RELATIVE EFFECTS OF PLUMAGE COLORATION AND VEGETATION DENSITY ON NEST SUCCESS[1]

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Abstract. Many passerine species are highly dichromatic with brightly-colored males and cryptically-colored females. Bright plumage in males is commonly thought to arise as a result of sexual selection by females such that males with bright coloration possess high fitness. However, bright plumage potentially could expose males to increased predation risk. Consistent with this idea, males of many highly dichromatic passerine species do not incubate. I tested whether brightly-colored males avoid incubation to reduce the probability of visual predators locating their nest. This hypothesis predicts greater hatching success for clutches incubated by cryptically-colored individuals than by brightly-colored individuals. The Northern Cardinal (*Cardinalis cardinalis*) is a common dichromatic species that breeds throughout the eastern U.S. I placed two button-quail (*Turnix sp.*) eggs in each of 203 simulated cardinal nests. Dull brown cardboard, simulating a female cardinal, was placed over about half of all clutches. Bright red cardboard, simulating a male cardinal, was placed over the other clutches. Nest success was highest for well-concealed nests (87%) and lowest for nests in open habitat (54%). Nests containing red cardboard did not have significantly lower success than nests with brown cardboard, nor did I detect a significant color × vegetation-density interaction. My analysis may have had insufficient power to detect an effect of color on nest success; alternatively, brightly-colored males that do not incubate may achieve benefits unrelated to predation risk.

Key words: Cardinalis cardinalis, incubation, nest success, Northern Cardinal, plumage coloration, predation, sexual selection.

INTRODUCTION

Plumage dichromatism commonly is thought to arise through sexual selection with females preferring brightly-colored males (Darwin 1871, Butcher and Rowher 1989, Andersson 1994). However, males with bright coloration could experience increased risk of predation if those males are more easily detected (Andersson 1994, Götmark and Hohlfält 1995). Verner and Willson (1969) suggested that males of dimorphic species are less likely to incubate than are males of monomorphic species. Brightly colored males may be constrained to avoid incubation to reduce the probability of a visual predator discovering them or their nest (Verner and Willson 1969). Alternatively, males of dimorphic species may not experience reduced fitness by incubating, but choose to avoid incubation perhaps in an effort to procure other mates. For example, Møller and Birkhead (1994) found that male plumage brightness across species was positive-

ly correlated with degree of extrapair copulations.

The hypothesis that brightly-colored males are constrained to avoid incubation predicts a negative correlation between nest success and plumage brightness of incubating individuals. Martin and Badyaev (1996) detected a negative correlation between nest success and female plumage brightness after pooling data from the literature on nest success of warbler (*Parulinae*) and finch (*Carduelinae*) species in which only the female incubates. However, correlations provide relatively weak inference (Romesburg 1981). For example, plumage brightness is related to nest height (Martin and Badyaev 1996). A negative correlation between plumage color and nest success potentially could reflect higher predation rates in more open nest habitat regardless of plumage color. I tested the hypothesis that brightly-colored males are constrained to avoid incubation using a manipulative experiment in an effort to obtain strong inference (Romesburg 1981).

The Northern Cardinal (*Cardinalis cardinalis*) is a highly dichromatic passerine common throughout the eastern U.S. and southern Ontar-

io. Males possess bright red plumage, whereas the plumage of the female is a duller reddish brown. Incubation in cardinals usually is performed by the female (Terres 1979). I used artificial nests and simulated male and female cardinals to test whether incubation by males reduced nest success.

METHODS

I studied 203 simulated cardinal nests in spring and summer 1997 at the USGS Patuxent Wildlife Research Center in Laurel, Maryland. An *a priori* power analysis revealed that a one-tailed 2 × 2 chi-square test with 200 nests and alpha = 0.10 would have power = 0.92 to detect the difference between 60% success for females and 40% success for males (Cohen 1988). Nests consisted of open, circular wicker baskets with a 7 cm inside diameter at the top and 3.5 cm diameter at the bottom. Nests were 3 cm deep. All baskets were dyed brown using fabric dye and allowed to dry for several days prior to being placed in the field. Jute twine was threaded through the sides of the baskets and used to position them in vegetation. Baskets were in place for at least one night before eggs were placed in them. Cotton balls were dyed brown and used to line nests.

