APPLIED ASPECTS OF AVIAN REPRODUCTION AT FORT HOOD, TX

BY

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THESIS

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Chapter 1

The impact of military disturbance on Northern Cardinal reproductive ecology

Abstract

Military bases support a wide variety of breeding birds, including key populations of endangered species; yet all past research assessing the impact of military disturbance has focused on raptors and no study has examined military effects on reproduction. We set out to fill these knowledge gaps by investigating the direct impact of on-ground military disturbance on Northern Cardinal (*Cardinalis cardinalis*) social structure, parental investment, offspring quality, stress hormone concentrations, and productivity. We compared birds among sites with high and low levels of military activity and found no evidence than any aspect of cardinal reproductive ecology is being affected. Cardinals did, however, appear to alter their nest defense based on the abundance of American Crows (*Corvus brachyrhynchos*), and this nest predator was much more abundant on low disturbance sites. If a potential predator actively avoids military disturbance it could actually confer an advantage to local passerines. While our findings are a promising result for cardinals on military bases, this disturbance-tolerant species was chosen to provide a conservative measure of military effects and more sensitive species may respond differently.

Introduction

Anthropogenic disturbance is known to adversely affect the behavior (e.g., Gutzwiller et al. 1994), physiology (e.g., Fowler 1999; Maxwell 1993) and breeding success (e.g., Boyle and Samson 1985) of birds. The effects may be especially serious in natural areas where the local abundances of wildlife are comparatively high. One area where we know little is the role of military disturbance on avian breeding ecology. Whereas disturbance from military training might affect birds in much the same way as other human activities (Gutzwiller and Hayden 1997), this issue is important because many military bases support key populations of threatened and endangered species (Boice 2006), such as Red-cockaded Woodpeckers on Fort Bragg, NC, and Black-capped Vireos at Fort Hood, TX. This outcome is a result of habitat preservation that more than

compensates for the negative effects of training activities that take place on military installations. Although bases have a net positive effect on birds via habitat preservation, the military may be able to improve the quality of these habitats by altering the timing or intensity of their training activities.

Insight into this topic based on past research is limited in two ways. First, all past studies have focused solely on raptors, thereby overlooking any effects on smaller birds. Second, no study has directly addressed how military disturbance might affect avian reproduction. We aimed to fill these knowledge gaps by investigating the direct impacts of on-ground military disturbance on passerine social structure, parental behavior, offspring quality, stress hormone concentrations, and productivity.

Using Northern Cardinals (*Cardinalis cardinalis*) as a focal species, we investigated whether birds integrate the level of disturbance into their perception of the quality of a given habitat. If so, we hypothesized that birds perceive areas with substantial military training as low quality habitat. This could affect both which birds nest in the habitat and how they perform when there. If training is ongoing prior to the breeding season, less dominant, lower quality individuals may be forced to nest in disturbed areas. This should be reflected by those birds being smaller (Burton and Evans 2001), initiating nests later (Perrins 1970), and laying smaller clutches (Lack 1968) than birds in undisturbed areas. If birds nesting in disturbed areas perceive the habitat as low quality, parental investment theory predicts they should also invest less in their offspring than birds in undisturbed habitat (Trivers 1972). We tested this hypothesis using nest defensive behavior and nestling provisioning.

Parents defending nests should balance the benefit of the current brood surviving against the cost to themselves through loss of future reproductive success due to injury or death (Montgomerie and Weatherhead 1988). If military disturbance lowers the perceived value of a given habitat, parents on sites with high disturbance should value their young less and therefore risk less defending them. We examined two aspects of nest defense. First, we determined how closely incubating females allowed us to approach their nests before flushing. Birds allowing a closer approach are assumed to be putting themselves at greater risk to avoid revealing their nest location (Gunness et al. 2001). Therefore, we predict that birds nesting in areas of high military disturbance would flush sooner than

birds in undisturbed areas. This trend could potentially be obscured due to the opposing force of habituation. We do not predict habituation by cardinals to effect flush distances, however, since the tendency to habituate to repeated human intrusion has not been supported in passerines (e.g., Weatherhead 1989). Secondly, we examined active nest defense by presenting nesting birds with two different nest threats, a human and a crow. We presented two threats to assess whether behavioral responses were threat-specific or generalized, owing to the perception of low habitat quality.

The second aspect of parental care we investigated was nestling provisioning. Previous work has shown that birds decrease provisioning in response to anthropogenic disturbance (Fernandez and Azkona 1993; Steidl and Anthony 2000). Thus, we predicted that cardinals in areas with military disturbance would perceive the value of their nestlings to be lower and therefore reduce provisioning effort. This should result in those nestlings gaining mass more slowly than nestlings in undisturbed habitat.

The parental behaviors we investigated are measures of an integrated behavioral response to military disturbance that is likely mediated by proximate changes in physiology. To explore whether the stress of military disturbance causes physiological changes in cardinals, we focused on corticosterone (CORT). The traditional view of the CORT response is that increased exposure to acute human disturbance elevates baseline levels of this hormone (e.g., Wasser et al. 1997). Recent studies, however, report that the prolonged exposure to acute stressors reduces baseline CORT concentrations (e.g., Cyr and Romero 2007; Homan et al. 2003; Rich and Romero 2005). Similarly, they showed suppressed stress-induced CORT concentrations in individuals exposed to chronic stress (e.g., Homan et al. 2003; Rich and Romero 2005; Romero and Wikelski 2002). Therefore, we predicted that birds occupying sites with high exposure to military disturbance would be chronically stressed and therefore display decreased baseline and stress-induced CORT levels.

Reduced nest defense in areas with military disturbance would increase the predation risk of those nests, because nest defense has been shown to deter nest predation (e.g., Greig-Smith 1980; Weatherhead 1990). Therefore, we predicted that nests in disturbed areas will have decreased daily nest survival and decreased fledging success. Because nest failure directly attributable to military training (e.g., nests destroyed by

vehicles) is not considered here, our prediction is that birds' perception of a highly disturbed area as low quality habitat could actually be a "self-fulfilling prophecy." If birds reduce parental care based on their perception that the habitat is low quality, it could lead to increased predation and reduced productivity, thereby effectively decreasing the quality of the habitat.

Methods

Study area

We conducted this study in 2007 and 2008 at Fort Hood, in central Texas. Prior to the 2007 breeding season, we established one study site with relatively high military disturbance and one site with relatively low military disturbance. We defined military disturbance as recurrent training on foot, in vehicles and tracked vehicles, or at occupied encampments. Hereafter we refer to areas with high levels of military activity simply as "high disturbance". We used our past experiences on the base and recommendations of personnel familiar with training locations to select these two sites. In 2008, we established three additional sites with a history of high disturbance and two more sites with low disturbance. We retained the 2007 low disturbance site, but could not use the high disturbance site from 2007 because the habitat had been substantially altered. In selecting sites we sought to keep habitat structure reasonably comparable between the levels of disturbance; resulting sites ranged in size from approximately 11-150 ha. Throughout both field seasons, all biologists recorded the number and type of every military activity observed while working on a site to quantitatively assess the level of military disturbance. Each individual military activity was recorded only one time per day and time spent on each site was standardized when comparing activity levels between high and low disturbance sites.

