no double clutching) of those birds wearing the color, was compared to that of those not wearing the color. It was necessary to factor out high annual variance in fledging success (Walters et al. in press). We expressed fledging success as the deviation from the mean fledging success for each particular year. To reduce the non-normality of this dependent variable, analyses were conducted on the log of the deviation plus 3. Three was added to avoid taking logs of negative numbers or 0. Analyses of fledging success were carried out only on adult males birds over 2 yr of age and adult females over 1 yr of age. This avoided confounding high variance in the fledging success of young breeders (Manor et al. in prep.). Females usually breed a year earlier than males.

Sex ratios of fledglings were compared (Chi-square test) to determine any relationships among the presence or absence of a band color on the parents and the number of fledglings of each sex produced. The set of fledglings used consisted only of fledglings whose parents were both identified with color bands. Given this restriction, the offspring of parents of all ages available were used in the analyses. The same set of fledglings were used in both analyses, being partitioned in the 2 × 2 table according to parent band color.

The relationship between survival and band color was examined by comparing the numbers of individuals with and without a particular color band surviving from the nestling to fledgling stage, from fledgling to age 1, 1 to 2, etc. up to age 5. Annual survival was analyzed separately for each sex because the female is the dispersing sex and has lower survival (Walters et al. in press).

Results

Reproductive success.—Of 436 breeding attempts of male Red-cockaded Woodpeckers, those involving individuals wearing at least 1 red color band produced significantly fewer fledglings than those involving males that did

TABLE 1. Deviations from mean number of fledglings produced for each sex based on the presence or absence of a red color band. Deviations are computed from annual means to remove annual variation in fledging success. Probabilities of a greater F represent the Type III Sum of Squares, after variation in fledging success due to the presence or absence of red on a bird's mate had been accounted for.

	Red-banded			Non-red-banded			
Sex	n	Mean	1 SD	n	Mean	1 SD	$P > F$
Males	147	−0.061	1.05	289	0.193	1.09	0.01
Females	99	0.022	1.05	231	−0.077	1.02	0.63

not wear red bands (Table 1). This was true even after adjusting for variance in the dependent variable that could be accounted for by the presence or absence of a red color band on his mate. Based on 5 yr of data, red-color-banded males produced 0.25 fewer fledglings per breeding attempt than those without red bands. The amount of variability for which red accounts in the model was small ($r^2 = 0.015$), but the presence or absence of red accounted for a significant proportion of the variance explained by the model. Our goal was to identify sources of variation related to band color, not to generate a predictive model of fledging success. Red-banded males did not do worse because of more frequent nest failures (0 fledglings produced). Of 289 non-red-banded-male breeding attempts, 69 (23.9%) were failures, while 43 (29.2%) of 147 red-banded-male breeding attempts failed ($\chi^2 = 1.47$, df = 1, $P = 0.22$).

In contrast, the 330 breeding attempts by females showed an opposite trend. The red-banded females produced, on average, 0.10 more fledglings per attempt than those without red. This difference was not significant statistically (Table 1). There are more males than females involved in the analyses because young birds were excluded, and females breed at an earlier age and have a higher mortality rate than males (Walters et al. in press). No other colors were related significantly to fledging success for either males or females.

It has not been demonstrated whether helpers at the nest effect fledging success in Red-cockaded Woodpeckers. However, to ensure that the result from the male fledging success analysis above was not due to helper bias, we compared the number of helpers at red-banded and non-red-banded males' nests. The mean number of helpers per breeding attempt was 0.35 for red-banded males ($n = 147$) and 0.45 for non-red-banded males ($n = 289$). This difference was not significant ($P = 0.12$, Wilcoxon 2-sample test).

Although we restricted our analyses to males > 2 yr of age, an age bias could still account for observed differences in fledging success. However, the mean age of 31 known-aged red-banded males used in the analysis of males did not differ significantly from 58 known-aged non-red-banded males ($P = 0.875$, Wilcoxon 2-sample test).

