

IS RED COLORATION OF MALE NORTHERN CARDINALS BENEFICIAL DURING THE NONBREEDING SEASON?: A TEST OF STATUS SIGNALING¹

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Abstract. I tested the hypothesis that bright colors may function as signals of status during the nonbreeding season, offsetting possible costs associated with such traits. Male Northern Cardinals (*Cardinalis cardinalis*) do not defend territories during the nonbreeding season and unfamiliar individuals interact over food resources. To test whether red coloration functions as a signal of status among unfamiliar individuals, I manipulated male coloration by a reddening, a lightening, or a sham control treatment to decouple color from other characteristics that might influence dominance. I observed interactions among males from these treatment groups at a single food source. During the trials, dominant individuals gained mass at a higher rate than subordinate individuals, suggesting a benefit of dominance. There was no effect of treatment or manipulated coloration on the initial or final dominance rank, indicating that males are not using red coloration as a signal of status. However, in the final dominance rank, males with naturally redder plumage were more dominant to those that originally had duller plumage. These results suggest that although red coloration is an indicator of dominance, adult males are not using it alone as a signal of status in controlling food resources.

Key words: *Cardinalis cardinalis*, coloration, competition, dominance, Northern Cardinal, sexual dimorphism.

INTRODUCTION

Among dimorphic species of birds, conspicuous coloration throughout the year has often been viewed as a consequence of sexual selection during the breeding season coupled with the constraint of a single molt in a year (Butcher and Rohwer 1989). However, Rohwer (1975, 1982) proposed that coloration may signal status and fighting ability, thereby mediating competition between individuals over resources during the nonbreeding season. Although Rohwer (1975) initially focused on explaining variable plumage present only in the nonbreeding season, the hypothesis has wider applicability for explaining benefits of conspicuous coloration present throughout the year (Møller 1987, Butcher and Rohwer 1989).

Northern Cardinals (*Cardinalis cardinalis*) are sexually dimorphic. Males have a bright red breast, whereas females are primarily a buffy brown. Although some related dimorphic species acquire conspicuous plumage only during the breeding season, cardinals have a single an-

nual molt after the breeding season and are not seasonally dimorphic (Pyle et al. 1987).

It is possible that male cardinals obtain a benefit of red color during the nonbreeding season. Although they defend territories during much of the pre-breeding and breeding season, winter flocks of cardinals have been reported from throughout the species' range (Kinsler 1973, Ritchison and Omer 1990). The extent of aggression between and among age and sex classes is not known. However, male cardinals interact with unfamiliar individuals during the winter, both as flock membership changes and as new individuals move into the area. Under these conditions, males may use red color as a status signal when establishing dominance relationships between unfamiliar individuals.

I examined whether the red coloration of adult male Northern Cardinals functions as a signal of status in interactions over food resources during the winter. Male color was manipulated to decouple color from other factors, such as male size, and the interactions of unfamiliar individuals were observed to determine the role of color in the establishment and maintenance of dominance hierarchies.

METHODS

The 30 males used in the experiment were captured between 21 October 1993 and 14 February

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1994 using baited traps at eight sites within Tompkins County, New York (42°27'N, 76°26'W). Males were marked with two color bands: males within a trial had bands of the same color but in different combinations on the legs so that individuals could be identified while controlling for possible effects of band color (Burley et al. 1982). I did not use red or orange color bands.

MEASURING COLORATION AND MORPHOLOGY

At the time of capture, morphological and coloration measurements (referred to as natural coloration) were taken. To quantify male coloration, I used methods described previously (Wolfenbarger 1999b). Briefly, I used the color chip series of the *Methuen Handbook of Color* (Kornerup 1967). The color chip series provides a measure of three components of color—hue, tone, and intensity. The hue component ranked color on a scale from yellow (5) to intense red (11). The tone component quantified the amount of black present (1 [all black] to 6 [none]). The intensity component indicated the degree of saturation of pigment (1 [little] to 8 [complete]). For all of these components, a higher score indicated a redder or brighter color.