Focal Species

Northern Cardinals were used as a focal species because they are abundant and they nest both in areas with frequent human activity and in relatively undisturbed areas. The fact that cardinals do nest in areas with frequent activity suggests they are at least somewhat tolerant of disturbance, although they could have poor success nesting in

disturbed areas. Cardinals should therefore provide a relatively conservative measure of the effects of military training.

Nest Monitoring

We used parental cues to locate Northern Cardinal nests from mid-March until late August during both years of the study. Although nest searching was conducted by all biologists from dawn until mid-afternoon unless they were performing other specified duties, sites were large enough that not every cardinal nest was found. Nests of other open cup nesting passerines were also located and monitored in 2008 to determine if variation seen in cardinal productivity was consistent among species. These species included Bell's Vireo (*Vireo bellii*), Black-capped Vireo (*Vireo atricapillus*), Blue-gray Gnatcatcher (*Polioptila caerulea*), Northern Mockingbird (*Mimus polyglottos*), Painted Bunting (*Passerina ciris*), and White-eyed Vireo (*Vireo griseus*). Located nests were checked approximately every other day, with more frequent visits when the nestlings approached fledging to allow accurate determination of nest fates. To determine clutch initiation dates for nests found after the onset of incubation we backdated from the date of hatching. Because the earliest known second nest attempt in either year was started on May 6, we only considered nests initiated prior to the beginning of May to be first attempts.

Nest Defense

We conducted active nest defense trials up to three times during a nesting attempt: incubation, early nestling, and late nestling. We included multiple observations of nest defense to a given threat because studies of songbirds have shown no change in defense intensity with multiple trials (e.g., Weatherhead 1989); however, nest defense increases as nests age (Montgomerie and Weatherhead 1988) and we therefore had to account for nest age by including it as a covariate in our analyses. A trial consisted of exposing cardinal nests sequentially to a human and a model American Crow (*Corvus brachyrhynchos*), both of which cardinals respond to as nest threats. To prevent cardinals from responding to the researcher during placement of the crow threat we quickly set up the model crow when the parents were not nearby. We randomly determined the order of the threats with a 2 h break between their presentations. The first threat was presented between 2 and 2.5 h after sunrise. Following detection by either parent, we recorded the

latency (time elapsed) to detection, total number of vocalizations, duration of response by each parent, and closest approach to the threat by each parent. Each behavior was scored on a scale from 1 to 5, with higher values representing a stronger response (Table 1.1). The scores of these six variables were then compiled into a composite nest defense score, ranging from 0 to 30. By recording multiple behavioral traits we were able to generate a more accurate overall 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 15-25m from the nest the previous day.

Because differences in the abundance of crows among study sites could potentially affect how cardinals respond to crow models, we used the number of crows detected on each site in 2008 as an index of relative abundance. Each biologist recorded every crow seen or heard while working on a site, while trying to avoid counting the same individual more than once per day by only recording crows in areas where no others had been detected that day. Time spent on each site was standardized when comparing crow abundances between high and low disturbance sites.

Flush distances of incubating cardinals were also recorded during nest checks to determine whether birds in areas with high disturbance take less risk to defend their young, therefore displaying longer flush distances than undisturbed birds. Researchers approached the nest at a steady walking pace with arms at their sides to avoid inconsistencies in the perceived threat by the birds. Since only female cardinals incubate, flush distances of males were not recorded.

Nestling Provisioning

To test the prediction that birds on high disturbance sites would provision their nestlings less, we monitored nestling provisioning from a blind using a spotting scope (20-60x magnification) trained on the nest. Observations were made for 1 h during the interval between successive presentations in nest defense. We used the second hour of the interval to ensure that the birds had resumed normal activity following the first nest threat presentation. In addition to recording the number of feeding visits by each parent, we also estimated food load size. 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 trial by multiplying the number of visits per hour by the average prey size. If we could not determine the prey size its load value was recorded as the average of all other loads values recorded during the hour of observations. In 2008 we briefly removed and weighed cardinal nestlings when approximately six days old to establish the relationship between provisioning effort and nestling mass.

Blood Collection and Estimating Stress Hormone Concentrations

We attempted to capture all focal breeding birds using mist-nets and conspecific playbacks, but primarily males were captured. Small sample sizes for females led us to exclude them from all analyses. Blood samples were taken from each captured adult to determine whether military disturbance decreases cardinal baseline and stress-induced CORT levels. We accomplished this by pricking the brachial vein with a hypodermic needle and collecting up to 60 µl of upwelling blood in heparinized microhematocrit tubes. The first blood sample was taken within 3 minutes of the bird hitting the net to reflect baseline hormone concentrations, as it has been shown that CORT levels during this time reflect stress prior to capture, rather than stress due to capture (Romero and Romero 2002). Birds were then placed into an opaque cloth bag for 30 minutes and another blood sample was then taken to measure stress-induced CORT levels. Blood flow was slowed after each bleed by applying light pressure to the vein with a cotton ball. Microhematocrit tubes containing blood were quickly refrigerated. Body measurements were subsequently taken on each individual and tarsus lengths were compared between levels of disturbance to assess whether smaller individuals were competitively excluded from low disturbance sites. A U.S. Fish and Wildlife Service aluminum leg band was also placed on each bird's leg along with a unique combination of plastic color bands before releasing the birds.

Within 24 hours of collection, microhematocrit tubes were spun at 1545 G for 10 minutes in a Zipocrit centrifuge to separate plasma before extracting it using a 50 µl Hamilton syringe. Plasma samples were then placed into 0.5 ml eppendorf tubes and stored in a 0 degree Fahrenheit freezer. CORT concentrations were later measured by radioimmunoassay after extraction with dichloromethane as previously described (Wingfield et al. 1992). Baseline CORT samples not taken within 3 minutes of capture

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and two samples with values more than three standard deviations from the mean were excluded from analyses.

Statistical Methods

Daily survival rates of nests were estimated with the logistic-exposure model (Shaffer 2004); we modeled cardinal data separately and pooled all other open cup nesting passerines. We compared estimates of nest defense (active nest defense and flush distance), nestling provisioning (feeding rate and feeding score), fledging success (number of fledglings per egg), and clutch size between birds occupying high and low disturbance sites using a mixed model repeated-measures analysis with the territory as the unit of replication. Bonferroni corrections were used for estimates of active nest defense when comparing nest threats for a given disturbance treatment and when comparing disturbance treatments for a given nest threat. Julian date, time after sunrise, age of young, and number of young were included as covariates in the analysis of nest defense (Montgomerie and Weatherhead 1988) and provisioning, whereas Julian date, number of eggs, and age of eggs were included as covariates for flush distance (Albrecht and Klvana 2004; Osiejuk and Kuczynski 2007). Despite the fact that multiple studies have shown no impact of previous exposure on passerine 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 the adults 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. Differences in baseline and stress-induced CORT concentrations were also determined with a mixed model repeated-measures analysis with Julian date as a covariate (Romero 2002). Bonferroni corrections were employed when comparing disturbance levels for either baseline or stress-induced samples. Differences in average nestling mass, date of initiation of first clutch, and adult tarsus length between disturbed and undisturbed birds were evaluated using a mixed model ANOVA with day of year, number of nestlings, and age of nestlings included as covariates for average nestling mass. Mixed model analyses were employed because disturbance treatment and nest threat were fixed models, while the individual birds which were monitored were randomly determined.