Mate choice.—If red-banded males were perceived as unattractive, then red-banded males might show a higher mate-switching rate than non-red-banded males. This was not indicated by this analysis. Red-banded males showed a mean annual mate-switching rate of 0.74 ($n = 75$, 1 SD = 0.29) and non-red-banded males had a rate of 0.76 ($n = 142$, 1 SD = 0.28). This difference was not significant (Wilcoxon 2-sample test, $P = 0.76$). The switching rates did not differ significantly for any other colors. Switching rates of 1 implies a new mate annually.

Occasionally male Red-cockaded Woodpeckers occupy a territory but fail to attract a mate (Walters et al. in press). An analysis of all after-hatch-yr males showed no relationship between the probability of occupying a territory alone and wearing a red color band ($n = 1{,}017$, $\chi^2 = 1.41$, $P = 0.24$). The absence of a white band was related to occupying a territory alone, and white-banded birds were more likely to have a mate ($n = 1{,}017$, $\chi^2 = 6.32$, $P = 0.012$).

TABLE 2. Number of male and female fledglings produced by red- and non-red-banded males and females relative to expected frequencies (parenthetic) if male presence or absence of red was independent of fledgling sex ratios.

	Female fledgling	Male fledgling
Male parent color		
Non-red	309 (322.9)	336 (322.1)
Red	142 (128.1)	114 (127.9)
Female parent color		
Non-red	323 (321.4)	319 (320.6)
Red	128 (129.6)	131 (129.4)

TABLE 3. The probabilities of red-, white-, and light-green-banded nestlings reaching fledgling age.

	n	Prob. fledging	*P*-value[a]
Red	530	0.789	
Non-red	1,288	0.838	0.011
White	557	0.851	
Non-white	1,261	0.812	0.044
Light-green	544	0.794	
Non-light-green	1,274	0.837	0.029

[a] Significance of χ^2 statistic for contingency table analysis.

Offspring sex ratio.—Between 1980 and 1985, 901 fledglings were produced by parents who were both color-banded. Non-red-banded male parents produced 47.91% females and 52.09% males (Table 2). Red-banded males produced 55.47% females and 44.53% males. This relationship between sex ratio and the presence or absence of red on the male parent was statistically significant ($\chi^2 = 4.19$, df = 1, $P = 0.041$). No other colors showed a significant relationship to offspring sex ratio.

For the same 901 fledglings, non-red-banded female parents produced 50.31% females and 49.69% males (Table 2). Red-banded females produced 49.42% females and 50.58% males. There was no relationship between the presence and absence of a red band on the female parent and sex ratio of fledglings ($\chi^2 = 0.081$, df = 1, $P = .776$). No other colors had a statistically significant relationship to offspring sex ratio.

Survival.—With 6 yr of data we were able to examine age-specific annual survival through age 5. Red-color-banded nestlings were significantly less likely to reach the fledgling stage (Table 3). However, we do not know whether the actual death occurred in the nest, or subsequent to fledging and before a researcher visited the group. Groups were usually visited within 1 week of the last fledging bird. Red-banded birds were significantly less likely to survive from the time of banding as a nestling to the time of the first sighting as a fledgling. We did not analyze sexes separately because nestlings could not be sexed at the time of banding. Nestlings with light-green bands were also less likely to survive this period, and nestlings wearing a white band were more likely to survive this period. Neither relationship was as strong as that for red bands (Table 3).

There was no relationship between annual age-specific survival of red- and non-red-banded males through age 5 (Table 4). Similarly, red bands did not affect the age-specific survival of females during that time (Table 4). A purple band was related to an increased probability of a fledgling reaching age 1 for both males ($\chi^2 = 4.495$, $n = 504$, df = 1, $P = 0.026$) and females ($\chi^2 = 4.418$, $n = 481$, df = 1, $P = 0.036$). This result for purple was not observed for older age classes, nor did the presence or absence of any other color relate to age-specific annual survival.

