

NORTHERN CARDINAL SEXES DEFEND NESTS EQUALLY

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ABSTRACT.—We exposed nesting Northern Cardinals (*C. cardinalis*) to models of three predators of cardinal eggs or nestlings (black rat snake [*Elaphe obsoleta*], Blue Jay [*Cyanocitta cristata*], and eastern chipmunk [*Tamias striatus*]). We attempted to determine relative contributions to nest defense by males and females during the mid-nestling stage of the nesting cycle. For all defense variables monitored, mean responses did not differ between the sexes, although females spent more time in attendance at the nest. Latency to response to the models was strongly correlated between mates, but responses by mates appeared to be independent at the nest. There was little evidence for stimulus-specific defense. Parent bird responses to the predator models and to a mounted Mourning Dove (*Zenaida macroura*, a “non-threat”) likewise did not differ. Active defense of nests may be of limited importance to reproductive success in this cardinal population. Received 7 May 1996, accepted 20 Oct. 1996.

Mates of biparental species invest considerable time and energy in the production of independent offspring (Clutton-Brock 1991). However, studies of parental care in many passerines suggest that male and female parental roles can differ; the sexes may contribute disproportionately to brooding, nestling feeding, or to other components of care, including nest defense (e.g., Breitwisch 1988, Rytönen et al. 1993). Theoretically, individuals of both sexes act to maximize their own reproductive success (Trivers 1972). Such a strategy can produce apparently cooperative behavior between mates, as males and females invest in the same offspring. However, individuals need not invest equally, despite the shared benefit of offspring production (e.g., Maynard-Smith 1977).

The sexes may be predicted to differ in their parental effort if their costs and benefits of that effort are unequal (Montgomerie and Weatherhead 1988). For example, male-biased operational sex ratios (as often found in passerines; see Breitwisch 1989) may lead to unequal levels of care between the sexes (Trivers 1972, Breitwisch et al. 1986). Further, individual characteristics (e.g., age, experience, body condition, certainty of parentage) may differ within pairs, causing mates to differ in their ability or willingness to engage in parental care (Redondo 1989). Additionally, males and females of dichromatic species may face very different risks in engaging in some aspects of parental care. The presence of the more “visible” sex at or near the nest may increase the probability of

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attraction of a visually-orienting predator dangerous to the nest contents or the adult bird (Skutch 1976).

The Northern Cardinal (*C. cardinalis*) is a monogamous and biparental passerine which builds open-cup nests within several meters of the ground (e.g., Kinser 1973). Cardinals are highly dichromatic, males having brilliant red plumage, while females have brown plumage. In our study population, the rate of nest predation was severe, and little influenced by nest location (Filliater et al. 1994). Thus, parental defense of nest contents may be crucial for reproductive success in this population. Given the potential for males and females to differ in their levels of activity around the nest because of inequalities in the costs and benefits of doing so, we investigated the relative contributions of the sexes to the active defense of their nests. Our primary goal was to examine sex differences in defensive behavior, an important component of avian parental care (Montgomerie and Weatherhead 1988).

STUDY AREA AND METHODS

We conducted this study in 1992 and 1993 at the Aullwood Audubon Center and Farm, a National Audubon Society property ca. 15 km NW of Dayton, Ohio (see Filliater et al. 1994 for site description). Defense levels were measured for 24 breeding pairs by presentation of a predator model at the nest during the mid-nestling stage (nestlings aged 3–8 days post-hatch). At this stage in the breeding cycle, both sexes visit the nest with or without food for the nestlings (pers. ob.); females brooded nestlings periodically as well. Each pair was exposed to only one of three different predator models [taxidermic mounts of an Eastern Chipmunk (*Tamias striatus*) and Blue Jay (*Cyanocitta cristata*), and a black rubber snake ca 1.2 m in length colored to resemble a black rat snake (*Elaphe obsoleta*)]. The response of each pair to a taxidermic mount of a Mourning Dove (*Zenaidura macroura*, a “non-threat”) was also measured. In 1992, experimental trials were conducted with 18 different breeding pairs. Each of the three predator models was used at six different nests. In 1993, six additional trials were conducted with the snake model to which was attached a monofilament line. This was used to move the head of the snake model slightly, ca once per minute while in place at the nest (e.g., Siderius 1993, Maloney and McLean 1995). Each pair tested in 1993 was exposed to the stationary dove model as before.