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

Results

We located and monitored 123 cardinal nests along with 31 nests of other open cup nesting passerines and obtained nestling masses from 29 of the cardinal nests. We were also able to capture 52 adult cardinals, primarily in 2008; 14 of these were females and 38 were males. Of those birds captured, CORT samples were taken from 30 males and 2 females. We conducted 206 active nest defense trials (103 with each threat) on nests from 55 territories, obtained 173 flush distances from 61 female cardinals, and conducted 94 observations of nestling provisioning on nests from 56 territories.

Military Disturbance and Crow Abundance

Sites designated as high disturbance had more than a 10-fold greater quantity of personnel, vehicles, large vehicles, and track vehicles than the low disturbance sites. The military activity on high disturbance sites was episodic, with high levels of sustained presence separated by brief lulls in activity. No encampments or long-term occupation by troops was ever detected on a low disturbance site. We detected 474 American Crows on the low disturbance sites but only 87 on the high disturbance sites, suggesting this species was over five times more abundant on sites with low disturbance.

Individual Quality

Contrary to our prediction that smaller birds would be competitively excluded from low disturbance sites, adult male cardinals were the same size at each level of disturbance, with respect to tarsus length (high disturbance: $\bar{x} = 28.03$, 95% CI = 27.61-28.46, $n = 16$, low disturbance: $\bar{x} = 28.30$, 95% CI = 27.83-28.77, $n = 13$, $F_{1, 27} = 0.72$, $p = 0.40$). Also contrary to our prediction, birds occupying high disturbance areas did not initiate their first clutch at a later date (high disturbance: $\bar{x} = 105.88$, 95% CI = 101.16-110.60, $n = 25$, low disturbance: $\bar{x} = 105.10$, 95% CI = 99.95-110.24, $n = 21$, $F_{1, 44} = 0.05$, $p = 0.82$) or produce smaller clutches (high disturbance: $\bar{x} = 3.05$, 95% CI = 2.85-3.25, $n = 36$, low disturbance: $\bar{x} = 3.29$, 95% CI = 3.08-3.50, $n = 36$, $F_{1, 78} = 2.70$, $p = 0.10$) than undisturbed birds.

Nest Defense

Birds at all sites followed the expected trend of increasing nest defense as the age of the nest increased (Fig. 1.1). When analyzed independently of type of threat, adult cardinals defended their nests similarly on high ($\bar{x}$ = 18.55, 95% CI = 17.51-19.56) and low ($\bar{x}$ = 19.52, 95% CI = 18.48-20.56, $F_{1, 202}$ = 1.77, p = 0.18; Fig. 1.1) disturbance sites. Likewise, when the nest threats were analyzed separately, we observed that cardinals from the two levels of disturbance did not differ in their response to the crow ($F_{1, 203}$ = 0.13, p = 1.0; Fig 1.2) or human ($F_{1, 203}$ = 2.51, p = 0.23; Fig. 1.2) threats. Nor did incubating females flush at different distances on high and low disturbance sites ($F_{1, 170}$ = 0.24, p = 0.62; Fig. 1.3).

Unexpectedly, when adult responses to each threat were analyzed by disturbance level, we observed that birds responded differently to human and crow threats on the low disturbance sites ($F_{1, 203}$ = 6.47, p = 0.02; Fig. 1.4), but not on sites designated high disturbance ($F_{1, 203}$ = 1.89, p = 0.34; Fig. 1.4).

Nestling Provisioning and Offspring Quality

Cardinals did not decrease their nestling provisioning on high disturbance sites, either in feeding rate ($F_{1, 92}$ = 0.20, p = 0.65; Fig. 1.5) or feeding score ($F_{1, 92}$ = 1.40, p = 0.24; Fig. 1.5). Similarly, offspring did not have lower mean nestling masses in high disturbance nests ($\bar{x}$ = 17.65, 95% CI = 16.16-19.13, n = 15) than in low disturbance nests ($\bar{x}$ = 17.59, 95% CI = 16.06-19.13, n = 14, $F_{1, 27}$ = 0.00, p = 0.96).

Corticosterone Response

Adult cardinals consistently displayed elevated CORT concentrations in response to capture and 30 minutes of restraint in both groups ($F_{1, 51}$ = 87.77, p = 0.00; Fig. 1.6), as expected. CORT levels, however, did not differ between disturbance levels for either baseline ($F_{1, 51}$ = 0.00, p = 1.00) or stress-induced ($F_{1, 51}$ = 1.53, p = 0.44) samples (Fig. 1.6).

Productivity

An analysis of cardinal productivity showed that nests in areas with high disturbance did not have lower daily survival rates or decreased fledging success (Table 1.2). Similarly, the daily nest survival rates of other open cup nesting passerines were

comparable between levels of disturbance and the fledging success of birds occupying high disturbance sites was not decreased (Table 1.2).

Discussion

The impact of military disturbance on passerine reproductive ecology appears to be minimal based on our experiments with Northern Cardinals. Again, cardinals were chosen to provide a conservative measure of military effects based on their tolerance of human disturbance. Therefore, even though the results of this study are promising for bird species that inhabit military bases, it is possible that less adaptable species would be unable to cope with this disturbance without displaying altered behaviors and decreased fitness. Although we did not collect data on the breeding behavior of other species we did show that our results for cardinal nest success and productivity are consistent with other open cup nesting species (including 7 nests of the endangered Black-capped Vireo), suggesting that other passerines may be similarly unaffected.

Another explanation for the lack of military effects is that our small birds may not respond as strongly to human disturbance as larger species because alert distance increases with body size (Blumstein et al. 2005). This could also clarify why American Crows seem to alter their distribution to avoid military disturbance but cardinals do not. It could, however, be because crows alter their behavior to the level of persecution (Knight et al. 1987) and frequent hunting in this rural part of Texas has caused them to avoid military personnel with weapons. Regardless of the reason, a decrease in the abundance of crows or any other nest predator would actually confer an advantage of military training for nesting passerines. We saw no difference in nest predation to support this idea, but the effect could have been obscured by predation from species less likely to avoid military disturbance, such as fire ants and snakes, the primary nest predators in the area (Stake and Cimprich 2003). By considering whether predators are impacted by military disturbance biologists may be able to gain insight that would be overlooked in studies of the nesting birds themselves.

The observed abundance of crows on low disturbance sites may explain why cardinals respond differently to the threats on the low disturbance sites but not on the high disturbance sites. This difference was primarily driven by a dramatic increase in the

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birds' response to the crow on low disturbance sites, where crows were most abundant, suggesting that cardinals adjust their defensive response to local crow abundance. The reason that a comparable adjustment to human abundance was not detected may be that crows pose a genuine threat to cardinal offspring, whereas military personnel do not.

While this study increases our understanding of military training's impact on avian ecology, multiple questions remain unanswered. For example, we know little about the effects of military disturbance on local avian community structure except that indirect effects of habitat modification may exist. By advancing our understanding of military disturbance's ecological impacts we can ensure that bases persist as important refuges for avian wildlife.

