

A TEST OF RADIO-TRANSMITTER EFFECTS ON PARENTAL INVESTMENT AND PRODUCTIVITY IN THE NORTHERN CARDINAL

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Abstract. Researchers often attach radio transmitters and other devices to free-living birds without a clear understanding of the possible consequences for their study organisms or their data. Although transmitters may affect parental investment (nest defense and offspring provisioning), this possibility has received little attention. We tested this hypothesis by placing mock radio transmitters on male Northern Cardinals (*Cardinalis cardinalis*) and comparing their behavior to that of uncaptured birds and procedural controls. Birds with transmitters defended their nests less vigorously than did uncaptured birds but did not modify their provisioning effort. This behavioral modification appears to have ultimately influenced predation rates, as nests of birds with transmitters had lower daily survival rates and were less likely to fledge offspring. Control birds that were captured, handled, and bled had intermediate levels of nest defense and productivity that were statistically indistinguishable from those of birds receiving other treatments, suggesting that capture, restraint, and blood collection may affect birds in ways that are independent of transmitters' effects. Interestingly, we also found limited evidence that females mated to males with transmitters increased their provisioning effort, possibly in compensation for a perceived reduction in their mate's care. Because attachment of a transmitter (and potentially blood sampling) directly affected the behavior and reproduction of birds with transmitters and may have indirectly affected the behavior of their mates, we suggest researchers cautiously balance the benefits of such methods against potential data biases and impairment of reproduction.

Key words: blood sampling, *Cardinalis cardinalis*, mate conflict, nest defense, offspring provisioning, reproduction, telemetry.

Evaluación de los Efectos del Radiotransmisor en la Inversión Parental y la Productividad en *Cardinalis cardinalis*

Resumen. Los investigadores a menudo colocan radiotransmisores y otros artefactos a las aves silvestres sin un entendimiento claro de las posibles consecuencias para sus organismos de estudio o sus datos. Aunque los radiotransmisores pueden afectar la inversión parental (defensa del nido y aprovisionamiento de los pichones), esta posibilidad ha sido poco estudiada. Evaluamos esta hipótesis colocando radiotransmisores falsos en machos de *Cardinalis cardinalis* y comparando su comportamiento con el de aves no capturadas y con controles de procedimiento. Las aves con radiotransmisores defendieron sus nidos menos vigorosamente que las aves no capturadas, pero no modificaron su esfuerzo de aprovisionamiento. Esta modificación comportamental parece haber influenciado en última instancia las tasas de depredación, ya que los nidos de las aves con radiotransmisores tuvieron menores tasas de supervivencia diaria y tuvieron una menor probabilidad de producir polluelos. Las aves control que fueron capturadas, manipuladas y sangradas presentaron niveles intermedios de defensa del nido y de productividad que fueron estadísticamente indistinguibles de aquellos de las aves que recibieron otros tratamientos, sugiriendo que la captura, la detención y la colecta de sangre pueden afectar a las aves de modos que son independientes de los efectos de los radiotransmisores. Encontramos cierta evidencia de que las hembras en pareja con machos con radiotransmisores aumentaron sus esfuerzos de aprovisionamiento, posiblemente en compensación por la percepción de una reducción en el cuidado por parte de la pareja. Debido a que la colocación de un radiotransmisor (y potencialmente el muestreo de sangre) afecta directamente el comportamiento y la reproducción de las aves con transmisores y puede haber afectado indirectamente el comportamiento de sus parejas, sugerimos que los investigadores balanceen con cuidado los beneficios de estos métodos contra el sesgo potencial de los datos y la complicación de la reproducción.

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INTRODUCTION

Using radio transmitters to collect behavioral and ecological data from free-living birds has become common since the introduction of radio telemetry (LeMunyan et al. 1959, Cochran and Lord 1963). Researchers using radio telemetry often either ignore or are uncertain about the potential effects of transmitters on their study organisms, and thus about possible biases in the data they collect. Multiple studies have revealed negative effects of transmitters on avian survival (e.g., Marks and Marks 1987), reproduction (e.g., Foster et al. 1992), energetic expenditure and body condition (e.g., Greenwood and Sargeant 1973), and behavior (e.g., Hooge 1991, all these reviewed in Barron et al. 2010). One aspect of behavior that has received little direct attention in this regard, however, is parental investment, despite its importance to reproductive success and survival (Trivers 1972). Some insight is provided by studies in which birds were handicapped with added weights or clipped feathers to increase the costs of flight. Many of these studies reported negative effects on parental investment (e.g., Whittingham et al. 1994, Sanz et al. 2000, Griggio et al. 2008). Because these handicaps are not directly equivalent to a transmitter attached to a bird, the assumption that transmitters have similar effects may be tenuous. In this study we experimentally investigated whether transmitters affect two components of parental investment (nest defense and offspring provisioning) by the Northern Cardinal (*Cardinalis cardinalis*).

