

FEMALE MATE CHOICE IN NORTHERN CARDINALS: IS THERE A PREFERENCE FOR REDDER MALES?

L. LAREESA WOLFENBARGER^{1,2}

ABSTRACT.—I tested whether female Northern Cardinals (*Cardinalis cardinalis*) associated with redder males in two laboratory experiments, one using males with unaltered plumage and the other using males with plumage altered by a lightened or reddened treatment. Females exhibited no preference for redder males. Given the long duration over which pair formation can occur in natural populations and the importance of territory quality to reproductive success, a female may choose a mate based on other morphological characteristics or aspects of his territory rather than on only red coloration. Received 27 May 1998, accepted 22 Oct. 1998.

Ornate plumage characteristics in birds are generally assumed to have arisen through sexual selection and, specifically, through female mating preferences or competitive interactions between males (Darwin 1871, Andersson 1994). A growing number of studies has demonstrated that females prefer males with brighter coloration (Hill 1990, Sætre et al. 1994, Sundberg 1995) as well as with other exaggerated plumage characteristics, such as longer crests (Jones and Hunter 1993) and longer tails (Andersson 1982, 1992; Møller 1988, 1992; Evans and Hatchwell 1992).

Northern Cardinals (*Cardinalis cardinalis*) are highly dichromatic. Males vary from orange to scarlet red. Male coloration varies both in overall hue and in evenness of breast coloration. In contrast, females are primarily a light brown but have small and variable amounts of red in the crest and breast; all females also have red coloration on the wings and tail.

In addition to being highly dichromatic, cardinals are territorial and socially monogamous. Males feed females substantially during nest construction, a time coinciding with egg production (Kinser 1973). Males also feed nestlings at higher rates than do females (Filiater and Breitwisch 1997, but see Linville et al. 1998). Because coloration derived from carotenoids is dependent on diet in birds (Goodwin 1950, Hill 1992), red coloration in cardinals could signal information to the female

regarding a male's foraging abilities, age, or overall phenotypic quality.

In this study, I address whether female preferences may account for the maintenance of red coloration in male Northern Cardinals. I used two laboratory experiments to test whether female cardinals preferred to associate with redder males during the breeding season.

METHODS

The experiments were conducted on the Cornell University campus, Ithaca, New York, from mid February through April 1995. Males and females used in the experiments were captured between 14 January and 16 April 1995 using baited traps and mist nets at 6 sites within Tompkins County, New York (42° N, 76° W). Individuals were marked uniquely with one color band. Because previous studies have demonstrated that red color bands can influence behavior of individuals in other species (Burley et al. 1982, Hagan and Reed 1988, Metz and Weatherhead 1991), I did not use red or orange color bands.

Prior to trials males were housed in two indoor flight aviaries (3.6 × 3.6 × 3.0 m) with skylights and incandescent lighting synchronized to dawn and dusk. Females were housed in a similar third aviary (5.2 × 3.6 × 3.0 m). Aviary rooms were both visually and acoustically isolated from each other. The temperature of each aviary ranged between 10 and 12° C. Food and water were provided *ad libitum*.

Measuring coloration.—To measure male coloration, I used methods described elsewhere (Wolfenbarger in press). Briefly, I used the color chip series of the Methuen Handbook of Color (Kornerup 1967) to quantify breast coloration of males. 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 [from little (1) to complete (8)]. I used a grid that divided the breast into eight 1 × 4 cm rectangles and

¹ Section of Neurobiology and Behavior, Cornell Univ., Ithaca, NY 14853-2702.

² Present address: Dept. of Biology, Univ. of Maryland, College Park, MD 20742; E-mail: LW137@umail.umd.edu

TABLE 1. Male color and morphology differences in male cardinals used in natural trials.