Japanese Quail (*Coturnix coturnix*) eggs, which are sometimes used in dummy nest studies, are larger than cardinal eggs and might be too large to be eaten by eastern chipmunks (*Tamias striatus,* Haskell 1995) or white-footed mice (*Peromyscus leucopus,* DeGraaf and Maier 1996), both potential nest predators. I used button-quail (*Turnix* sp.) eggs which are only slightly smaller than cardinal eggs (Harrison 1975). Two button-quail eggs were placed in each basket. Clutch size in cardinals is 2–5 eggs (Bent 1968, Harrison 1975), with a mean in Maryland of 2.4 (Robbins and Blom 1996).

Each model cardinal consisted of a 5 × 11 cm piece of corrugated cardboard folded down the middle along the short axis. Models generally protruded from the top of a nest by 4 cm, and were held in place in a nest solely by friction. For male cardinal models, I glued a 5 × 11 cm piece of bright red construction paper to the top surface of the cardboard. Dull brown construction paper was used for female cardinal models. Construction paper was selected to match the dorsal plumage of cardinals as depicted in Peterson (1980). Color of cardboard

was randomly assigned to each nest. A reflectance spectrophotometer with a range of 400–700 nm (Color Mate Colorimeter, Milton Roy, Rochester, New York) was used *a posteriori* to compare red and brown cardboard to the back, breast, and crown coloration of an actual male and female cardinal specimen using the opponent color coordinate system (L, a, b; where L measures brightness, $a > 0$ measures redness, and $b > 0$ measures yellowness, see Graves 1998 for details). I also estimated the 3-dimensional difference, d, between red and brown paper and the estimated difference between male and female cardinals using the equation:

$$d = ([L_{male} - L_{female}]^2 + [a_{male} - a_{female}]^2 + [b_{male} - b_{female}]^2)^{0.5}$$

Nests were placed throughout a 1.5 km² portion of the central tract of the research center. The study area consisted mostly of open fields crossed by wooded streams and fence rows and was bordered by woodland (Hotchkiss and Stewart 1947). Several ponds were scattered throughout the area. Northern Cardinals were abundant. I attempted to place nests in cardinal habitat, generally shrubs along a fence row or field-forest ecotone (Stewart and Robbins 1958, Filliater et al. 1994). All nests were placed between 0.6 and 2.5 m of the ground; most were approximately 1.5 m above ground level. Nests were spaced ≥ 30 m, and usually ≥ 70 m apart. I recorded nest locations with detailed field notes. Nest markers were not used. Neither Conner et al. (1986) nor Filliater et al. (1994) detected a relationship between nest concealment and nest success of actual cardinal nests. Thus, initially I did not formally estimate nest concealment prior to placing eggs in the field, although I did casually record whether some nests appeared either particularly conspicuous or so concealed as to be difficult to relocate. Before 50 nest trials were completed, I began to suspect from my initial results that nest success was related to nest concealment. I subsequently devised a qualitative classification of nest concealment. If a nest was visible from most (generally ≥ 50%) horizontal directions at a distance of 3 m, then habitat was considered open. Habitat was considered closed if a nest was not visible in most (generally ≥ 75%) horizontal directions at a distance of 1 m. All other nests were considered partially concealed. Nest concealment was estimated formally prior to egg place-

ment (and color assignment) for 153 of the 203 nest trials, after egg placement for the first 50 trials, and after the fate of 33 nests was known. Thorns were considered present generally if they were found within 20 cm of the nest.

Cardinals in Maryland nest from early April–late August, peaking late April–early July (Stewart and Robbins 1958). My first nest trials began April 27; the last ones ended August 18. Some authors have reported variation in nest success across the breeding season (Picman 1988, Sloan et al. 1998). I grouped nests into early (initiated April 27–May 15, $n = 65$), middle (initiated May 29–June 12, $n = 69$), and late (initiated July 19–August 3, $n = 69$) breeding season.

Cardinals incubate for 12–13 days (Harrison 1975). I defined a successful nest as one in which both eggs remained in the nest and intact for 13 days. If either egg was missing or broken before 13 days had passed, then the nest was considered to have failed. Each nest in the early group was checked 6.9 times on average; nests in the other two groups were checked an average of 3.3 times. During each nest visit, I removed each egg and carefully examined it for signs of predation. Occasionally the cardboard cover was found out of the nest with both eggs still present and intact. In these instances the cover was replaced and the nest trial continued until 13 days had elapsed since egg placement.