Given the importance of nest predation for most birds (Ricklefs 1969), and that nest defense can deter predation (e.g., Greig-Smith 1980, Weatherhead 1990), alteration of nest defense could negatively affect a bird's fitness (Montgomerie and Weatherhead 1988). In this study we provide the first test of the prediction that birds with transmitters defend their nests less vigorously, possibly because of physical limitations or energetic costs.

As with nest defense, transmitters may cause a reduction in offspring provisioning due to physical impairment associated with the transmitter's additional energetic burden (Sanz et al. 2000). In the only study to investigate transmitter effects on passerine provisioning, Neudorf and Pitcher (1997) found no difference in provisioning by female Hooded Warblers (*Setophaga citrina*). A potential limitation of their study was that they considered only feeding rate, possibly missing differences associated with size of the food load. Here we examine provisioning effort as a composite of both feeding rate and size of food loads.

Another potential effect of transmitters that has received little attention is an indirect effect on the mate of the bird carrying a transmitter. Chase (1980) predicted that in species with biparental care, if some factor (such as energetic costs caused by transmitters) causes an animal to reduce its parental care, its mate should compensate for that reduction by increasing the care it provides (Harrison et al. 2009). Two studies of offspring provisioning support this prediction in single-brooded seabirds (Wanless et al. 1988, Paredes et al. 2005), whose reproductive

strategies may necessitate compensation if reproductive success in a season is to be greater than zero (Paredes et al. 2005). In contrast, species like the cardinal that are capable of producing multiple broods in a year may forgo such compensation to invest energetic resources in the subsequent brood (Trivers 1972). We examined this possibility by determining whether the mates of birds with transmitters compensated for any reduction in offspring provisioning or nest defense.

Finally, we investigated whether transmitters affected daily nest survival, probability of fledging young, and fledging success (fledglings produced per egg). We predicted that transmitters should reduce productivity if they cause a decrease in nest defense, because the intensity of nest defense is often positively correlated with nest success (e.g., Greig-Smith 1980, Weatherhead 1990, but see Redmond et al. 2009). Because parental activity can attract predators and increase nest predation (Martin et al. 2000), we expected that if transmitters decreased offspring provisioning then birds with transmitters could actually suffer less nest predation. If females compensate for a reduction in their mate's parental care, however, that would offset changes in productivity resulting from transmitter effects on males.

METHODS

FOCAL SPECIES

The Northern Cardinal is a 45-g passerine that nests in open cups, usually 1–2 m above ground, in diverse habitats through most of the eastern United States (Halkin and Linville 1999). Females do most of the nest construction and are sole incubators of eggs, although both sexes feed and defend offspring (Halkin and Linville 1999). Cardinals are capable of producing multiple broods within a breeding season and renest following nest failure or fledging of young (Halkin and Linville 1999).

NEST MONITORING

We conducted this study in 2007 and 2008 at Fort Hood, in central Texas (31.2° N, 97.8° W). We worked on two sites in 2007 and six in 2008 (including one of the 2007 sites) that were isolated from each other. The sites ranged in size from 11 to 150 ha. By observing parental behaviors, we located Northern Cardinal nests at each site from mid-March until late August. Nests were checked approximately every other day, with more frequent visits when nestlings approached fledging to ensure accurate determination of nest fates.