For each male I measured color in eight breast regions. I used a grid that divided the breast into eight, 1×4 cm² regions and placed the grid posterior to the black bib of the male. Within each of the eight regions of the breast, patches of dull colors were often interspersed in a brighter red background. I scored the brightest and dullest color in each of the eight regions of the grid. For each component of color (hue, tone, and intensity) and for each measurement (brightest or dullest color), I used the sum of the eight regions in analyses. Because hue and intensity are not consistently correlated in male cardinals and because duller birds have more variable plumage coloration on the breast (Wolfenbarger 1999b), the association between dominance rank and each component (hue, intensity, tone) of dull and bright color scores was tested separately rather than using a composite score. All males exhibited the maximum tone scores possible (no black present) for both bright and dull breast measurements; therefore, the relationship between color tone and dominance rank was not tested.

I measured length of black bib, and width of

black bib at the widest region, using methods described by Møller (1987b). Tarsus length, crest length, and bib measurements were taken using dial calipers to the nearest 0.1 mm. Crest length was measured from the feathers at the proximal end of the nares to the most distal feather on the crest.

PLUMAGE MANIPULATION TREATMENTS

After measuring natural plumage coloration, I manipulated male coloration in one of three treatments. The treatments differed in what was applied to the breast; handling procedures were identical among treatments. For the “reddened” treatment, a mixture of 1 part Divina 20 Volume Creme Developer and 3 parts Clairol Professional Hi Power Tint 670^R (i.e., Torch Crimson) was placed on the breast. A “lightened” treatment consisted of applying to the breast Wella Color Charm—Ultra Blonde mixed with Divina 20 Volume Creme Developer in a 1:1 mixture. As a “control” treatment, developer was applied to the breast (by itself, developer did not alter breast coloration). After 25 min, the breast was rinsed with water, and the individual was placed in a holding cage (0.8 × 0.3 × 0.4 m) overnight in an indoor animal facility.

Before manipulations, male coloration scores among treatment groups were similar and did not differ significantly from each other (Table 1). After the color modifications, reddened males had significantly higher hue scores than lightened males (Table 1). Treatments did not differ significantly in intensity scores for either the dull or bright breast measurement (Table 1); therefore, I analyzed only hue treatment effects on dominance for hue scores only.

Although it is possible that manipulated color faded over the course of a male's captivity, this possibility was not evaluated. But because manipulated color was measured just prior to a male's release at the end of each trial, color differences reported represent the minimum differences present during the trials. Prior to release, I measured body mass.

REFLECTANCE SPECTRA OF UNMANIPULATED AND MANIPULATED PLUMAGE

Because vision in birds includes the perception of ultraviolet light (Goldsmith 1990), I measured reflectance spectra on 15 specimens from the Cornell University Vertebrate Collections that

TABLE 1. Mean (\pm SD) differences among treatments in male coloration prior to manipulations (natural coloration) and after manipulation (manipulated coloration). Data were compared with the Quade test, a nonparametric two-way analysis of variance. For differences in hue after the manipulation, post-hoc comparisons were made using ranks in a Fisher least significant difference test (Conover 1980).

Male color score	Treatment		
	Reddened	Control	Lightened
Natural coloration			
Dull breast			
Hue	67.6 \pm 8.4	63.6 \pm 2.4	64.6 \pm 6.4
Intensity	60.4 \pm 2.1	60.7 \pm 2.1	60.6 \pm 2.7
Bright breast			
Hue	78.6 \pm 8.1	74.1 \pm 3.3	74.1 \pm 7.4
Intensity	63.7 \pm 0.9	63.2 \pm 0.9	63.5 \pm 0.8
Manipulated coloration			
Dull breast			
Hue	70.6 \pm 6.4	64.5 \pm 3.2	63.9 \pm 5.6*
Intensity	63.3 \pm 1.3	61.5 \pm 1.7	61.7 \pm 2.9
Bright breast			
Hue	79.8 \pm 5.4	73.5 \pm 2.8	72.0 \pm 4.9*
Intensity	64.0 \pm 0	63.2 \pm 0.9	63.7 \pm 0.7

* $P < 0.05$.

consisted of 11 unmanipulated and 4 manipulated specimens that I deposited (2 lightened, 1 control, 1 reddened) to determine whether the manipulations altered plumage reflectance outside the range of natural variation. I chose to measure specimens that originated from the same area around Ithaca, New York, where experimental birds were obtained, and the specimens chosen had been acquired by the collections no earlier than 1993. A reflectance probe containing six 200- μ m fibers (Ocean Optics, Inc., Model S2000, George H. Drysdale and Associates, Inc., Cincinnati, Ohio) measured spectral components from 250–880 nm at 0.38 nm intervals in an area 1.75 mm in diameter, using illumination from a tungsten-halogen (visible light source) and a deuterium (UV light source) lamp simultaneously. The probe was held at a 90° angle relative to the plumage and was placed 5 mm from the surface by using a metal sheath that excluded external light. Data integration time was set at 30 msec.