Tables and Figures

Table 1.1. Designation of scores for each variable measured in active nest defense trials. The variables latency to detection and total vocalizations were recorded for the pair of cardinals, whereas the response duration and closest approach variables were recorded independently for male and female parents. The scores of these six variables were compiled into a composite nest defense score, ranging from 0 to 30.

Variable	Value	Score
Latency to Detection	0-10 minutes	5
	10.01-20 minutes	4
	20.01-30 minutes	3
	30.01-40 minutes	2
	>40 minutes	1
	>60 minutes	0
Response Duration	241-300 seconds	5
	181-240 seconds	4
	121-180 seconds	3
	61-120 seconds	2
	1-60 seconds	1
	0 seconds	0
Total Vocalizations	401+	5
	301-400	4
	201-300	3
	101-200	2
	1-100	1
	0	0
Closest Approach	0-3.9 m	5
	4-7.9 m	4
	8-11.9 m	3
	12-15.9 m	2
	16+ m	1
	Never Approached	0

Table 1.2. Daily nest survival rate and mean number of fledglings produced per egg for Northern Cardinals and other open cup nesting passerine species occupying sites with high and low levels of military disturbance. Values in parentheses are the number of territories used in calculating the number of fledglings per egg. Calculations of daily survival rates are based on 123 total nests for cardinals (obs. days = 768) and 31 total nests for other passerines (obs. days = 147).