CAPTURE AND DEVICE ATTACHMENT

We attached transmitters to males only because they were easier to capture with mist nets and conspecific playback and we wanted to be consistent in which member of the pair received a transmitter. Males in our study were included in one of three categories. Individuals that were never captured were considered to be "no treatment." We randomly assigned all captured males to one of two treatments. In the "control" group, males

were captured but no transmitter was attached. In the “transmitter” group, males were captured and a mock transmitter was attached. Males in the “control” and “transmitter” groups were captured shortly after their nest was found, usually during incubation. When males of both these groups were captured we collected up to 60 μ L of blood from the brachial vein for unrelated research and banded each bird with a U.S. Fish and Wildlife Service aluminum leg band and a unique combination of color bands before placing the birds into an opaque cloth bag. Thirty minutes after capture we collected another blood sample. At this point we released “control” birds but attached a mock transmitter to “transmitter” birds before releasing them. We used mock transmitters rather than real transmitters because our goal was to assess the effects of carrying a “transmitter,” not to conduct a telemetry study. Therefore, we identified effects related to bearing the artificial load while eliminating any possible disturbance associated with tracking.

Mock transmitters were identical in dimensions, shape, and mass to actual radio transmitters used on cardinals (JDJC Corp., Fisher, IL), but were constructed by attaching a metal wire antenna 0.8 mm in diameter and 110 mm in length to an cylindrical wooden body 8 mm in diameter and 25 mm in length with JB Weld. Like real transmitters, the mock transmitters were rounded at the ends to minimize drag, and we flattened the underside to better conform to the bird’s body. In 2007 we piloted the method of attaching devices dorsally with eyelash glue (Raim 1978), but low retention times limited its utility, so we excluded those individuals from all analyses. This led us to change in 2008 to a leg harness made of dissolvable suture (Doerr and Doerr 2002) that we covered in thin cord to minimize skin abrasion. We attached harnesses to the transmitters through small tunnels at the anterior and posterior ends of the transmitter. To ensure the fit was appropriate, we tightened the harness until it was snug to the bird but would still allow a 2-mm toothpick to be inserted under the transmitter (Doerr and Doerr 2002). The average mass of the entire package was 1.6 g (SD = 0.2), which was approximately 4.0% of the birds’ body mass (SD = 0.3%), thus conforming to the “<5% rule” that is often required for avian telemetry studies.

NEST DEFENSE

We conducted nest-defense trials no sooner than 2 days following capture and performed trials up to three times during a nesting attempt (minimum 2 days between repeated trials), during incubation, the early nestling phase (young 1–5 days old), and the late nestling phase (young 6–10 days old). A trial consisted of exposing cardinal nests sequentially to a human observer and a plastic decoy of an American Crow (*Corvus brachyrhynchos*) 1–2 m from the nest, both of which cardinals respond to as threats. Our use of two threats was based on unrelated research on behavioral responses to anthropogenic vs. natural disturbance (Barron et al. 2012). We randomly determined the order of presentation of the threats and had a 2-hr break between their presentations. The

first threat was consistently presented between 2 and 2.5 hr after sunrise. We did not conduct nest-defense trials if it was raining. Following detection of the threat by either parent, we recorded the latency to detection, total number of vocalizations, duration of response, and closest approach to the threat by each parent. Each behavior was scored on a scale from 1 to 5, with greater values representing a stronger response (Table 1). We then summed the scores of these three variables to produce a composite nest-defense score, ranging from 0 to 15 for each individual parent and 0 to 30 for the pair. By recording multiple behavioral traits and deriving a composite score we sought to generate a more complete estimate of nest defense (Gunness and Weatherhead 2002). After 5 min the threat was removed and the researcher left the area. Observations made during exposure to the crow were from a small, camouflaged blind set up approximately 15–25 m from the nest the previous day.

NESTLING PROVISIONING

We monitored nestling provisioning from the same blind through a spotting scope (20–60 \times magnification) trained on the nest. Observations were made in the early nestling (1–5 days old) and late nestling (6–10 days old) stages

TABLE 1. Scores for each variable measured in nest-defense trials. The scores of these variables were added together to produce a composite nest-defense score ranging from 0 to 15 for males and females independently and 0 to 30 for the breeding pair.

Variable	Value for an individual	Value for a pair	Score
Latency to detection	n/a	0–10 min	5
		10.01–20 min	4
		20.01–30 min	3
		30.01–40 min	2
		40.01–60 min	1
		>60 min	0
Total vocalizations	201+	401+	5
	151–200	301–400	4
	101–150	201–300	3
	51–100	101–200	2
	1–50	1–100	1
	0	0	0
Response duration ^a	241–300 sec	241–300 sec	5
	181–240 sec	181–240 sec	4
	121–180 sec	121–180 sec	3
	61–120 sec	61–120 sec	2
	1–60 sec	1–60 sec	1
	0 sec	0 sec	0
Closest approach ^a	0–3.9 m	0–3.9 m	5
	4–7.9 m	4–7.9 m	4
	8–11.9 m	8–11.9 m	3
	12–15.9 m	12–15.9 m	2
	16+ m	16+ m	1
	Never approached	Never approached	0