DATA ANALYSES

Data were analyzed using the program SURVIV (White 1983). Nests were grouped into 35 cohorts, each representing a different color × period × vegetation density × thorn combination. Cohort size was the number of nests in each combination. For each cohort, the number of nests that succeeded out of the total number of nests placed was used to estimate the probability of surviving. I began the analysis with the most general model in which all 35 cohorts were allowed to have different survival probabilities. I then tested for an effect of time, then thorns, then vegetation density. When testing for an effect of a particular variable, I compared models with and without survival constrained equal for all cohorts that differed only by that variable. For example, when testing for an effect of time, I compared the most general model with a model in which survival of the "red × early × open × no thorns" cohort was constrained equal to survival of the "red × middle × open × no

thorn" and "red × late × open × no thorns" cohorts, and so on. Models were compared using a likelihood ratio test and Akaike Information Criteria (AIC_c, Burnham and Anderson 1998). If the constrained model had a lower AIC_c value than the general model, then I concluded the variable being tested did not significantly affect survival. If no effect of a particular variable was detected, then that variable was "removed" from subsequent analyses by retaining the relevant constraint statements, and the constrained model became my new most general model against which I tested for effects of the next variable of interest.

Once all variables had been tested and the final model was constructed, I attempted to estimate confidence in the results by setting male success equal to the product of female success and a coefficient (β), then examining the 95% confidence interval on that coefficient (Gerard et al. 1998). For example, if 40% of red nests were successful and 60% of brown nests were successful, then $0.4 = \beta \cdot 0.6$, and $\beta = 0.67$, suggesting that red cardinals had 33% lower nest success (1–0.67) than brown cardinals in all habitats combined. However, if 95% confidence intervals on β encompassed one, then I would have no evidence that color affected survival probabilities. A test for a color × vegetation density interaction was conducted by comparing a model with habitat-specific coefficients (β_{open}, $\beta_{partial}$, and β_{closed}) vs. a model with one coefficient across habitats ($\beta_{open} = \beta_{partial} = \beta_{closed} = \beta$). Values presented for survival rates and β coefficients are means ± SE.

RESULTS

A posteriori comparisons of red and brown paper with an actual male and female cardinal specimen indicated that the colors I used were more similar to the breast plumage than the dorsal plumage of real cardinals (Table 1). The estimated 3-dimensional difference in color between red and brown paper ($d_{paper} = 31.7$) was larger than that for male and female back color ($d_{back} = 17.4$), but smaller than that for male and female breast color ($d_{breast} = 55.4$), and was closest in magnitude to the estimated difference in crown color ($d_{crown} = 26.6$).

Because no effect of time was detected, survival of nests in all three breeding-season periods were constrained equal. I did not detect an effect of thorns either. However, vegetation den-

TABLE 1. Comparison of red and brown cardboard with back, breast, and crown color of an actual male and female cardinal measured using a reflectance spectrophotometer, and L, a and b of the opponent-color coordinate system. Here, L measures brightness, a measures redness, and b measures yellowness (see Graves 1998 for details).

Color metric	Red paper	Brown paper	Male			Female		
			Back	Breast	Crown	Back	Breast	Crown
L	40.08	54.66	29.21	39.29	29.79	37.41	58.10	30.37
a	37.26	9.15	17.21	49.71	35.01	2.09	2.92	11.54
b	16.04	14.01	12.42	40.09	25.68	9.90	17.18	13.28

sity was significantly correlated with survival. Nest success was 54 ± 8% in open habitat, 73 ± 4% in intermediate habitat, and 87 ± 5% in closed habitat. Success was significantly lower in open habitat than in intermediate habitat, and significantly lower in intermediate habitat than in closed habitat. I deleted all nests in the early period and reran the analysis to test whether I may have biased my results when retroactively assigning the first 50 nests to a habitat category. Results were similar and led to the same conclusion.

Nests containing red paper did not have significantly lower success than nests with brown paper (Table 2). Habitat-specific estimates of nest success for red cardinals compared to brown cardinals were β_{open} = 0.74 ± 0.23, $\beta_{partial}$ = 0.92 ± 0.11, and β_{closed} = 1.20 ± 0.17, meaning, for example, that red cardinals had an estimated 26 ± 23% lower nest success than brown cardinals in open habitat. However, in each habitat type, equal success for red and brown cardinals (for example, β_{open} = 1.0) was encompassed by the 95% confidence intervals on those coefficients (0.28–1.20, 0.71–1.14, and 0.85–1.54 for β_{open}, $\beta_{partial}$, and β_{closed}, respectively), providing no evidence of an effect of color on nest success. Also, β = 1.04 ± 0.08, meaning red and brown cardinals had virtually identical nest success in all habitats combined. Finally,

TABLE 2. Estimated nest success by color and habitat.