| Species | Disturbance | Daily Survival Rate | | Number of Fledglings per Egg | | | |
		Mean	95% CI	Mean (n)	95% CI	F	P
Cardinalis cardinalis	High	0.942	0.921-0.958	0.32 (51)	0.21-0.44		
						0.30	0.59
	Low	0.945	0.924-0.961	0.37 (51)	0.25-0.48		
Other passerines	High	0.944	0.896-0.971	0.35 (13)	0.22-0.67		
						0.49	0.49
	Low	0.944	0.892-0.972	0.50 (14)	0.19-0.81		
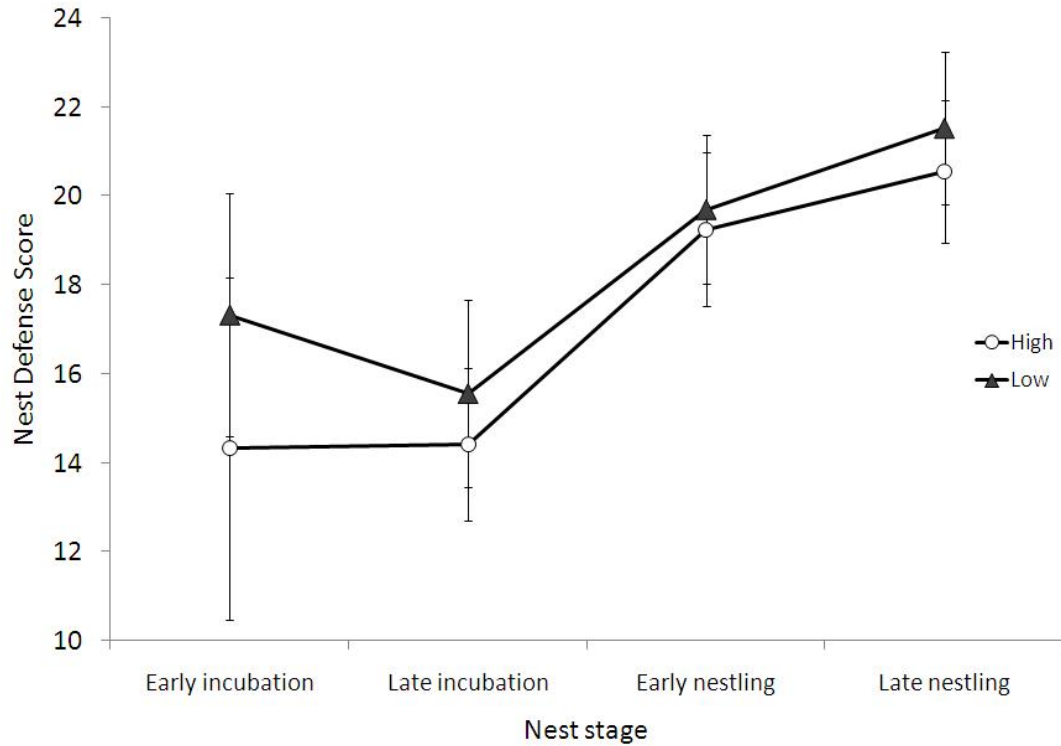
Figure 1.1. Mean nest defense scores (±95% confidence intervals) of adult cardinals with young in multiple nest stages on high and low disturbance sites. Nest defense scores are a composite of latency to detection, number of vocalizations, duration of response, and closest approach. Nest stages are early incubation (1-8 days), late incubation (9-16 days), early nestling (17-21 days), and late nestling (22-26 days). This analysis includes 206 nest defense trials (105 high disturbance, 101 low disturbance) from 55 territories (27 high disturbance, 28 low disturbance), with these trials divided between the crow and human nest threat.
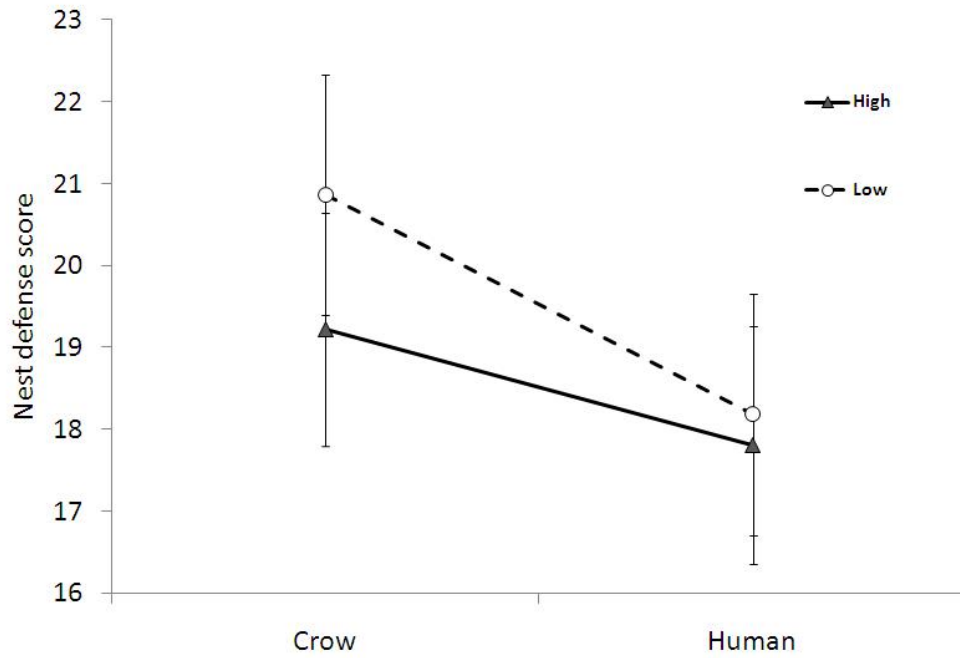
Figure 1.2. Mean nest defense scores (±95% confidence intervals) of adult cardinals to each threat type between sites with high and low disturbance. Nest defense scores are a composite of latency to detection, number of vocalizations, duration of response, and closest approach. A total of 207 nest defense trials (105 high disturbance, 102 low disturbance), divided approximately equally between nest threats, are included from 28 territories from each disturbance level.
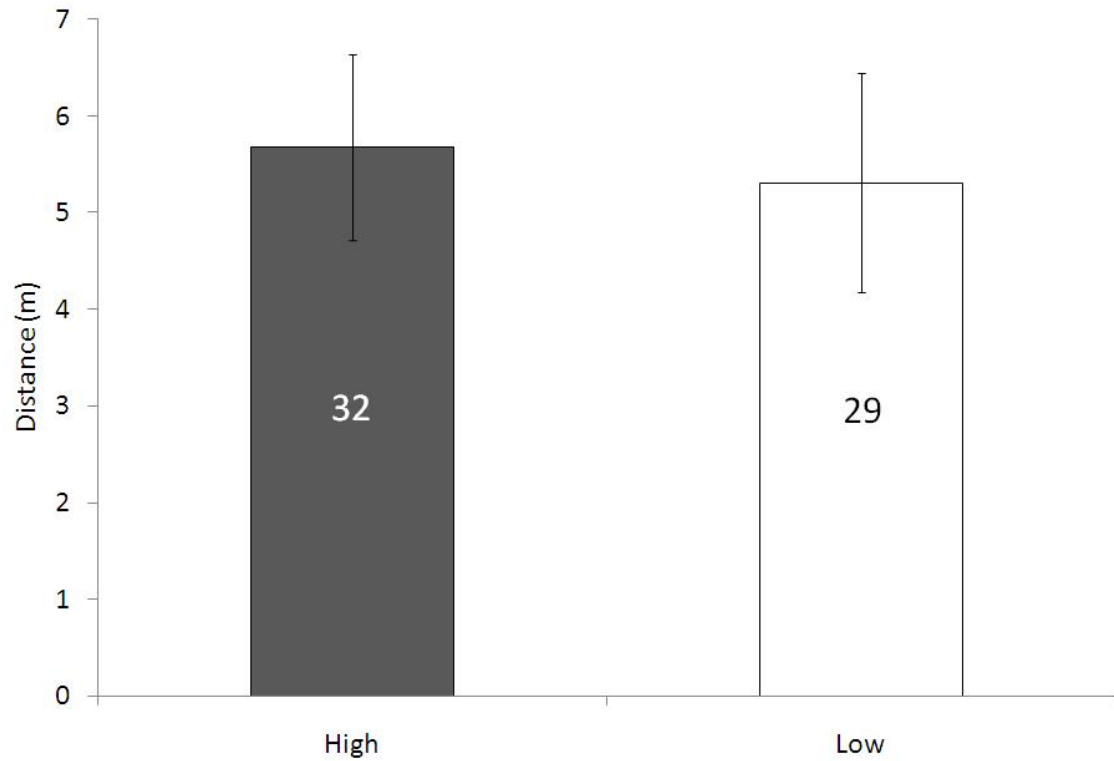
Figure 1.3. Mean flush distance (±95% confidence intervals) of incubating females inhabiting high and low disturbance sites. A total of 173 flush distances were recorded, with 101 high disturbance and 72 low disturbance. Values within bars represent the number of females from which flush distances were recorded on each site.
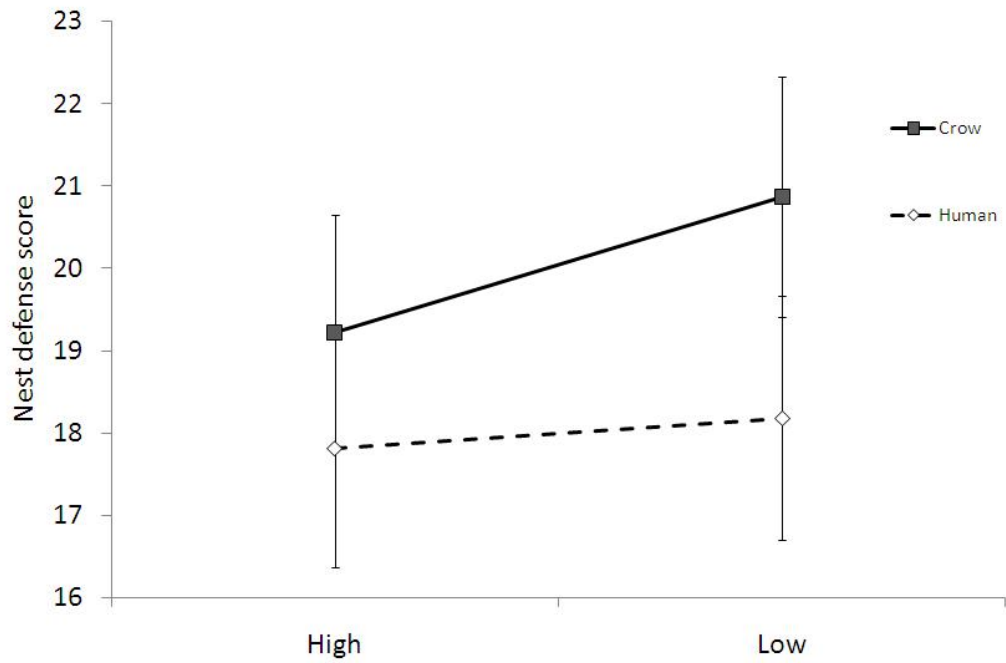
Figure 1.4. Mean nest defense scores (±95% confidence intervals) of adult cardinals from high and low disturbance sites for crow and human nest threats. Nest defense scores are a composite of latency to detection, number of vocalizations, duration of response, and closest approach. Observations were made at 28 territories from each military level, with a total of 207 nest defense trials (105 high disturbance, 102 low disturbance), divided approximately equally between nest threats.
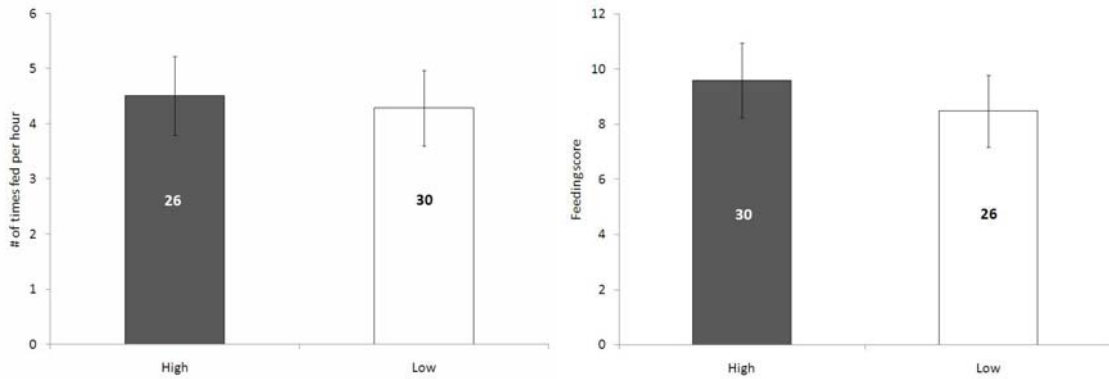
Figure 1.5. Mean number of feeding visits per hour (±95% confidence intervals) and feeding scores (±95% confidence intervals) of adult cardinals on high and low disturbance sites. Feeding score equals number of feeding visits multiplied by average prey size. A total of 94 observations of provisioning are included, 45 from high disturbance sites and 49 from low disturbance sites. Values within bars represent the number of territories where observations were made.