^aIndependent values for male and female included in a pair’s composite score for nest defense.

during the second hour of the 2-hr interval between successive nest-defense trials to ensure that birds had resumed normal activity following the first nest-threat presentation. Observations were not conducted if it was raining. In addition to recording the number of feeding visits by each parent, we also estimated the size of the food load. Loads were given a value of 1 if they were completely contained within the parent's bill, 2 if they protruded slightly from the bill, and 3 if they protruded obviously from both sides of the bill. We calculated a feeding score for each parent in each trial by multiplying its number of feeding visits per hour by their average size of the prey. If we could not determine a load's size we excluded it from calculations of mean load size. Although a transmitter's effects on provisioning could also affect mass at fledging, we lacked sufficient data to investigate this possibility.

STATISTICAL ANALYSIS

We estimated daily survival rates for nests of birds from each treatment by the logistic-exposure method (Shaffer 2004). We did not include nest stage, date, and year as covariate factors in the model because our samples were balanced across treatments and the inclusion of these tangential factors would have decreased power to detect effects of treatment. We compared estimates of nest defense, nestling provisioning, and fledging success by treatment with linear mixed-model repeated-measures analyses with pairs as the random factor and treatment as the fixed factor. We used the Bonferroni correction for multiple pairwise comparisons among treatments. Julian date, time after sunrise, and age of young were included as covariates in the analyses of nest defense (Montgomerie and Weatherhead 1988) and nestling provisioning. We also controlled for number of young by including it as a covariate in nest-defense analyses and reporting feeding scores per nestling. Although multiple studies have shown no effect of previous exposure on passerines' nest defense (Weatherhead 1989), there has been some debate over this issue (Knight and Temple 1986, Siderius 1993). Therefore, we also included the number of times parents had been exposed to a researcher prior to the trial as a covariate of nest defense, including both regular nest visits and previous nest-defense trials. We then calculated effect sizes to provide an estimate of the magnitude of transmitter effects relatively independent of sample sizes, because researchers increasingly recognize that such measures of the magnitude of an effect are more meaningful than estimates of statistical significance (Johnson 1999, Nakagawa and Cuthill 2007). We report effect sizes as Cohen's d , which allowed us to use Cohen's (1988) interpretation of these values: less than 0.5 indicates a small effect, 0.5 to 0.8 a medium effect, and above 0.8 a large effect. For bimodal nest-survival data we also calculated odds ratios to infer whether the odds of nest predation differed by treatment. For all analyses we used the program NCSS (Hintze 2007), except those of daily survival rates, which we

analyzed with SAS 9.1.3 (SAS Institute 2003). All means are given \pm 95% confidence intervals.

All methods were approved by the University of Illinois Institutional Animal Care and Use Committee.

RESULTS

We captured 37 male Northern Cardinals, 11 of which received mock radio transmitters (the 3 birds that received glued mock radio transmitters are not part of this total and are omitted from analyses; see Methods) and 23 of which served as procedural controls. Additionally, 88 male cardinals were observed but never captured and were classified as "no treatment" birds. We located and monitored 116 nests (94 no treatment, 11 control, 11 transmitter) in 101 territories (84 no treatment, 9 control, 9 transmitter). The discrepancy between the total number of territories and the sum of territories from each treatment arose because one male received a control treatment after its "no treatment" nest failed. We made 93 observations of nestling provisioning (79 no treatment, 10 control, 4 transmitter) on nests from 55 territories (47 no treatment, 5 control, 3 transmitter) and conducted 274 nest-defense trials (207 no treatment, 44 control, 23 transmitter) on nests from 73 territories (56 no treatment, 9 control, 8 transmitter), with these trials approximately evenly divided between the crow and human nest threats.