	Relative color score		Z (P) ^a
	Lower $\bar{x} \pm$ SD (n)	Higher $\bar{x} \pm$ SD (n)	
Bright breast hue	73.9 \pm 7.0 (8)	81.7 \pm 4.3 (8)	2.81 (0.005)
Dull breast hue	65.9 \pm 6.4 (8)	71.9 \pm 4.0 (8)	2.81 (0.005)
Bright breast intensity	62.9 \pm 0.9 (3)	63.2 \pm 0.6 (3)	— ^b
Dull breast intensity	61.1 \pm 3.1 (7)	62.7 \pm 0.9 (7)	2.64 (0.008)
Morphological traits (in mm):			
Tarsus length	24.3 \pm 0.7 (10)	24.1 \pm 1.0 (10)	0.82 (> 0.05)
Crest length	36.8 \pm 3.5 (10)	35.8 \pm 1.9 (10)	0.46 (> 0.05)
Tail length	99.9 \pm 5.0 (10)	98.4 \pm 3.7 (10)	0.46 (> 0.05)
Black bib length	19.8 \pm 4.6 (10)	20.2 \pm 4.3 (10)	0.65 (> 0.05)
Black bib width	21.8 \pm 1.1 (10)	22.0 \pm 1.1 (10)	0.46 (> 0.05)

^a Z-value is from Wilcoxon matched pairs signed rank test.

^b In 7 trials, male scores for bright breast intensity were identical.

placed it immediately posterior to the black bib and measured coloration in each of these regions. Because male cardinals often had clumps of orange, yellow, or even tan feathers interspersed within a background of red feathers, I recorded the highest ("Bright" breast score) and lowest color score ("Dull" breast score) for hue, tone and intensity in each of the 8 regions. For all of these components a higher score indicates a redder or brighter color. Among the birds I used, there was greater variation among males in the color of dull regions relative to bright regions (Wolfenbarger, in press). I tested the repeatability of the color scoring method by using specimens in the Cornell Vertebrate Collections, and found the method to be highly repeatable (Wolfenbarger 1996).

For analyses of the association between measures of female association and male coloration, I summed each component of color (i.e., hue, tone, intensity) for the eight regions and used separate scores for the bright and dull color measurements. In this experiment, all males except two exhibited the maximum tone scores possible for both bright and dull breast measurements; therefore, the relationship between color tone and female association was not tested. Similarly, there was very little variation in bright breast intensity. Therefore, I used three variables: bright breast hue, dull breast hue, and dull breast intensity to characterize male coloration.

Although other studies have created a composite score from color chips (Linville et al. 1998), I used these components separately for two reasons. Hue and intensity were not consistently correlated in this population of cardinals (Wolfenbarger 1996), and combining these scores would result in identical scores for males that actually had different hue and intensity scores. Second, the relative importance of hue, intensity and tone for color perception of cardinals is not known. Any weighting of these components becomes problematic for the interpretation of negative results since one obvious alternative would be that the weighting factor might be incorrect.

Morphological measurements.—I measured the fol-

lowing on males: tarsus length, tail length, crest length, maximum length of black bib (after Møller 1987), and width of black bib. All were measured to the nearest 0.1 mm except tail length which was measured to the nearest 0.5 mm.

Experiment 1: natural plumage trials.—Ten trials were conducted to test whether females spent more time with males having higher natural plumage scores. Males and females in each trial were captured at least 4 km apart to reduce the possibility that males and females had interacted prior to the experiment. Males and females were tested in the order that they were captured from the field so that males spent similar lengths of time in captivity (approximately 7 days for natural trials and 18 days for manipulated trials), but within a trial males and females had spent similar amounts of time in captivity. No apparent change in behavior was associated with when males and females were captured or how long they spent in captivity.

In each trial males differed primarily in hue scores. Within a trial males differed significantly in bright and dull breast hue (Wilcoxon matched-pairs test: Bright hue: $Z = 2.81$, $P < 0.05$; Dull hue: $Z = 2.81$, $P < 0.05$; Table 1). There were also significant but small differences in dull breast intensity between males in a trial ($Z = 2.64$, $P < 0.05$; Table 1). The lack of differences in bright breast intensity (Table 1) reflects the limited natural variation of breast intensity in male cardinals. I analyzed bright and dull breast measurements separately because male rankings based on bright and dull measurements were not identical.