All experimental trials were begun between 06:00–09:30 EST. Two persons were involved in each trial. One person handled the models and then withdrew from the immediate area. The second individual remained stationary on the ground, behind vegetation if possible, and recorded observations from a distance of 10–12 m from the nest. Before model presentation, parental nest visits were monitored (average duration 84 min) to ensure that both parents were attending the nest. Once both parents were out of view, the first model was placed at nest height, ca 1 m from and facing the nest. The model was placed so that it appeared to be resting on a limb or twig. The use of the dove or predator model first was alternated between trials.

The duration between model placement and parent bird return averaged 9 min (range: 1–33 min). Once either or both parent birds returned to within 10 m of the nest, data were collected for 3 min. Observations of parent bird defensive response and location relative to the nest and model were spoken into a tape recorder and were collected separately for mates if both responded. After 3 min, the handler approached and removed the model. Undisturbed

(no model in place) nest visits were again monitored, for an average of 105 min (range: 86–178 min). After this period, the second model (either dove or predator) was placed as before. Again, one or both parent birds returned after a short duration (\bar{x} = 13 min), and their response was monitored for 3 min. Once the second model was removed, post-trial nest visits were then monitored (\bar{x} = 35 min).

The first variable monitored was the duration between model placement and parent bird return to within 10 m of the nest (response time: RT). Because parent birds did not always feed the nestlings when visiting the nest, we took RT as a measure of the latency for parent bird discovery and response (e.g., Curio and Regelmann 1987). We also measured the portion of the 3-min response period for which a bird remained within 10 m of the nest (time present: TP). Parent bird distance to the model was estimated and recorded each time a bird changed its location; from these data parent bird closest (CDM) and furthest distance to the model (FDM) were determined. Parent bird distance to the model at the end of each 15 sec interval during the 3-min response period was also noted; these interval-end distances were averaged to provide mean distance to the model (MDM).

Parent bird calling rate (CR, calls/min) was also determined. Only one type of call (variously described as “chip” or “click”) was counted. These calls are known to be used in situations of agonism or alarm (Lemon 1968, Kinser 1973) and made up the vast majority of cardinal vocalizations during nest visits (PMN, unpubl. data). In addition, any threat displays or attacks on the model were noted.

Many nests visits by both sexes before, between, and after model presentations were observed. Visit frequency, mean duration, and calls/visit were tabulated for both sexes to allow an assessment of overall nest attendance and call usage during these undisturbed (no model present) nest visits. Brood characteristics (size and age) were also recorded to determine the cues by which the sexes may determine their defense levels.

A total of 24 pairs of birds was sampled. However, responses by only one member of a pair were common. Likewise, some birds made no nest visits between or after model presentations. As such, sample size varies among analyses. To simplify presentation, for some analyses a single value N_i is given to reflect the total number of individuals sampled (up to a maximum of 24 of each sex) in an incomplete block design (Sokal and Rohlf 1981, p. 394).

Nonparametric statistical tests (Siegel and Castellan 1988, SAS Institute 1990) were employed. Paired analyses were used when possible (e.g., mates within pairs or a bird acting as its own control). However, the frequent lack of response by one member of a pair necessitated the use of non-paired analyses in some cases.

Variable means were compared by the Wilcoxon matched-pairs, signed ranks test (T value reported) for paired comparisons and by the Mann-Whitney U -test (U value reported) for $k = 2$ independent cases. Variable mean comparisons for $k > 2$ independent cases were by the Kruskal-Wallis one-way ANOVA (H value reported). The G -test (G_{adj} reported) or binomial test was used to measure association; Spearman rank correlations (r_s reported) were used to examine the strength of variable correlations.

All tests were two-tailed unless otherwise stated. The α value for significance of statistical tests was set at $P = 0.05$ for singular comparisons. The comparison-wise error rate (Chandler 1995) was conservatively reduced to α/k for k simultaneous comparisons.