NEST DEFENSE

We found an effect of treatment on males' nest defense (Fig. 1a; Tables 2 and 3), but there was no difference between responses to a person vs. those to a model crow ($F_{1,202.8} = 0.1$, $P = 0.76$) and the treatment effect was consistent across these threats (treatment \times threat $F_{2,202.4} = 0.2$, $P = 0.81$). Birds with transmitters defended their nests approximately half as aggressively as did "no treatment" birds ($F_{1,85.4} = 7.9$, $P = 0.02$; Fig. 1a; Table 3). Control males responded intermediately, however, and their level of defense did not differ significantly from that of either "no treatment" ($F_{1,45.3} = 2.5$, $P = 0.36$; Fig. 1a; Table 3) or transmitter birds ($F_{1,67.7} = 1.6$, $P = 0.62$; Fig. 1a; Table 3).

Females' responses did not differ by treatment (Fig. 1a; Tables 2 and 3), suggesting they did not compensate for the treatment's effects on their mate's nest defense. Females also responded to the crow and human threats similarly ($F_{1,183.2} = 2.6$, $P = 0.11$), and this response was consistent across treatments (treatment \times threat $F_{2,182.6} = 0.5$, $P = 0.59$).

Transmitters therefore had an overall effect on nest defense (Fig. 1b; Tables 2 and 3), with transmitter pairs defending their nests less aggressively than "no treatment" pairs ($F_{1,85.5} = 8.0$, $P = 0.02$; Fig. 1b; Table 3). Defense of offspring by control pairs, however, was similar to that of both "no treatment" ($F_{1,43.4} = 3.8$, $P = 0.17$; Fig. 1b; Table 3) and transmitter pairs ($F_{1,66.8} = 1.1$, $P = 0.87$; Fig. 1b; Table 3).

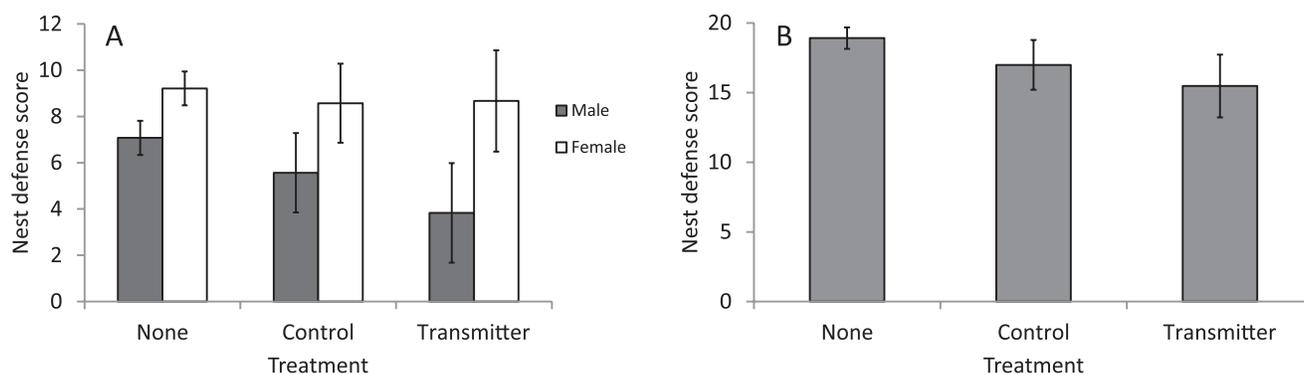


FIGURE 1. Mean nest-defense scores ($\pm 95\%$ confidence intervals) of cardinals from each treatment (a) split by sex and (b) total. Calculations of nest-defense scores are detailed in Table 1.

NESTLING PROVISIONING

Although males with transmitters provisioned nestlings slightly less than those from other treatments, the effect on their provisioning was relatively small (Fig. 2a; Tables 2 and 3). Females mated to males with transmitters, however, fed nestlings almost twice as much as other females did, although high predation rates during incubation limited sample sizes and may have prevented us from detecting a significant effect (Fig. 2a; Table 2). Effect sizes substantiate the importance of this pattern by indicating large increases in provisioning by females mated to males with transmitters (Table 3) but only a small difference between females mated to “no treatment” and control birds (Table 3). Consequently, compensatory feeding within a treatment produced similar overall (male + female) provisioning in all treatments (Fig. 2b; Tables 2 and 3).

PRODUCTIVITY

The daily survival rate of nests belonging to birds with transmitters was much lower than that of “no treatment” birds (odds ratio = 2.59, 95% CI = 0.88 to 7.65; Table 4). Furthermore,

TABLE 2. Influence of treatment of male cardinals (no treatment, control, transmitter) on nest defense and nestling provisioning of males, females, and pairs. Nest defense was estimated by the composite score detailed in Table 1. Nestling provisioning was estimated by multiplying the number of feeding visits per nestling by the average load size.