Reflectance was measured as the proportion of light reflected relative to a white standard (a glossy white floor tile). For each specimen, two regions of the breast were measured. At each location, 20 spectra were measured and aver-

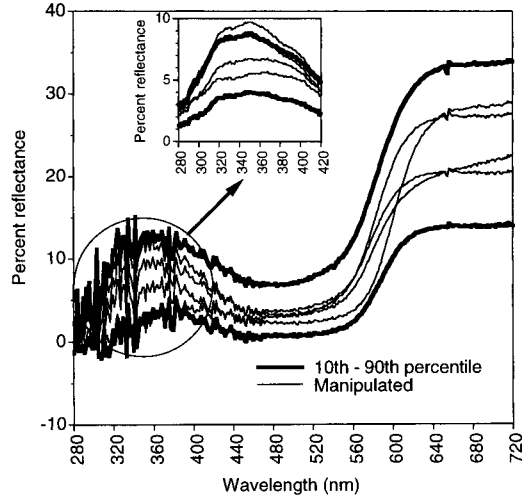


FIGURE 1. Percent reflectance of breast plumage of manipulated and unmanipulated male Northern Cardinals relative to a white standard. The 10th and 90th confidence limits for 11 unmanipulated specimens (2 lightened, 1 control, 1 reddened) fall within the 10th and 90th confidence limits. Reflectance spectra from 280–720 nm were obtained using illumination from a tungsten-halogen (visible light source) and a deuterium (UV light source) lamp simultaneously. Inset shows data obtained from using only the deuterium.

aged. At lower wavelengths, spectral data were subject to higher noise levels due to fewer photons emitted by the UV light source relative to visible light. I repeated spectral measurements using only the deuterium lamp to obtain more precise estimates of reflectance between 280–400 nm although these restricted conditions do not mimic a natural light environment. For these measurements I used a 1 mm reading distance and data integration time of 130 msec. Spectra of manipulated specimens were within the 90% confidence interval of the unmanipulated specimens when using the visible and UV light sources simultaneously (Fig. 1). When using only the UV light source, three of the four manipulated specimens were within the 90% confidence interval and one individual was similar to the most reflective unmanipulated individuals.

EXPERIMENTAL DESIGN

I conducted 10 trials, each involving three males. Males were used only once. For each trial, I recorded dominance interactions among three males whose breast plumage had been manipulated by one of three treatments: reddened,

lightened, or a sham control. I conducted each trial for 4 successive days and on each day I observed male interactions for 2 hr or until a minimum of 10 dominance interactions were recorded between each dyad.

To minimize the possibility that males were familiar with each other, the three males in each trial originated from different sites that were at least 2.5 km apart ($\bar{x} \pm SD = 9.5 \pm 3.6$ km). Males were housed and tested in outdoor aviaries (5 × 3 × 4 m). These aviaries were visually but not acoustically isolated from each other. Males were assigned to trials as they were captured from the wild so that they were in captivity for similar times (range 7–12 days) and in similar environmental conditions before a trial. Prior to beginning a trial, food and water were available *ad libitum*. Each aviary also had several branches and small conifers as perch sites.

Trials began when three males were introduced into an aviary used only for the dominance trials. These males had not previously interacted with one another although they may have been housed with males used in other trials.

Age-related dominance is common, especially among birds (Balph et al. 1979, Rohwer et al. 1981). To minimize effects of age, I eliminated first-year birds from the trials, using plumage criteria to identify them (Pyle et al. 1987).

QUANTIFYING INTERACTIONS

I observed male interactions on each day of a trial. Prior to making observations, individuals were not allowed access to food for 1 hr to increase the number of interactions between dyads. The initial observation period began immediately after releasing the three males into the testing aviary. One tray of food was placed in a central position in the aviary and observations were conducted from behind a one-way mirror. During nonobservation periods, two trays of food were provided, one near each end of the aviary.

All active interactions between individuals, either at the food tray or at perch sites, were recorded. These included chasing and supplanting as described by Kinser (1973). I considered an individual to have “won” an interaction if he chased or supplanted another individual either at the food tray or a perch site. In dyads, individuals were considered dominant if they won more interactions than they lost.