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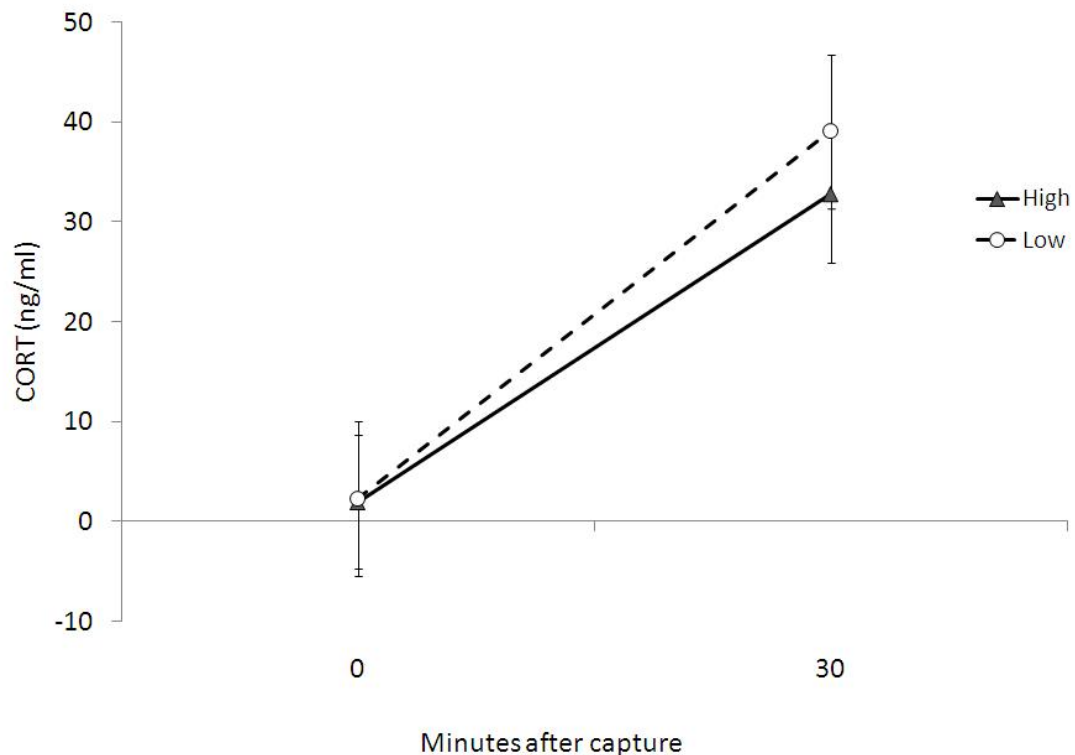
Figure 1.6. Mean corticosterone levels (±95% confidence intervals) of male cardinals occupying high and low disturbance sites. The 0 minute time includes birds bled within 3 minutes of capture and represents baseline levels, whereas the 30 minute time represents stress-induced levels. High, 0: n=16, High, 30: n= 15, Low,0: n=14, Low, 30: n=14.

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Chapter 2

Impact of radio transmitters on Northern Cardinal parental investment and productivity

Abstract

Researchers commonly use radio transmitters to collect ecological data from free-living birds with the assumption that these devices do not alter their natural behavior or ecology. We tested this assumption for Northern Cardinal (*Cardinalis cardinalis*) parental investment (nest defense and offspring provisioning), because such behaviors have been mostly ignored in past studies with passerines. We placed mock radio transmitters on male cardinals and compared their behaviors to uncaptured birds and similarly handled procedural controls. Birds with transmitters showed a strongly significant decrease in their nest defense and an insignificant decrease in provisioning effort. These responses were not a result of capture and restraint, as uncaptured birds and procedural controls had similar estimates for both behaviors. An insignificant increase in provisioning effort by mates of birds with transmitters hinted that compensation by unmarked females may minimize transmitter effects on current productivity. This idea is supported by our similar estimates of daily nest survival and fledging success between birds with and without transmitters. The increased energy expenditure of compensating mates could limit their future reproductive potential, representing an indirect effect of radio transmitters.

Introduction

Using radio transmitters to collect ecological data from free-living animals has become common since the introduction of radio-telemetry (Cochran and Lord 1963; LeMunyan et al. 1959). Ornithological studies increasingly use radio telemetry as technological advancements have made transmitters small enough for use on birds such as passerines. A major assumption of studies using this technology is that transmitters do not alter the natural behavior or ecology of the birds. If this assumption is wrong, radio transmitters could harm the birds and produce unreliable data. Multiple studies have revealed negative impacts of transmitters on avian survival (e.g., Marks and Marks 1987),

reproduction (e.g., Foster et al. 1992), body condition (e.g., Greenwood and Sargeant 1973), and behavior (e.g., Hooge 1991). One aspect of behavior that has received little attention in this regard, however, is parental investment, despite its importance to reproduction and survival (Trivers 1972). Here we investigate whether transmitters affect two components of parental investment (nest defense and offspring provisioning) by Northern Cardinals (*Cardinalis cardinalis*).

Given the importance of nest predation for most birds (Ricklefs 1969), and that nest defense can potentially deter predation (e.g., Greig-Smith 1980; Weatherhead 1990), alteration of normal nest defense could have negative implications for a bird's fitness (Montgomerie and Weatherhead 1988). There are two ways that transmitters might affect nest defense. First, transmitters could cause birds to defend their nests less aggressively simply because the cost of carrying the transmitter makes normal defense physically more difficult. Alternatively, and perhaps less intuitively, if birds with transmitters perceive their own survival value to be diminished, that could favor increased investment in their current brood (Trivers 1972), and therefore increased nest defense (Montgomerie and Weatherhead 1988). Neither of these predictions has been tested previously.

As with nest defense, offspring provisioning could either be reduced due to physical impairment associated with transmitters, or increased because transmitters cause birds to favor current reproduction over future reproduction. In the only study to investigate transmitter effects on passerine provisioning, Neudorf and Pitcher (1997) found no difference in provisioning between females with and without transmitters. A potential limitation of their study was that they considered only feeding rate, potentially missing differences associated with food load size. Here we examine both feeding rate and the size of food loads.

A potential effect of transmitters that has not been previously investigated is an indirect effect on the mate of the bird that is carrying a transmitter. If the bird with a transmitter reduces its parental investment, its unmarked mate could potentially compensate by increasing their own investment (Johnstone and Hinde 2006). To examine this possibility we determined whether transmitters caused a change in the nest defense or offspring provisioning of the mate of the bird with the transmitter.