RESULTS

Response to models.—An assumption of this experiment was that the parent birds responded to the presence of the models near their nest. This was tested by comparing the number of calls given by parent birds on

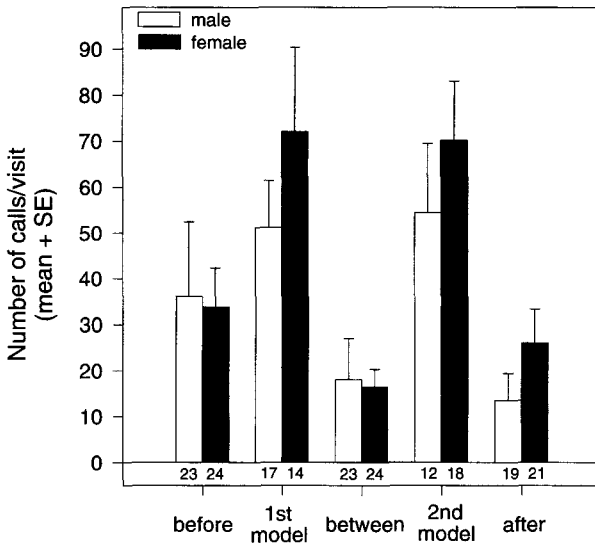


FIG. 1. Grand mean + SE of the number of "chip" calls given on nest visits by Northern Cardinals before, between, after, and during model presentations. Number of birds sampled given below bars.

visits to the nest when *any* of the models was present with the number of calls given on nest visits before, between, and after model presentations (visits during which females brooded nestlings were excluded).

Males gave similar numbers of calls on nest visits before, between, and after model presentations ($H = 2.12$, $N_t = 23$, $df = 2$, NS) as did females ($H = 3.38$, $N_t = 24$, $df = 2$, NS; Fig. 1). Males gave similar numbers of calls to the first and second models ($U = 89.5$, $N_t = 16$, NS) as did females ($U = 124.0$, $N_t = 18$, NS). However, more calls were given during model presentations than when no model was present both by males ($T = 11.0$, $N = 18$, $P = 0.0013$) and by females ($T = 23.0$, $N = 23$, $P = 0.0014$). Both sexes called at higher rates during nest visits when models were in place (males, $T = 43.0$, $N = 19$, $P = 0.04$; females, $T = 53.0$, $N = 21$, $P = 0.03$). In addition, nest visit mean duration was greater, when models were in place, for both males ($T = 24.0$, $N = 19$, $P < 0.005$) and females ($T = 28.0$, $N = 21$, $P = 0.0025$). These results suggest that parent birds clearly responded to the presence of the models, but that encountering a model at the nest had no apparent lasting effect on the birds' behavior.

Our planned comparisons were to examine male-female response differences. Because several predator models were used to elicit defensive behavior, we first examined within-sex defensive behavior among the

predator model types for each of the response variables monitored (for example, male response time was compared among the different predator model types). For both males ($H = 1.03$ to 4.97 , $N_t = 17$, $df = 3$, all NS) and females ($H = 2.33$ to 8.53 , $N_t = 16$, $df = 3$, all NS), no model-specific behaviors were detected. This suggests that response data may reasonably be pooled among the predator models for each sex.

We then compared responses to the predator versus the dove models for each sex. The strongest inference of predator-dove model response differences is obtained from paired data of individuals which responded to both models (for example, comparison of individual male response times to the dove and predator models). For all variables, the responses given by males ($T = 10.0$ to 20.0 , $N = 9$, all NS) and females ($T = 5.0$ to 30.0 , $N = 11$, all NS) to the control and predator models did not differ. A total of 12 males and 16 females responded to the dove model; a total of 17 males and 16 females responded to the predator models. Unpaired analyses (which make use of all available data) of all defense variables monitored likewise suggest no difference in response to the dove or predator models for either sex (males, $U = 74.5$ to 97.5 , all NS; females, $U = 89.5$ to 122.0 , all NS).