For each trial I constructed two dominance hierarchies, one from the initial observation (day 1) and the other from the remaining three observation days because dominance hierarchies did not change after the second day of observation. Three dyads (each in three different trials) did not engage in active interactions during the initial 2-hr observation period, and in one case a dyad (from a fourth trial) won an equal number of active interactions. For these dyads, I used the available data on the order in which individuals fed (from 3–4 feeding bouts) to determine dominance.

STATISTICAL ANALYSES

I analyzed whether coloration was correlated with dominance in the initial or the final (days 2–4) dominance ranking. For analyses of hue and dominance, I used the Page test for ordered hypotheses with multiple treatments, predicting that males with higher color scores should have higher dominance ranks (Page 1963). I used the Quade test which is a nonparametric two-way analysis of variance to analyze differences among treatment groups before and after coloration manipulation (Conover 1980). For other morphological variables, I also used the Page test with the prediction that males with larger tarsi, crests, and black bibs would be most dominant. There was no *a priori* prediction about the relationship between body mass and dominance rank, and I used the Friedman test to analyze whether mass at the beginning or end of a trial was associated with dominance rank (Conover 1980).

I used a sequential Bonferroni adjustment for each relationship between hue and dominance rank that I tested because I used both a bright and dull measurement of hue (Rice 1989). Values listed are means \pm SD.

RESULTS

COLORATION AND DOMINANCE

The three treatment conditions were not significantly associated with dominance rank in either the initial or final dominance hierarchy (Page test, initial: $L = 119$, $P = 0.59$; final: $L = 114$, $P = 0.91$, Table 2). Because the sham control treatments were not necessarily intermediate in color between the reddened and lightened treatments, I also analyzed the relationship between manipulated hue scores and dominance. Manipulated hue score also did not correlate with dom-

TABLE 2. Effects of treatment group and natural plumage coloration on dominance rank. For each trial males were ranked for dominance by treatment hue or natural coloration prior to manipulation. Each set of nine cells categorizes the males from all 10 trials by these rankings (i.e., of the 10 males in the lightened treatment group, 5 were ranked lowest in the initial hierarchy; 1 male was intermediate in dominance; and 4 males had the highest dominance ranking).

	Dominance rank		
	Lowest	Middle	Highest
Treatment groups			
Initial hierarchy			
Lightened	5	1	4
Control	1	5	4
Reddened	4	4	2
Final hierarchy			
Lightened	2	4	4
Control	1	6	3
Reddened	7	2	3
Natural coloration, dull breast hue			
Initial hierarchy			
Least red	5	2	3
Middle	2	5	3
Most red	3	3	4
Final hierarchy			
Least red	6	1	3
Middle	2	8	0
Most red	2	1	7

inance rank on the first or last day of trials, indicating that males did not use breast treatment coloration in establishing either the initial or final dominance hierarchy (initial: $L_{\text{bright}} = 123$, $P = 0.25$, $L_{\text{dull}} = 117$, $P = 0.75$; final: $L_{\text{bright}} = 123$, $P = 0.25$, $L_{\text{dull}} = 121$, $P = 0.41$).

In the final dominance hierarchy, natural breast hue of the males did correlate with dominance rank: males with the reddest coloration prior to the manipulation were most dominant, although one of the relationships was nonsignificant with a Bonferroni adjustment (dull breast score: $L = 128$, $P = 0.04$; bright breast score: $L = 128$, $P = 0.04$, Table 2). By contrast, this relationship was not evident on the first day of the trial although there was a trend for males with higher natural breast hue to have higher dominance rank in the initial hierarchy (dull breast score: $L = 123$, $P = 0.25$; bright breast score: $L = 127$, $P = 0.06$, Table 2).

Numbers of interactions varied greatly among trials. Initial hierarchies were based on a mean of 4 active interactions (SD = 4.0). Final dom-

inance hierarchies were based on as few as 4 active interactions between dyads to as many as 50 ($\bar{x} = 14.7 \pm 10.6$). No circular relationships (i.e., $A > B$ and $B > C$, but $C > A$) existed in any of the hierarchies.

In 6 of the 10 trials, the dominance hierarchy of seven dyads changed between the first observation period and the second observation. These changes were not associated with coloration differences between dominant and subordinate individuals. Also, these changes were not associated with assigning the initial dominance rank for four dyads according to feeding order, for only one of the seven changes in rank involved one of these dyads.