Trials were conducted in a rectangular experimental aviary (5.0 \times 1.4 \times 1.75 m) divided by netting into three main compartments. Males were placed at opposite ends of the aviary and a female was placed in the center compartment (2.5 \times 1.4 \times 1.75 m). The female compartment was divided into three equal areas so that females could associate with either male or spend time in a middle area where she could not interact visually with either male. Opaque barriers within the female area were used to divide the compartment. These prevented a male from observing a female in-

TABLE 2. Male color and morphology differences in male cardinals used in manipulated trials.

	Lightened male $\bar{x} \pm SD (n)$	Reddened male $\bar{x} \pm SD (n)$	Z (P) ^a
Color score before manipulation:			
Bright breast hue	75.7 ± 7.4 (10)	80.5 ± 6.5 (10)	1.89 (0.059)
Dull breast hue	68.9 ± 4.9 (10)	70.9 ± 3.5 (10)	1.99 (0.046)
Bright breast intensity	63.0 ± 0.7 (10)	63.1 ± 0.9 (10)	0.30 (> 0.05)
Dull breast intensity	61.5 ± 3.1 (10)	62.3 ± 0.9 (10)	0.34 (> 0.05)
Color score after manipulation ^b :			
Bright breast hue	72.9 ± 5.4 (9)	86.1 ± 4.3 (9)	2.69 (0.0072)
Dull breast hue	66.6 ± 6.4 (8)	77.3 ± 4.8 (8)	2.52 (0.011)
Bright breast intensity	62.8 ± 0.9 (5)	63.8 ± 0.7 (5)	0.68 (> 0.05)
Dull breast intensity	61.2 ± 0.9 (9)	63.0 ± 0.8 (9)	2.69 (0.0072)
Morphological traits (in mm):			
Tarsus length	24.0 ± 0.9 (10)	24.4 ± 0.8 (10)	0.83 (> 0.05)
Crest length	35.4 ± 2.5 (10)	37.1 ± 2.9 (10)	1.17 (> 0.05)
Tail length	99.7 ± 4.3 (10)	98.6 ± 4.5 (10)	0.35 (> 0.05)
Black bib length	20.4 ± 4.1 (10)	19.6 ± 4.8 (10)	0.56 (> 0.05)
Black bib width	21.7 ± 0.9 (10)	22.1 ± 1.3 (10)	0.82 (> 0.05)

^a Z-value is from Wilcoxon matched pairs signed rank test.

^b Males that have identical scores are not included in means of color scores after manipulation.

teracting with the male on the opposite side, but did not restrict female movement. I considered a female as interacting with a male when she spent time in the area adjacent to the male compartment as opposed to the center area. To minimize the possibility of side preferences, all aspects of the male compartments as well as the female compartment were symmetrical. A single perch was provided in each male compartment and three perches in the female compartment, one in each area. Food and water were provided *ad libitum* in each male compartment and in the middle area of the female compartment.

Each trial lasted 29 hours. For each trial a female was placed in the experimental aviary for a one hour acclimation period without the presence of males. A male was introduced to each side of the aviary and the experiment proceeded for 26 hours. At the end of 26 hours, the positions of the two males were switched and the female interacted with males for an additional two hours.

Females were videotaped during four different observation periods: (1) for one hour with no males present (Pretrial Period), (2) for the first two hours (0 Hour Period) after introduction of the males, (3) from 24–26 hours after introduction of the males (24 Hour Period), and (4) from 26–28 hours of the trial (Reversed Period). In sum, each female was taped for 6 hours with the two males present and for one hour prior to the introduction of males. After completion of a trial, males and females were returned to their respective aviaries.