Male-female responses.—For those pairs which responded in tandem to the predator models, male and female responses did not differ for any of the response variables monitored ($T = 6$ to 17 , $N = 9$, all NS). Only response time to the predator models was correlated between mates ($r_s = 0.96$, $N = 9$, $P < 0.01$). Nonpaired analyses were used to examine the full set of response data available (responses from 20 males and 21 females; as no differences in response between the dove and predator models were found, response data were pooled by individual). Again, for each of the defense variables measured, no differences between male and female responses were found ($U = 133$ to 206 , all NS).

Both mates in a pair responded during four of 24 dove model presentations and nine of 24 predator model presentations (binomial test, NS). We found no association between model type (dove or threat) and the frequency of response by the sexes ($G_{adj} = 0.10$, $df = 1$, NS) or between model type and the sex of the first-arriving bird ($G_{adj} = 0.12$, $df = 1$, NS; Table 1).

No birds made contact with the snake model. However, the snake model elicited “fluff-out” (threat) displays (see Lemon 1968, Kinser 1973) from one of nine responding males and one of nine responding females (not mates), a distinctive “chitter” call (described in Lemon [1968] as a mark of agonism) from three males and two females, and one mixed-species mobbing. The jay model was struck bodily by one of four responding males and one of three responding females (not mates). One of

TABLE 1
MALE AND FEMALE RESPONSE PHENOLOGY TO DOVE AND PREDATOR MODELS^a

Model	F alone	F first, then M	F = M	M first, then F	M alone
Dove	12	1	2	1	8
Predator	7	4	2	3	8

^a Given are the number of model presentations which followed each pattern of parent bird response sequences.

16 responding females struck the dove model. No birds attacked or displayed at the chipmunk model.

Brood characteristics and defense.—Modal brood size in this population was two (Filliater and Breitwisch 1997), which represents the brood size of 12 of the 24 pairs tested here. The duration of female response (Time Present) was the only aspect of either male or female defense which was strongly correlated with brood size ($r_s = 0.64$, $N = 16$, $P < 0.01$). Male closest (CDM: $r_s = -0.57$, $N = 17$, $P < 0.025$) and mean (MDM: $r_s = -0.59$, $N = 17$, $P < 0.025$) distances to the models were negatively correlated with brood age. No measure of female defense was correlated with brood age.

The relationship between defense and the subsequent success of the nest (in terms of the number of young fledged) was also examined for each sex. FDM values during model presentations were strongly and negatively related to the subsequent success of that nest; i.e., females which stayed close to the nests during model presentations produced more young ($r_s = -0.63$, $N = 16$, $0.005 < P < 0.01$, 1-tailed test). No measure of male defensive response was strongly correlated with this measure of nest success ($r_s = -0.45$ to 0.36 , $N = 17$, all NS).

Nest attendance.—A total of 506 nest visits over nearly 100 h of observation on these 24 pairs of birds was logged. Data for one male were excluded as he made no trips to the nest despite being nearby. Males and females made similar numbers of visits ($T = 69.0$, $N = 20$, NS), but visit duration was much greater for females than for males ($T = 41.0$, $N = 23$, $P < 0.005$). As such, overall attendance (proportion of observation time spent at the nest) was greater for females than for males ($T = 59.0$, $N = 23$, $P < 0.025$).

DISCUSSION

While the use of model predators to elicit avian parental defensive responses has been criticized as being artificial or inappropriate (e.g., Knight and Temple 1986), models are advantageous for a number of reasons. Living predators may provide an inconsistent stimulus, due either

to their being restrained or for physiological (e.g., Hamerstrom 1957) or other reasons, and can be very difficult to present efficiently (D. Winkler, pers. comm.). Alternatively, stuffed mounts can be presented in a consistent fashion and have been used extensively (e.g., Knight and Temple 1988, Neudorf and Sealy 1992, Rytkönen et al. 1993, Maloney and McLean 1995). Given that parental nest visitation behavior was noticeably affected by the presence of models at the nest, we feel justified in concluding that parent birds did indeed respond to the models, be they recognized merely as "intruders", or more specifically by type (e.g., "avian intruder" versus mammal or snake), or by species.