Finally, we investigated whether transmitters affect cardinal productivity, in the form of daily nest survival rate and fledging success (fledglings produced per egg). If there is an effect the most likely outcome would be that transmitters reduce productivity, although depending on which of the predictions outlined above are supported, productivity could be unaffected by transmitters or could even increase. We predicted that transmitters would reduce productivity if they cause a decrease in nest defense, since the intensity of nest defense is positively correlated with nest success (e.g., Greig-Smith 1980; Weatherhead 1990). Because parental activity can attract predators and increase nest predation (Martin et al. 2000), we expect that if transmitters decrease offspring provisioning then birds with transmitters would have increase productivity. Although this decrease in provisioning could also decrease fledging mass, we lack sufficient data to investigate this possibility. Compensation by females would offset any changes in productivity that would have resulted from transmitter effects on male parental behaviors.

Methods

Nest Monitoring

We conducted this study in 2007 and 2008 on seven sites ranging from 11-150 ha at Fort Hood, in central Texas. We used parental cues to locate as many Northern Cardinal nests as possible on each site from mid March until late August. Nests were checked approximately every other day, with more frequent visits when the nestlings approached fledging to ensure accurate determination of nest fates.

Capture and Device Attachment

We restricted transmitter attachment to males because they were easier to capture using a mist-net with conspecific playback and we wanted to be consistent in which member of the pair received a transmitter. We randomly assigned each pair for which we found a nest to one of three treatments. In the "no treatment" group birds were not captured. In the "control" group, males were captured but no transmitters were attached. In the "transmitter" group, males were captured and a transmitter was attached. Males in the "control" and "transmitter" treatments were captured shortly after the nest was found, which was usually during incubation. When males were captured we collected up to 60 µl of blood from the brachial vein for an unrelated research objective and banded each bird

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with a USFWS aluminum leg band and a unique combination of color bands before placing the birds into an opaque cloth bag. Blood collection has no major negative effects on wild birds (Sheldon et al. 2008) and should therefore not influence our results. Thirty minutes after capture we collected another blood sample and then released "control" birds. "Transmitter" birds received a mock transmitter before being released. We used mock transmitters rather than real transmitters because our goal was to assess the effects of carrying a "transmitter" and not to conduct a telemetry study. Mock transmitters were similar in size, shape, and mass to actual radio transmitters and were constructed by attaching a 0.8 mm metal wire antenna to an 8 mm cylindrical wooden body using JB Weld. The average mass of the entire package was 1.6 grams (SD = 0.2), which was approximately 4.0% of the birds' body mass (SD = 0.3%). In 2007 we attached devices dorsally using eyelash glue (Raim 1978), but the low retention times caused us to change to a harness made of dissolvable suture (Doerr and Doerr 2002) in 2008.

Nest Defense

We conducted nest defense trials up to three times during a nesting attempt: incubation, early nestling, and late nestling. A trial consisted of exposing cardinal nests sequentially to a human and a model American Crow (*Corvus brachyrhynchos*), both of which cardinals respond to as nest threats. We randomly determined the order of the threats with a 2 h break between their presentations. The first threat was consistently presented between 2 and 2.5 h after sunrise. Following detection by either parent, we recorded the 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 higher values representing a stronger response (Table 2.1). The scores of these three variables were then compiled into a composite nest defense score, ranging from 0 to 15. By recording multiple behavioral traits we were able to generate a more accurate overall 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 15-25m from the nest the previous day.

Nestling Provisioning

We monitored nestling provisioning from a blind using a spotting scope (20-60x magnification) trained on the nest. Observations were made for 1 h during the interval between successive presentations in nest defense trials. We used the second hour of the interval to ensure that birds had resumed normal activity following the first nest threat presentation. In addition to recording the number of feeding visits by each parent, we also estimated food load size. 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 their number of visits per hour by their average prey size. If we could not determine the prey size its load value was recorded as the average of all other loads values recorded during the hour of observations.

Statistical Methods

We analyzed daily survival rates of nests using a logistic-exposure model (Shaffer 2004). Differences in estimates of nest defense, nestling provisioning (feeding rate and feeding score), and fledging success among birds from each treatment were analyzed with a mixed model repeated measures analysis using the pair as the unit of replication. We used Bonferroni corrections for multiple comparisons between the treatments. Julian date, time after sunrise, age of young, and number of young were included as covariates in the analysis of nest defense (Montgomerie and Weatherhead 1988) and nestling provisioning. Although multiple studies have shown no impact of previous exposure on passerine 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. Mixed model analyses were employed because treatment and nest threat were fixed models, whereas the individual birds that were monitored were randomly determined.

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

Results

Nest Defense

We found a significant effect of treatment on male nest defense ($F_{2, 271}$ = 10.61, p < 0.001), but there was no difference between responses to a person vs. a model crow ($F_{1, 271}$ = 0.58, p = 0.45) and the treatment effect was consistent across these threats ($F_{1, 271}$ = 0.32, p = 0.72). Comparisons between treatments confirmed that birds with transmitters defended their nests less aggressively than both no treatment ($F_{1, 271}$ = 19.73, p < 0.001; Fig. 2.1) and control birds ($F_{1, 271}$ = 6.08, p = 0.04; Fig. 2.1), but there was no difference between the control and no treatment birds ($F_{1, 271}$ = 3.41, p = 0.20). Females did not show a compensatory increase in nest defense when their mates had transmitters because their responses did not differ among treatments ($F_{2, 271}$ = 0.21, p = 0.81). The covariates age of young ($F_{1, 265}$ = 32.09, p < 0.001) and number of previous trials ($F_{1, 265}$ = 10.10, p = 0.002) significantly affected male nest defense, but not female nest defense.

Nestling Provisioning

Males with transmitters provisioned approximately half as much as no treatment and control birds, although high predation rates during incubation limited our sample sizes and prevented us from detecting a significant effect of treatment on feeding rate ($F_{2, 93}$ = 1.21, p = 0.30; Fig. 2.2) or feeding score ($F_{2, 91}$ = 1.42, p = 0.25; Fig. 2.2). The trend of increased provisioning by mates of males with transmitters suggests that females may compensate by increasing their own feeding rate ($F_{2, 93}$ = 1.83, p = 0.17; Fig. 2.3) and feeding score ($F_{2, 90}$ = 1.21, p = 0.06; Fig. 2.3).

Productivity

Birds with transmitters did not have altered productivity as indicated by either daily nest survival rates or fledging success (Table 2.2).

Discussion

Our results indicate that transmitters cause male Northern Cardinals to reduce their parental investment. We found clear evidence of decreased nest defense by males with transmitters, and a non-significant trend for males with transmitters to decrease provisioning. The similarity in behavior between no treatment and control birds indicates

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that capturing and restraining birds was not responsible for the behavioral changes observed in birds with transmitters.

Despite the decrease in parental investment by males with transmitters we did not find evidence that transmitters caused a decline in nest productivity. Two factors may have contributed to this result. First, although past studies have found a positive correlation between nest defense intensity and nest success, the effect can be small and detectable only with relatively large samples (e.g., Weatherhead 1990). Our limited sample of nests from the transmitter treatment could have prevented us from detecting an effect of decreased nest defense. Second, although there was some evidence that males with transmitters fed their offspring less, there was also limited evidence that their mates compensated for this reduced paternal care. By compensating for their mates, females would have minimized the impact of their mates' reduced contribution.