Experiment 2: manipulated plumage trials.—The 30 individuals used in the natural plumage experiment were also used in the manipulated plumage experiment, but within each experiment individuals were used only once. Males and females for each trial were unfamiliar with each other because they were housed

in different aviaries prior to the trial and were introduced in novel combinations for the two experiments. For each pair of males in a manipulated trial, one was randomly assigned to a reddened plumage treatment and the other to a lightened plumage treatment. Trials proceeded as in experiment one. At the conclusion of the manipulated trials, all individuals were released at the original site of capture.

Plumage manipulation methods.—Prior to the manipulation, males were anesthetized with 1.5 mg/kg of Midazolam injected into the pectoralis muscle. This dosage induced a state of light anesthesia: males closed their eyes but opened them in response to external stimuli such as having a wing extended. No mortality was associated with using the anesthesia.

For the “reddened” treatment, a mixture of 1 part Divina 20 Volume Creme Developer and 3 parts Clairol Professional Hi Power Tint 670[®] was placed on the feathers for 25 minutes. A “lightened” treatment consisted of applying Clairol Professional 7th Stage Creme Hair Lightener mixed with Divina 20 Volume Creme Developer in a 1:1 mixture to the feathers for 25 minutes. In both treatments males were rinsed and were dried with a hair dryer. The males were alert within an hour of the injection and were released back into an aviary within 2 hours. Trials were conducted at least four days after the males were manipulated.

Manipulated plumage coloration scores.—Although treatments were assigned randomly, plumage hue scores before the manipulation were significantly higher for males in the reddened treatment group (Wilcoxon matched-pairs test: Natural bright hue: $Z = 1.89$, $P = 0.06$; Natural dull hue: $Z = 1.99$, $P < 0.05$; Table 2). There was no significant difference in the intensity scores prior to the manipulation (Natural bright intensity: $Z = 0.30$, $P > 0.05$, Natural dull intensity: $Z = 0.034$, $P > 0.05$; Table 2). After plumage manipula-

tions, differences between hue scores for reddened and lightened treatment groups were significant (Manipulated bright hue: $Z = 2.69$, $P < 0.05$, Manipulated dull hue: $Z = 2.52$, $P < 0.05$; Table 2). Males in the reddened treatment had significantly higher intensity for the dull breast measurement but not for the bright measurement (Manipulated bright intensity: $Z = 0.68$, $P > 0.05$; Manipulated dull intensity: $Z = 2.69$, $P < 0.05$; Table 2). Little variation in manipulated tone scores existed: all except two individuals had the maximum possible tone scores. Reflectance spectra (from 280–750 nm) of manipulated plumage were within the range of natural variation in plumage reflectance that occurs at these wavelengths (Wolfenbarger, unpubl. data). As in experiment one, dull and bright breast measurements were analyzed separately.

Analyses of experiments.—For the periods videotaped, the time a female spent in each area of the experimental aviary was measured either during the trial via a monitor connected to one camera or after the trial from the videotapes. The monitor was located in a room visually and acoustically isolated from the experimental aviary. For each sampling period, I determined the number of trials in which the female spent more time with the male having the higher color score for each period videotaped (0 Hour, 24 Hour, Reversed). I used the 0 Hour and 24 Hour samplings to assess female preferences and the pretrial and reversed sampling periods to assess whether females had site preferences in the aviary.

For the 0 Hour and 24 Hour periods, I used a one-tailed binomial test to determine whether the number of trials in which a female spent more time with the redder/brighter male was significantly greater than expected by chance (50%; Conover 1980). The test statistic T refers to the number of trials in which the female spent more time with the male with the higher color score (Conover 1980).

Because males were randomly assigned to trials, there were trials in which hue or intensity scores were identical. I eliminated these from analyses because neither male was redder or brighter using my measurements. I also eliminated sampling periods in which the difference in amount of time spent with males was less than 2 minutes (i.e., the female showed no preference for a particular male).