Variable	df	<i>F</i>	<i>P</i>
Nest defense			
Male	2, 60.3	4.54	0.01
Female	2, 35.1	0.30	0.74
Pair	2, 58.7	5.09	0.01
Nestling provisioning			
Male	2, 46.4	0.44	0.65
Female	2, 50.5	1.54	0.22
Pair	2, 46.0	0.14	0.87

TABLE 3. Estimates of the magnitude of effects (Cohen’s *d*) of treatment of male cardinals on nest defense and nestling provisioning of males, females, and pairs. Nest defense was estimated by the composite score detailed in Table 1. Nestling provisioning was estimated by multiplying the number of feeding visits per nestling by the average load size. The effects implied by Cohen’s *d* are generally interpreted as <0.5 = small, $0.5-0.8$ = medium, >0.8 = large.

Comparison	Male <i>d</i>	Female <i>d</i>	Pair <i>d</i>
Nest defense			
Transmitter vs. no treatment	1.08	0.18	1.09
Transmitter vs. control	0.66	0.04	0.55
Control vs. no treatment	0.58	0.25	0.71
Nestling provisioning			
Transmitter vs. no treatment	0.35	0.98	0.26
Transmitter vs. control	0.77	1.37	0.12
Control vs. no treatment	0.33	0.23	0.16

their nests were less than half as likely to fledge young (transmitter = 18%, no treatment = 44%; odds ratio = 3.53, 95% CI = 0.72 to 17.23), and they fledged a smaller proportion of young (Table 4). Although this latter pattern lacked statistical significance, its moderate effect size ($d = 0.47$) suggests its biological importance. The level of productivity of control birds was intermediate, as estimated by probability of fledging young (27%), daily nest-survival rates (Table 4), and fledging success (Table 4).

DISCUSSION

Our results provide clear evidence that the combination of transmitter attachment and blood collection caused male Northern Cardinals to reduce their nest defense below that of uncaptured birds, a novel finding establishing that transmitters have subtle behavioral effects frequently overlooked by researchers. As nest defense can be positively correlated with nest success (Montgomerie and Weatherhead 1988), this pattern identifies a potential mechanism for the detrimental

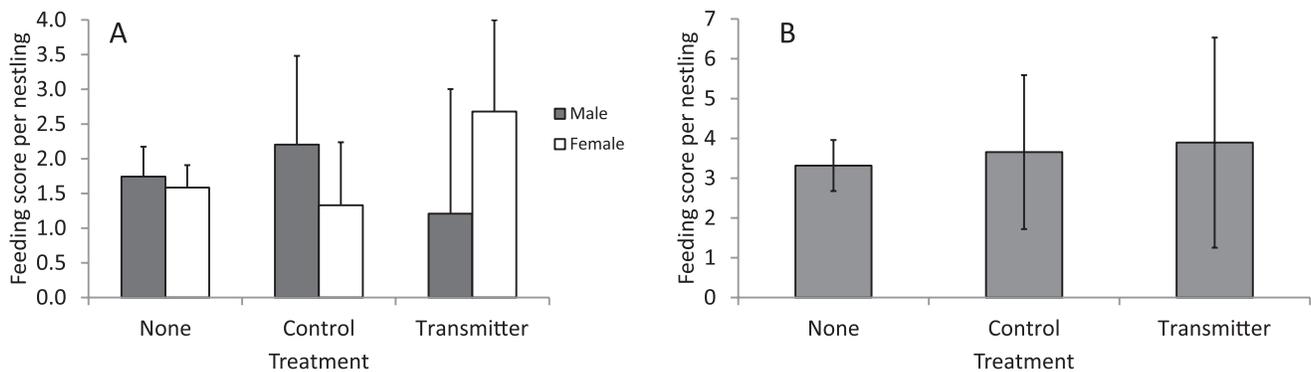


FIGURE 2. Mean feeding score per nestling ($\pm 95\%$ confidence intervals) of cardinals from each treatment (a) split by sex and (b) total. Feeding score per nestling equals number of feeding visits per nestling multiplied by average load size.

effects on reproduction observed in this and other studies. While further research is necessary to uncover the underlying cause of reproductive impairment, this study does demonstrate negative consequences for the fitness of birds with transmitters.