Cardinal defensive responses.—Parent birds responded similarly to *all* of the models presented. This is a rather unexpected finding, given that a number of passerines have previously been shown to tailor their defensive response to the apparent threat posed by different stimuli (e.g., Buitron 1983, Curio et al. 1983, Knight and Temple 1988) and to exhibit rapid, learned predator recognition (Maloney and McLean 1995). However, only the avian models (jay and dove) were struck, and only the snake model elicited threat displays and a group mobbing. This suggests that the models may have been perceived as being different and highlights the difficulty of comparing the "intensity" of different types of behaviors.

Previous studies of sex-differences in nest defense by other passerines (including the Northern Mockingbird [*Mimus polyglottos*; Breitwisch 1988] and Red-winged Blackbird [*Agelaius phoeniceus*; Knight and Temple 1988]) have demonstrated marked differences in male and female defensive behavior. However, by all measures of active defense monitored, males and females in this population appear to contribute equally to the defense of their nest during the mid-nestling stage. Although larger sample sizes might have helped to clarify male and female roles in providing defense, the lack of sex differences reported here is not simply a function of our effort, as marked sex differences in nest defense by other passerines have been demonstrated in studies employing similar methodologies and sample sizes (e.g., Breitwisch 1988, Knight and Temple 1988, Curio and Onnebrink 1995). Sex differences in nest defense may best be detected in species which provide intense defense; cardinal nest defenses generally appear to be of low intensity but are highly variable. In general, no model was ignored (including the dove model): parent birds increased their call rate and number of calls and lengthened visit duration when models were in place at the nests (see Results). However, no model consistently elicited intense responses from either sex.

Females exhibited greater nest attendance than did males, at least in part due to female brooding of young. Greater attendance by one sex is of consequence if the sex with higher nest attendance is more likely to

(at least initially) encounter and respond to an approaching threat to the nest contents. Responses by single birds were common but were not biased toward females. This suggests that the sexes may have equal probability of discovering a threat that arrives at the nest during parental absence. Once at the nest, mates' responses were generally independent; there was little indication that defensive behavior might be "matched" between mates, as suggested by Breitwisch (1988) for Northern Mockingbirds; nor was there evidence for differential parental effort by mates as suggested by Burley (1986) for sexually-selected species.

Our study was designed to use each member of a pair as a control for its mate, in order to account for differences among pairs in factors which may influence defense levels, such as brood size or age (see review in Montgomerie and Weatherhead 1988). The efficacy of this experimental design was weakened when both mates did not respond and non-paired analyses were necessary. However, the importance of brood size as a determinant of nest defense intensity is not always demonstrable (e.g., Hogstad 1993, Rytönen et al. 1995, Curio and Onnebrink 1995). Monogamous mates invest in a single brood of some size and age, but it remains possible for mates to respond to different cues relating to the brood (e.g., size versus age). The power of our tests of the influence of brood size and age is somewhat limited by the number of comparisons made, but the data suggest that males and females may indeed perceive or respond to different cues relating to brood characteristics.

Importance of defense.—Our results suggest that active defense played a relatively minor role in influencing nest success in this cardinal population. Although adults struck the predator models on several occasions, most defense was of much lower intensity (e.g., calls, some movements around nest area). Parent birds may have little ability to deter threats to their nests without assuming unacceptably high risk to themselves; this may be especially true of snakes, which are important predators of young birds (Skutch 1976, pers. ob.). Annual reproductive success in this population has been estimated at 15%, with predation as nearly the sole cause of nest losses (Filliater et al. 1994), but cardinals appear not to defend vigorously their current investment in a brood. Rather, reproductive success is achieved by rapidly renesting if the current clutch or brood is lost. Scott et al. (1987) have shown that cardinals can begin laying a new clutch in as few as four days ($\bar{x} = 5.5$ days) after nest failure and have relatively long breeding seasons. We have witnessed such rapid and repeated renestings in this population; individual pairs attempted six or more nests in a single season lasting ca. 130 days (PMN, unpubl. data). In this population, renesting may be a better option than intense defense of the current brood.

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