Among trials, differences in male coloration scores varied widely (range in differences: bright breast = 0–21, dull breast hue = 0–24, dull breast intensity = 0–8). Females may exhibit strong preferences (as measured by time spent with male) when differences between male coloration are large; whereas females may spend equal amounts of time with males whose color scores are similar. I used regression analysis to test whether the magnitude of the difference in color was related to the difference in the time a female spent with a particular male. In particular, I tested whether there was a positive relationship between the difference in color scores between the two males and the difference in the amount of time spent between the two males in the 0 Hour and 24 Hour sampling periods (Wilkinson

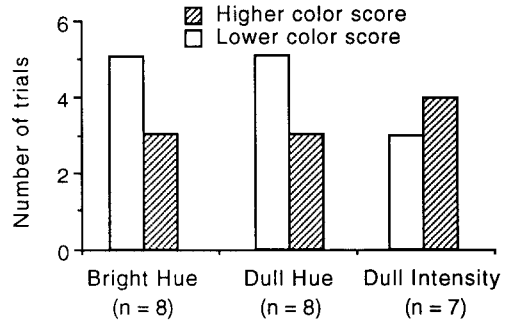


FIG. 1. Number of natural trials in which female spent more time with male having lower or higher color score during the 0 Hour Sampling period (Binomial test: all $P > 0.05$).

et al. 1992). Because the predicted difference in the amount of time spent with males of the same color is zero, the regression line was forced through the origin.

I tested whether females exhibited two types of potential site preferences: (1) a general preference among females for either the east or west side of the experimental aviary or (2) the likelihood that an individual female stayed on the same side of the aviary between consecutive sampling periods. I used the pretrial and reversed periods to assess the consistency of females' preferences for a particular side or male. Two-tailed binomial tests were used to determine whether females remained on the same side of the aviary between subsequent sampling periods in more than half of the trials (Conover 1980). I used a sequential Bonferroni adjustment for multiple comparisons (Rice 1989) because I used both dull and bright breast measures in analyses. A Wilcoxon matched pairs signed rank test was used to compare morphological variables between paired males (Wilkinson et al. 1992).

RESULTS

Natural and manipulated plumage experiment.—Of the 59 observation periods during the two experiments, females spent an equal amount of time (± 2 min) with both males in only 7 periods. During the remaining 52 periods, females spent an average of 45.8 (SE = 4.0) minutes more with one male than the other (range = 12–110 min, total possible = 120 min).

In the 0 Hour and 24 Hour sampling periods, females were as likely to associate with the relatively dull males as with brighter, redder males (Fig. 1, binomial test: 0 Hour: T Bright hue = 3, $P > 0.05$, $n = 8$; T Dull hue = 3, $P > 0.05$, $n = 8$; T Dull Intensity = 4, $P > 0.05$, $n = 7$; 24 Hour: T Bright hue = 5, $P > 0.05$, $n = 9$; T Dull hue = 3, $P > 0.05$,

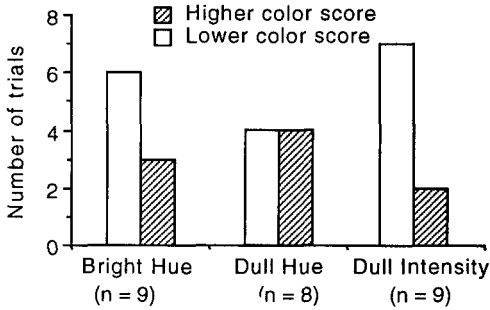


FIG. 2. Number of manipulated trials in which female spent more time with males having lower or higher color scores during the 0 Hour Sampling period (Binomial test: all $P > 0.05$).

$n = 9$; T Dull Intensity = 6, $P > 0.05$, $n = 7$). Similarly, in the manipulated plumage trials where color differences between males were greater, females did not consistently associate with males having higher coloration scores (Fig. 2; binomial test: 0 Hour: T Bright hue = 3, $P > 0.05$, $n = 9$; T Dull hue = 4, $P > 0.05$, $n = 8$; T Dull intensity = 2, $P > 0.05$, $n = 9$; 24 Hour: T Bright hue = 3, $P > 0.05$, $n = 9$; T Dull hue = 4, $P > 0.05$, $n = 8$; T Dull intensity = 2, $P > 0.05$, $n = 9$).