Color	Vegetation density	Number successful	Number failed	Estimated success[a] (%)
Red	Open	8	10	44 ± 12
Brown	Open	15	10	60 ± 10
Red	Intermediate	37	16	70 ± 6
Brown	Intermediate	40	13	75 ± 6
Red	Closed	29	2	93 ± 4
Brown	Closed	18	5	78 ± 9

[a] Estimates for red and brown were not significantly different.

the model with β was selected over the model with β_{open}, $\beta_{partial}$, and β_{closed}, indicating no significant color × vegetation density interaction.

DISCUSSION

Several studies have reported a correlation between concealment and success of real nests (Martin and Roper 1988, Johnson 1997). Other studies using real or artificial nests did not detect such a correlation (Howlett and Stuchbury 1996, Sloan et al. 1998). Filliater et al. (1994) found no correlation between nest concealment and success of actual cardinal nests in Ohio. My results indicate that nest concealment was important to clutch survival, at least in this model system.

Numerous possible reasons may exist for the different results of Filliater et al. (1994) and this study. Predator abundance and diversity may have differed between the two areas (Picman 1988, Yahner 1996). Filliater et al. (1994) did not estimate nest success through the hatching stage, but did report that 15% of cardinal nests fledged young in their study (Filliater et al. 1994). Low success through the fledging stage suggests that predation was more intense in their study area than mine. Nevertheless, an abundance and diversity of potential nest predators were present in my study area: red fox (*Vulpes fulva*), gray fox (*Urocyon cinereoargenteus*), raccoon (*Procyon lotor*), eastern gray squirrel (*Sciurus carolinensis*), eastern chipmunk, *Peromyscus sp.*, black rat snake (*Elaphe obsoleta*), American Crow (*Corvus brachyrhynchos*), Blue Jay (*Cyanocitta cristata*), House Wren (*Troglodytes aedon*), Grey Catbird (*Dumetella carolinensis*), and Brown-headed Cowbird (*Molothrus ater*). The size of my study area (1.5 km²) suggests that many individual predators of several different species may have been responsible for observed depredation.

Using artificial nests enabled me to have a

40% larger sample size, with resulting greater statistical power, than Filliater et al. (1994). I also was able to place nests in the broadest range of vegetation density possible. I placed 44 nests (22%) in habitat so open as perhaps to be biologically unrealistic. Little time was spent searching for real nests. However, none of the 19 actual nests, including 4 active cardinal nests, that I found during field work was in open habitat. The observed high predation rate on artificial nests in open habitat together with the absence of real nests in this habitat may reflect the ghost of predation past: adaptive selection of concealed nesting sites in response to intense predation of unconcealed nests in the past. A total of 54 artificial nests (27%) was placed in very dense vegetation. These nests had high success. Well-concealed real nests may be underrepresented in studies of predation if such nests have low detection probabilities.

Nevertheless, numerous possible biases are associated with using artificial nests to estimate actual predation rates, including presence of human scent, lack of bird scent, absence of bird activity around the nest, and unrealistic nest appearance and placement (see Wilson et al. 1998 and Sloan et al. 1998 for reviews). Some of these biases may have resulted in an over-estimate of actual nest success of cardinals in my study area. However, my primary objective was testing for a relative effect of bright vs. dull color on nest success, rather than estimating actual nest success *per se*. In so doing, all nests were treated the same except for density of the surrounding vegetation, color of the model cardinal, and frequency of nest visitation.

May 1997 was very windy, so I made frequent visits to nests that month to replace covers. I did not formally test for an effect of visitation rate on nest success. However, no difference in nest success was found between the three time periods used in this study despite more frequent nest checks in the early period (but see Major 1990).