The question of female age-specific survival from age 0 to 1 is the same as asking whether or not females disperse successfully. Most female Red-cockaded Woodpeckers either disperse to another group or die in their first year of life (Walters et al. in press). If band color affects social status or courtship behavior of females, the presence or absence of a color on females may influence the probability of becoming established in a group at age 1. From the age-specific survival analyses above we con-

TABLE 4. Annual age-specific survival probabilities in relation to the presence or absence of a red color band.

		Red		Non-red		
Sex	Age	Prob.	*n*	Prob.	*n*	*P*-value[a]
Males	0–1	0.412	155	0.424	354	1.00
	1–2	0.423	78	0.426	162	1.00
	2–3	0.417	36	0.452	84	0.84
	3–4	0.500	18	0.436	39	0.78
	4–5	0.500	2	0.461	13	1.00
Females	0–1	0.282	124	0.322	357	0.43
	1–2	0.386	44	0.422	116	0.85
	2–3	0.474	19	0.444	63	1.00
	3–4	0.461	13	0.409	22	1.00
	4–5	0.333	3	0.500	8	1.00

[a] Fisher's exact test comparing red to non-red survival.

clude that female fledglings wearing purple bands are more likely to successfully disperse.

DISCUSSION

We found that red color bands used on male Red-cockaded Woodpeckers can reduce their fledging success and affect sex ratios of their offspring. Nestlings with red bands had a lower probability of being resighted subsequent to fledging. However, controls normally desired of a field experiment designed to test the effects of color bands were not possible. We assumed that red bands were assigned to individuals in the population at random. In fact, both individual color bands and group colors were assigned in a haphazard rather than random fashion (J. Walters pers. comm.). Inspection of the location of red and non-red individuals revealed no obvious spatial pattern or correlation with habitat quality. In addition, the mean age of known-aged red-banded males in the analysis of male fledging success was not significantly different from known-aged non-red males, nor was there a difference in the number of helpers to red and non-red males. Thus fledging success differences between these 2 groups could not be attributed to age, group-size, or spatial biases.

In the fledging success analyses breeding attempts by the same individual in different years were treated as independent observations. We ignored the fact that some individuals may have been more fecund than others. The observations between red and non-red males were independent because birds never switched band color categories. There was no difference in the number of breeding attempts per individual in the 2 red color categories.

Red-banded males produced significantly fewer male offspring than males without red bands. This was consistent with the hypothesis that red bands are perceived as unattractive, and females may invest less parental care in male offspring when mated to an unattractive mate. This hypothesis could be tested by comparing time budgets of females mated to red-banded males with budgets of females mated to non-red-banded males.

Burley (1986a) found that colors applied to Zebra Finches that were naturally present in a congener were "non-preferred," possibly reflecting a role in the evolution of species recognition. This hypothesis was consistent for the Red-cockaded Woodpecker because the male has less red than males of all other southeastern U.S. species of woodpecker, and has the unique ability to conceal it at will. This capability could have evolved directly as a species recognition mechanism. It could be a secondary function, with the development of the original ability to conceal resulting from some other advantage. It is unlikely that the concealment evolved by chance or drift from the more primitive state of non-concealment. The species recognition hypothesis is consistent with our hypothesis that red is unattractive only if the red cockade is not used in courtship.

An alternative explanation is that the red cockade functions as a "coverable badge." Hansen and Rowher (1986) assert that the ability to hide or expose a "badge," such as the red epaulets of Red-winged Blackbirds (*Agelaius phoeniceus*), confers appropriate benefits to the signaler, depending on the social circumstances. Although this has not been formally studied in Red-cockaded Woodpeckers, behavioral observations (Blue and Repasky pers. comm.) indicate that display of the cockades is correlated with agonistic encounters with other family groups and with single intruders.