The power of binomial tests at the critical value is 95% at sample sizes of 8 and 9, and 70% with a sample size of 7. However, the power of all of these tests at the P -values of the results is less (25–36%) because of the small effect observed in the experiments. Results from at least 150 trials would be needed to find significant differences with such a minor effect (Conover 1980).

Magnitude of color differences and female association.—Within trials of both experiments, males varied widely in color differences, and it is possible that females only associated with redder or brighter males when color differences were large. If so, then the difference between coloration of males should be positively related to the difference in time a female spent with males within a trial. In contrast to this prediction, there were no positive or significant relationships between color score differences and differences in time spent with males in a trial for the natural or manipulated experiment during the 0 Hour and 24 Hour periods. In fact, all of the slopes were near zero or negative (range of $b = -0.36$ to 0.08, $n = 10$, all $P > 0.05$). Therefore as color

differences between males increased, females did not spend a greater amount of time with redder or brighter males.

Female behavior in the experimental aviary.—Males and females rapidly adjusted to the experimental aviary and females spent the majority of time during trials on the three perches rather than on the floor or netting. Typically within the first 15 minutes after males were introduced, females had visited each of the side compartments. Singing occurred in 7 of the 10 natural trials and 8 of the 10 manipulated trials, but I was unable to determine from the videotapes which male (or female) sang. In any one trial singing occurred for less than 5 minutes. When adjacent to a male compartment, females sat on perches for relatively long times but regularly interrupted these periods by flights back and forth between and within the two side male compartments. Such flights also occurred in the pre-trial periods.

Site preferences by females.—Females did not spend more time consistently on the east or west side of the experimental aviary (Wilcoxon test, two-tailed: natural trials: Pretrial $Z = 1.13$, $P > 0.05$, $n = 10$, 0 Hours $Z = 0.06$, $P > 0.05$; 24 Hours $Z = 0.05$, $P > 0.05$; Reversed $Z = 1.07$, $P > 0.05$; manipulated trials: Pretrial $Z = 0.41$, $P > 0.05$; 0 Hours $Z = 1.38$, $P > 0.05$; 24 Hour $Z = 1.07$, $P > 0.05$; Reversed $Z = 0.97$, $P > 0.05$). Between the pre-trial and 0 H periods, females did not exhibit a tendency to remain on the same side of the experimental aviary (binomial test, natural trials: $T = 3$, $P > 0.05$, $n = 8$, manipulated trials: $T = 5$, $n = 10$, $P > 0.05$). In the 0 H and 24 H periods, most females remained on the same side (binomial test, natural trials: $T = 5$, $n = 10$, $P > 0.05$; manipulated trials: $T = 8$, $n = 10$, $P = 0.01$) indicating that females were likely to associate with the same male in the 0 H and 24 H sampling periods. However, in the 24 H and the reversed sampling periods, females again spent the majority of time on the same side (binomial test, natural trials: $T = 7$, $n = 9$, $P = 0.02$; manipulated trials: $T = 6$, $n = 8$, $P = 0.035$), indicating that females did not consistently associate with the same male once the males' positions were reversed.

Morphological variables.—In the trials using natural plumage coloration, males with the

higher color score did not have a longer tarsus length, crest length, tail length, or black bib size (Table 1; Wilcoxon rank tests: all $P > 0.05$). Likewise, males in the reddened and lightened groups did not differ significantly in morphological measurements (Table 2, Wilcoxon rank tests, all $P > 0.05$).