Martin and Badyaev (1996) detected a negative correlation between female plumage brightness and nest success using pooled data for warbler and finch species taken from the literature. Results from the present study suggest that nest concealment is more important to nest success than is plumage brightness. Sloan et al. (1998) reported predation rates on uncovered artificial passerine nests 3–4 times that of real passerine

nests in shrub habitat within a northern hardwood forest. Concealing eggs with a cover may substantially increase success of artificial nests regardless of vegetation density or color of the covering. I did not test this possibility by including artificial nests without covers in this study. However, Linder and Bollinger (1995) reported that domed artificial Ovenbird (*Seiurus aurocapillus*) nests, placed on the ground, had higher survival than similar open-cupped artificial nests. In a study similar to mine, Haskell (1996) did not detect an effect of color on success of artificial nests in trees, although color did influence success of artificial ground nests. Haskell's (1996) different results between ground and tree nests also suggests that habitat effects on nest success may supercede effects of plumage color, although Haskell (1996) did not estimate nest concealment. Stutchbury and Howlett (1995) did not detect a correlation between degree of conspicuous plumage in female Hooded Warblers (*Wilsonia citrina*) and nest success. Some studies have reported that raptors were more likely to attack conspicuous avian prey (Götmark 1993, Götmark and Olsson 1997), while other studies found that raptors attacked bright avian prey less often than duller-colored individuals (Götmark 1996, Götmark et al. 1997). Filliater and Breitwisch (1997) found that male cardinals provide significant nestling care. The authors suggested that male cardinals do so without endangering the young. Furthermore, Ritchison et al. (1994) reported 14% (5 of 37) of cardinal nestlings in their study came from extra-pair fertilizations, consistent with the hypothesis that brightly-colored males that do not incubate may achieve benefits unrelated to predation risk, although the authors considered 14% to be a relatively low percentage compared to other passerines.

Although my results suggested that male cardinals are not constrained to avoid incubation, my study may have included biases additional to those usually associated with studies using artificial nests. My simulated cardinals did not resemble actual cardinals except in color, and even here I assume that I have reasonably duplicated plumage coloration (but see Bennett et al. 1994, Götmark 1996). Red paper did not fade in the field; however, brown paper tended to fade slightly ($L = 56$, $a = 12$, $b = 15$). Occasionally, fading was more noticeable, particularly in open habitat. Fading may have made brown paper

more conspicuous, increased predation rates on these nests, and reduced my ability to detect an effect of color on survival (Yahner and Mahan 1996). If fading had been directly responsible for predation of as few as 3 brown nests, this would have been enough to obscure a significant effect of plumage color on survival in open habitat (95% C.I. on β_{open}: 0.26–0.97). However, fading alone would have had to have been directly responsible for 46% (6 of 13) of failed brown nests in intermediate habitat to have obscured an effect of color on survival of these nests. This latter possibility seems intuitively improbable. Any bias associated with structural appearance of the models, if not their color, should have operated on all nests equally.

Another important possible limitation in this study was my inability to test for a movement × plumage color interaction that may attract predators to nests during the incubation stage (Götmark and Olsson 1997, Götmark et al. 1997). Absence of movement at my nest sites may have increased success of nests with red paper. Brown-headed Cowbirds are thought to locate nests by observing behavior of the host (Thompson and Gottfried 1976). It is not known if cowbirds disproportionately parasitize nests of brightly-colored hosts. Nor is the incubation behavior of female cardinals, in particular the amount of movement around the nest during the incubation stage, well known. Laskey (1944) reported that "during incubation, the male feeds the female, usually when she is off the nest" suggesting that a significant amount of movement around the nest may occur during incubation.

Although I did not detect a color × vegetation density interaction, there was some suggestion that the cost of incubation for brightly-colored males may be negatively-correlated with vegetation density ($\beta_{open} < \beta_{partial} < \beta_{closed}$) and my study was too weak to detect it. Detecting an effect of color on nest success with power = 0.90 for a one-tailed 2-×-2 chi-square test with alpha = 0.10 and β = 0.75 would require 314 nests, all placed in vegetation of uniform density. Detecting an effect of color with β = 0.80 would require 484 nests. These estimates of required sample size may be of use if experiments similar to mine are conducted in the future.

In conclusion, dense vegetation appeared to be much more important than plumage coloration in achieving high nest success in my study.

I failed to detect evidence that "incubation" by brightly-colored models reduced nest success. This may have been due to relatively low statistical power, absence of movement at nests, or possibly to reduced survival of some brown nests resulting from fading. Alternatively, brightly-colored males may simply choose not to incubate in an effort to procure other mates. Sample sizes required to achieve high power were calculated for tests using smaller effect sizes than were used in this study. Tests involving covers with other colors or patterns, placed in various habitat types, could improve our understanding of avian plumage and behavior. Ideally, the color of coverings should be selected a priori to match the reflectance of dorsal plumage of museum specimens of the species of interest. Marking the location of covered nests with similar-colored flagging tape nearby could be one way of simulating movement of adult birds near artificial nests.

ACKNOWLEDGMENTS

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