One reason that red leg bands on male Red-cockaded Woodpeckers could reduce fledging success is that red functions as a signal of aggression, and that this signal (displayed constantly by the leg bands) cannot be concealed at will. This unintended message could keep individuals in an abnormally agitated state and reduce the quality or quantity of parental care for the nestlings. Further, males with colored leg bands may incite more intergroup aggression because of their inability to express submissiveness. If the species recognition hypothesis operated in Red-cockaded Woodpeckers, we would expect an excess of red-banded males to occupy territories alone due to female confusion during pair formation.

Color banding is an essential tool for avian field studies. Therefore, workers must minimize potential effects of color-banding. It would be wise to avoid the use of colors which accentuate conspecific colors or sympatric congener colors. In addition, care should be taken to apply colors to individuals randomly to facilitate subsequent analyses of possible band effects. An examination of color-band effects should be routine, and results should be reported in the methods that color-band effects were, or were

not, detected. We suggest avoiding the use of red bands on the endangered Red-cockaded Woodpecker.

ACKNOWLEDGMENTS

We thank J. Walters, P. Doerr, and J. Carter for the use of their banding data. We thank J. Walters, K. Pollock, R. Repasky, the scientific staff of the Manomet Bird Observatory, N. Burley, and an anonymous reviewer for excellent contributions to the manuscript. Computer resources for data analyses were provided by the Manomet Bird Observatory; JMR's research was supported by NSF Grant BSR-8307090 to J. Walters and P. Doerr.

LITERATURE CITED

BRODSKY, L. M. In press. Ornament size influences mating success in Rock Ptarmigan. Anim. Behav.

BURLEY, N. 1981. Sex-ratio manipulation and selection for attractiveness. Science 211: 721–722.

———. 1985a. Leg band color and mortality patterns of captive breeding populations of Zebra Finches. Auk 102: 647–651.

———. 1985b. The organization of behavior and the evolution of sexually selected traits. Pp. 22–44 *in* Avian monogamy (P. A. Gowaty and D. W. Mock, Eds.). Ornithol. Monogr. 37.

———. 1986a. Comparison of the band color preferences of two species of estrilid finches. Anim. Behav. 34: 1732–1741.

———. 1986b. Sexual selection for aesthetic traits in species with biparental care. Am. Nat. 127: 415–445.

———. 1986c. Sex-ratio manipulation in color banded populations of Zebra Finches. Evolution 40(6): 1191–1206.

BURLEY, N., G. KRANTZBERG, & P. RADMAN. 1982. Influence of color banding on the conspecific preferences of Zebra Finches. Anim. Behav. 30: 444–455.

CARTER, J. H., III, R. A. STAMPS, & P. D. DOERR. 1983. Status of the Red-cockaded Woodpecker in the North Carolina Sandhills. Pp. 24–29 *in* Red-cockaded Woodpecker Symp. II (D. A. Wood, Ed.). Tallahassee, Florida, Florida Game and Fresh Water Fish. Comm. and USFWS.

HANSEN, A. J., & S. ROWHER. 1986. Coverable badges and resource defense in birds. Anim. Behav. 34(1): 69–76.

LIGON, J. D. 1968. Sexual differences in foraging behavior in two species of *Dendrocopus* Woodpeckers. Auk 85: 203–215.

———. 1970. Some factors influencing numbers of the Red-cockaded Woodpecker. Pp. 30–43 *in* The ecology and management of the Red-cockaded Woodpecker (R. L. Thompson, Ed.). Tallahassee, Florida, Bur. of Fish. and Wildl. and Tall Timbers Res. Stn.

MENGEL, R. M., & J. A. JACKSON. 1977. Geographic variation of the Red-cockaded Woodpecker. Condor 79: 349–355.

RIDGWAY, R. 1914. The birds of North and Middle America, part IV. Washington, D.C., Government Printing Office.

WALTERS, J. R. In press. The Red-cockaded Woodpecker. *In* Cooperative breeding in birds: long-term studies of ecology and behavior (W. D. Koenig and P. B. Stacey, Eds.). Princeton Univ. Press.

WALTERS, J. R., P. D. DOERR, & J. H. CARTER III. In press. The cooperative breeding system of the Red-cockaded Woodpecker. Ethology.