MORPHOLOGY AND DOMINANCE

Within trials, males with the longest tarsi were not the most dominant individuals in either the initial or final ranking, indicating that this measure of size did not influence control over food resources (Page test, initial hierarchy: $L = 121$, $P = 0.41$; final hierarchy: $L = 120$, $P = 0.50$). Similarly, crest length was not a predictor of higher dominance rank either in the first or final ranking (Page test, initial hierarchy: $L = 116$, $P = 0.81$; final hierarchy: $L = 116$, $P = 0.81$). Finally, neither a longer nor a wider black bib was associated with a higher dominance ranking (Page test, initial hierarchy: $L_{\text{length}} = 120$, $P = 0.50$, $L_{\text{width}} = 122$, $P = 0.37$; final hierarchy: $L_{\text{length}} = 116$, $P = 0.81$, $L_{\text{width}} = 120$, $P = 0.50$).

There was no association between body mass at the beginning of the experiment and final dominance rank (Friedman test, $T_{2,14} = 0.47$, $P = 0.64$), indicating that the heaviest male at the beginning of a trial was not necessarily most dominant by the end. However, a significant relationship did exist between dominance rank and body mass at the end of trials: individuals most dominant in the final hierarchy also had the highest mass at the end of trials (Friedman test, starting mass vs. initial hierarchy: $T_{2,16} = 0.18$, $P = 0.83$; final mass vs. final hierarchy: $T_{2,16} = 4.96$, $P = 0.02$). Similarly, dominant individuals in the final hierarchy were most likely to increase in mass from the first to last day of trials relative to males of lowest ranking (Friedman test, $T_{2,14} = 4.49$, $P = 0.03$, Fig. 2), so that at the end of the experiment dominant individuals were slightly heavier and had increased in mass during the experiment.

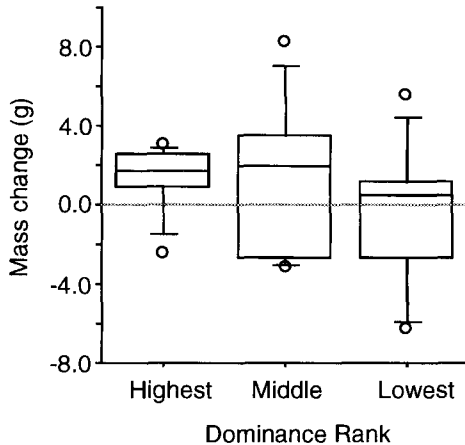


FIGURE 2. Change in body mass during dominance trials. Boxes represent 25th and 75th percentile with the median indicated by the horizontal line bisecting each box. "Whiskers," extending above and below boxes, encompass 10th and 90th percentile, and circles represent the range. The mass change of the highest and middle dominance ranks differ significantly from the lowest rank, but not from each other.

DISCUSSION

Manipulated coloration was not associated with dominance rank in either the initial or final dominance hierarchy (Table 2). If coloration is used as a status signal, then initial dominance rankings of unfamiliar individuals should be established according to coloration. In my experiment, dominance rank and manipulated color were not significantly correlated when males were first observing the color of unfamiliar males and setting up a hierarchy over access to food. Therefore, these results do not support the status-signaling hypothesis, for they indicate that males did not use manipulated coloration to initially assess relative dominance status.

These results contrast with Rohwer's (1985) classic work on Harris' Sparrows *Zonotrichia querula* where first year males dyed to resemble adults (more black on the throat) were dominant over controls when experimental and control individuals were previously unfamiliar with each other. Other studies using plumage manipulations have confirmed the function of variable coloration in signaling status between age and sex classes (Fugle et al. 1984, Järvi and Bakken 1984, Holberton et al. 1989), and it is common for males to be dominant over females and for individuals older than a year to be dominant over individuals less than a year (Balph et al.

1979, Rohwer et al. 1981). My experiment represented a conservative test of the status signaling hypothesis because males less than one year of age were excluded; therefore, red coloration may be used as a signal between first year males and older males but this remains untested. Limited evidence suggests that red coloration may correlate with age (Wolfenbarger 1999b), but other evidence indicates that variable environmental conditions among years may account for changes in coloration (Linville and Breitwisch 1997, Linville et al. 1998).