Surprisingly, control birds' levels of nest defense and productivity were intermediate, a finding that together with the decreased survivorship observed by Brown and Brown (2009) challenges previous evidence that neither capture and restraint nor blood collection have major negative effects on wild birds (Sheldon et al. 2008, Barron et al. 2010). It is unclear why capture and/or blood collection should affect nest defense but not provisioning behavior, but it does not appear to arise from differences in experience with humans since we found no interaction between treatment and threat (i.e., crow vs. human). Given that birds are likely to perceive being captured as a "predator encounter," the effect of that experience may be restricted to how they respond to predators subsequently. Consistent with nest defense deterring predators, we also found that procedural controls experienced intermediate levels of reproductive success. The possibility that capturing, handling, and bleeding birds might reduce nest

productivity because of less vigorous nest defense warrants further investigation.

The lack of a treatment effect on offspring provisioning corroborates the findings of Neudorf and Pitcher (1997), who reported no effects of radio transmitters on feeding by female Hooded Warblers. This suggests that among passerines males and females respond to transmitter attachment similarly, as Barron et al. (2010) suggested for all birds. Because greater uncertainty of parentage could make males more willing to decrease nestling provisioning when burdened with a transmitter (Slagsvold and Lifjeld 1990, Sanz et al. 2000), however, an appropriate test of this possibility requires comparing how transmitters affect parental care by males and females of the same species.

Patterns of provisioning did, however, suggest that females mated to transmitter males increased provisioning with respect to controls, although our samples were small, requiring further substantiation of this pattern. Such an increase in provisioning could stem from changes a bird observes in the appearance, behavior, or mobility of its mate, although it is surprising considering only males' nest defense was altered. Multiple processes, not mutually exclusive, could be responsible for this seemingly mismatched pattern of behavioral compensation. First, nest defense poses an inherent risk of immediate injury or death (Curio and Regelman 1985), whereas the costs of increased offspring provisioning are much more subtle and long-term (Trivers 1972), and parents may be less likely to compensate for more costly activities (Chase 1980). Second, compensation requires a reliable means of assessing a mate's investment. Whereas birds are able to track the nutritional needs of offspring (and thus their mates' provisioning effort) with cues such as nestlings' begging (Leonard and Horn 1996), the lack of a reliable means of assessing their mates' nest defense might leave birds less able to adjust this behavior. A model by Johnstone and Hinde (2006) similarly showed that compensation is more likely when parents can independently determine a brood's need accurately, as is the case with provisioning but

TABLE 4. Daily nest-survival rate and mean number of fledglings produced per egg for cardinals from each treatment. Calculations of daily survival rates are based on 748 observation days and an effective sample size (Rotella et al. 2004) of 1183.

Treatment	Daily survival rate		Number of fledglings per egg			
	Mean	95% CI	Mean (n^a)	95% CI	F	P
No treatment	0.95	0.93–0.96	0.37 (82)	0.28–0.46	1.17	0.32
Control	0.93	0.87–0.97	0.24 (9)	–0.02–0.51		
Transmitter	0.88	0.79–0.94	0.18 (9)	–0.09–0.45		

^aValues in parentheses indicate the number of territories included in repeated-measures analyses.

not nest defense. Finally, the high level of nest defense exhibited by females of all treatments could indicate that they lack the ability to elevate this behavior further.

Any compensation in provisioning effort by mates of radio-tagged birds could have long-term consequences beyond the scope of our study. For example, Paredes et al. (2005) proposed that compensation for a handicapped mate could make a pair more likely to divorce. It should also follow that even though compensatory feeding contributes to the success of the current brood, there could be a trade-off whereby the unmarked bird's future reproductive potential is reduced (Trivers 1972). Longer-term studies that examine the behavior of pairs over multiple breeding attempts and seasons are required for these possibilities to be assessed.

Whether or not future research confirms that transmitters have indirect effects on the mates of birds with transmitters, our results provide evidence that transmitters can have direct negative effects on passerines' parental investment and reproduction. As the birds we studied were not tracked, these results arise solely from the burden of transmitter attachment and may therefore underestimate the overall effects of transmitters if birds are negatively affected by the human disturbance inherent in radio tracking. This does not mean that transmitters cannot be used effectively in ornithological studies to generate information that would otherwise be unavailable. It does mean, however, that researchers should weigh the costs and benefits of using transmitters, where the costs apply both to the birds being studied and to the reliability of the data collected.

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