DISCUSSION

During the majority of observation periods, females spent significantly more time with one male. However, the two experiments provided no evidence to support the hypothesis that female Northern Cardinals prefer males with redder or brighter coloration. In trials using natural plumage coloration, females were as likely to spend more time with males having low color scores as with those having high color scores (Fig. 1). Similarly in the manipulated trials, where average plumage differences between males were greater than in the natural trials, females still did not spend more time with redder or brighter males (Fig. 2).

These results differ from other studies of female preference in passerines. Under aviary conditions analogous to the conditions I used, females of many species showed a preference for brightly colored males (Johnson 1988, Hill 1990, Enstrom 1993, Johnson et al. 1993, Sætre et al. 1994, Sundberg 1995; but see Rohwer and Røskaft 1989, Alatalo et al. 1990, Butcher 1991). Although bright plumage colors do not seem important in gallinaceous species, females show preferences for other male ornaments (Zuk et al. 1992, Buchholz 1995, Ligon and Zwartjes 1995, Mateos and Carranza 1995).

The individuals adapted well to captivity and appeared to be in breeding condition. The experiments were conducted at a seasonally appropriate time when pair formation occurs in central New York (pers. obs.). Behaviors associated with pair formation such as singing and slow flight displays occurred in the housing aviaries and during experimental trials, suggesting that males were responding to female presence.

Assigning female preference based on the total time spent with males has become a standard method in avian studies of female choice (Burley et al. 1982, Burley 1986, Hill 1990, Enstrom 1993, Johnson et al. 1993, Sundberg 1995). Observations of pair formation in the

field indicate that male and female cardinals interact extensively, consequently time spent with males should be a reasonable indication of mate preference (Kinser 1973).

While males in this study appeared to exhibit some behaviors associated with pair formation, female behavior was more ambiguous. Females flew toward the male area regardless of whether the male was present or not. The side of the aviary on which females spent more time changed from the pretrial to 0 hour sampling period, indicating that females did not immediately establish a preference for one side of the experimental aviary and may have responded to the addition of the males. However, females preferred the same side of the aviary during the 24 hour and reversed sampling periods, even though the males had switched sides. This suggests that after 24 hours individual males did not strongly influence where females spent more time.

With the sample sizes used, the power of the binomial test is high at the critical value. It is noteworthy that other choice experiments of this design have found significant female preferences with similar sample sizes (ranging from 7 to 21 females; Hill 1990, Enstrom 1993, Sætre et al. 1994, Sundberg 1995). This suggests that if a preference for red color exists, it is weak in comparison to color preferences found in other passerines.

The dietary basis of red coloration in male cardinals suggests that females could acquire information about a male's foraging abilities or ability to defend resources using coloration. Male color and his absolute effort in feeding nestlings are not related in cardinals (Linville et al. 1998), emphasizing the limitation of using red coloration alone to assess mates. However, females mated to brighter males fed nestlings less (Linville et al. 1998), suggesting that there may be advantages to pairing with brighter males.

My results provided no evidence for female preference for brighter or redder male plumage coloration as a single criterion for mate choice; however, the possibility remains that female cardinals assess mates using a combination of factors, including coloration, as has been found in other species (Zuk et al. 1990; Omland 1996a, b; Scheffer et al. 1996; Møller et al. 1998). The prolonged opportunities for direct interactions between males and females

prior to pairing (Kinser 1973) suggests that females may be able to use other male characteristics in mate choice, such as song or courtship behaviors. If females assess male condition, multiple ornaments or traits may provide more accurate information either through redundancy or because some ornaments are unreliable indicators of condition (Møller and Pomiankowski 1993). It also remains possible that females assess male coloration in some circumstances but not other. For example, females may use different criteria when choosing social mates and when choosing extra-pair mates.

Lastly, territorial resources may influence mate choices, but coloration may be relatively more important in mediating competition between males. Redder male cardinals acquire territories with denser vegetation density, and pairs on these territories produce more offspring, most likely because of reduced nest predation (Wolfenbarger in press). Given the importance of territory quality, females may directly assess a male's territory during pair formation rather than relying on plumage coloration alone for mate choices.

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