Studies focusing on variation within age classes provide little evidence for a link between more conspicuous plumage and higher dominance rank (Wilson 1992, Belthoff et al. 1994), including subsequent work on Harris' Sparrows that indicated status signaling is absent within age classes (Watt 1986, Jackson et al. 1988).

In cardinals, there is an association between a male's natural coloration (hue prior to manipulation) and his final dominance rank (Table 2). Therefore, red coloration was associated with gaining access to food resources in the winter, but males were not using coloration alone to assess the status of unfamiliar individuals. It remains possible that males may use red coloration in combination with other factors to assess each other's ability to defend a resource. Alternatively, dominance may influence color. As in other birds, the red coloration of male cardinals is carotenoid-based (Hudon 1991). These pigments cannot be synthesized by birds and are obtained from diet (Fox and Vevers 1960, Hill 1992, Witmer 1996), suggesting that more dominant males may be better able to obtain foods rich in carotenoids during the nonbreeding season when they are molting.

Neither skeletal size nor body mass of male Northern Cardinals was associated with dominance rank in either initial or final dominance rank. Similarly, crest length of male Northern Cardinals did not correlate with either initial or final dominance status. Therefore, males encountering each other for the first time do not appear to use these morphological traits to assess dominance status. Among avian species, dominant individuals are larger in some species (Baker and Fox 1978, Ketterson 1979), but not in others (Arcese and Smith 1985, Bryant and Newton 1996).

The bright red coloration of male cardinals is not the only possible ornament used in signaling

dominance. Recent evidence indicates that some birds have UV reflective plumage that is used as a signal (Andersson et al. 1998, Hunt et al. 1998). In cardinals, reflectance in the UV is weaker than that for wavelengths corresponding to orange and red coloration (Fig. 1). Manipulated individuals had normal levels of reflectance in the UV range. However, this experiment systematically altered only red coloration, and a signaling function for UV reflectance is possible. In at least three species, black bib size is correlated with dominance rank, and males with larger black bibs have higher dominance status (Rohwer 1985, Møller 1987, Senar et al. 1993). In this study, measures of black bib size did not correlate with dominance rank. However, males in my experiment differed on average only 4.2 ± 2.1 mm ($\bar{x}_{\max} = 17.3 \pm 2.4$ mm; $\bar{x}_{\min} = 13.3 \pm 2.7$) in maximum bib length and much less for bib width. Bib length may correlate with dominance between first year males and those older. In a wild population, maximum bib length increased between years an average of 8.1 ± 4.8 mm ($n = 12$), representing a 60% increase in bib length and suggesting that bib size may indicate age (unpubl. data).

Higher dominance status in male cardinals does have potential benefits. Over the course of the 4-day trials, dominant males gained significantly more body mass than did subordinate males even though mass at the beginning of the trials was not related to dominance rank. Maintenance of a minimum body mass during the winter months is likely to be a major factor in decreasing the risk of starvation (Baldwin and Kendeigh 1938, Ekman and Hake 1990, Rogers and Rogers 1990). Male cardinals of higher dominance rank should have higher winter survivorship as in other species (Baker and Fox 1978, Kikkawa 1980, Arcese and Smith 1985), possibly by allowing individuals to feed more efficiently or to feed in safer spots (Ekman 1987, Piper 1990, Keys and Rothstein 1991).

Although a growing body of literature indicates that conspicuous coloration functions during the breeding season (Andersson 1994), there is mixed support for benefits associated with retaining conspicuous plumage coloration throughout the year. For example, in the Great Tit *Parus major*, a larger breast stripe is preferred by females during the breeding season (Norris 1990) and also signals higher dominance status within age and sex classes at feeding sta-

tions during the nonbreeding season (Maynard Smith and Harper 1988). In contrast, female House Finches *Carpodacus mexicanus* prefer brighter males during the breeding season, but redder coloration does not correlate with dominance over food resources in the nonbreeding season (Hill 1990, 1991, Belthoff et al. 1994). Available evidence suggests that male cardinals also benefit from displaying red coloration during the breeding season although laboratory experiments revealed no evidence of female preferences for redder males (Wolfenbarger 1999a, 1999b).

The results presented here refute one hypothesis about the maintenance of year-round red coloration in Northern Cardinals. Adult male cardinals do not appear to use red coloration as a status signal in defending centralized food resources from other adult males during the nonbreeding season. However, naturally redder males were more dominant, and coloration may be used as a signal in other contexts, such as the acquisition and defense of breeding territories or in signaling to females or first-winter males.

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