Our results suggesting that transmitters cause cardinals to decrease offspring feeding rate differ from those of Neudorf and Pitcher (1997), who found no comparable trend in Hooded Warblers. The different outcome is not attributable to differences in transmitter weight because their transmitters were heavier relative to the birds (7-8.5%) than were ours (4%). In both studies transmitters were attached with leg-harnesses and in both species nestlings are fed by each parent. An obvious difference between studies is that we attached transmitters to males and they attached transmitters to females. This might explain our results if greater uncertainty of parentage makes males more willing to decrease nestling provisioning when burdened with a transmitter (Sanz et al. 2000; Slagsvold and Lifjeld 1990). An appropriate study to test this possibility would compare how transmitters affect parental care by males and females of the same species.

Johnstone and Hinde (2006) recently suggested that parents should respond to changes in their partner's cooperation with an incomplete compensatory change in the opposite direction when variation in brood need is less than variation in parental state. Cardinals may fit this pattern, as the rarity of nestling starvation and the wide range of adult body conditions (Barron, unpublished) suggests higher variation in parental state than in brood need. Furthermore, Chase (1980) predicted that any additional costs of cooperative behaviors (such as energetic costs caused by transmitters) would compel an animal to reduce such behaviors, causing a compensatory increase in the cooperative

behaviors of its mate. While the female mates of cardinals with transmitters did not compensate by increasing their intensity of nest defense, they did seem to increase their offspring provisioning to compensate for their males' decreased provisioning. This insignificant trend is inconclusive, however, and further research is required to determine its accuracy. Future studies should also determine whether males compensate similarly, since males and females can respond differently to changes in partner effort (Sanz et al. 2000). Although compensatory feeding would maintain the quality of nestlings in the current brood, this life-history trade-off could limit the unmarked bird's potential investment in future broods (Trivers 1972) and therefore represent an indirect effect of transmitters.

Our findings suggest that compensatory feeding by an unmarked mate may be required to maintain offspring quality and therefore researchers should avoid placing transmitters on both parents from a single nest. Studies that only investigate transmitter effects on indices of productivity could be missing important indirect effects on the compensating mate and should therefore be cautious about declaring no effect. The potential reduction in the long-term fitness of the bird with the transmitter and its mate reveals the importance of carefully weighing the costs and benefits of using this technology on sensitive, rare, or endangered species.

Tables and Figures

Table 2.1. Designation of scores for each variable measured in nest defense trials. The scores of these three variables were compiled into a composite nest defense score for both the male and female parent, ranging from 0 to 15.

Variable	Value	Score
Response Duration	241-300 seconds	5
	181-240 seconds	4
	121-180 seconds	3
	61-120 seconds	2
	1-60 seconds	1
	0 seconds	0
Total Vocalizations	201+	5
	151-200	4
	101-150	3
	51-100	2
	1-50	1
	0	0
Closest Approach	0-3.9 m	5
	4-7.9 m	4
	8-11.9 m	3
	12-15.9 m	2
	16+ m	1
	Never Approached	0

Table 2.2. Daily nest survival rate and mean number of fledglings produced per egg for birds from each treatment. Values in parentheses are the number of nests followed by the number of territories. Calculations of daily survival rates are based on 768 observation days.

Treatment	Daily Survival Rate		Number of Fledglings per Egg			
	Mean	95% CI	Mean (n)	95% CI	F	P
No Treatment	0.942	0.925-0.956	0.37 (91, 81)	0.28-0.46		
Control	0.953	0.909-0.976	0.24 (11, 9)	-0.02-0.51	0.85	0.43
Transmitter	0.943	0.900-0.969	0.24 (14, 12)	0.00-0.47		
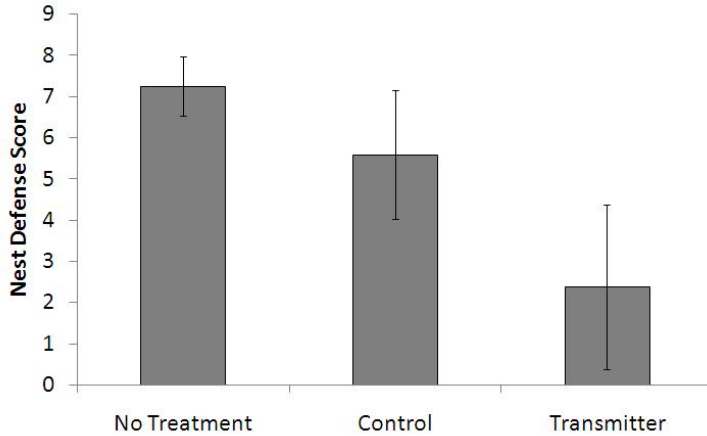
Figure 2.1. Mean nest defense scores (±95% confidence intervals) of male cardinals from each treatment. Nest defense scores are a composite of number of vocalizations, duration of response, and closest approach. This analysis is of 276 nest defense trials (207 no treatment, 43 control, 26 transmitter) from 72 territories (56 no treatment, 8 control, 8 transmitter), with these trials divided between the crow and human nest threat.

Figure 2.2. Mean number of feeding visits per hour (±95% confidence intervals) and feeding scores (±95% confidence intervals) of male cardinals from each treatment. Feeding score equals number of feeding visits multiplied by average prey size. We estimated feeding rates from 96 observations (80 no treatment, 11 control, 5 transmitter) from 57 territories (47 no treatment, 6 control, 4 transmitter). We estimated feeding scores from 94 observations (79 no treatment, 10 control, 5 transmitter) from 55 territories (46 no treatment, 5 control, 4 transmitter).
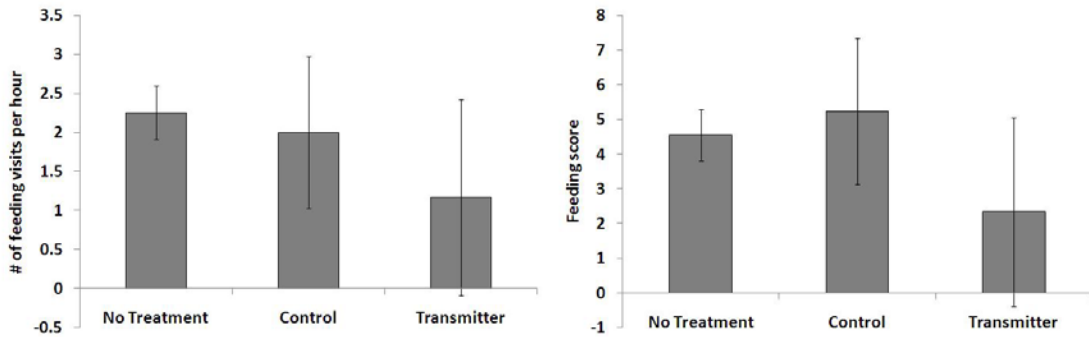
Figure 2.3. Mean number of feeding visits per hour (±95% confidence intervals) and feeding scores (±95% confidence intervals) of female cardinals from each treatment. Feeding score equals number of feeding visits multiplied by average prey size. We estimated feeding rates from 96 observations (80 no treatment, 11 control, 5 transmitter) from 57 territories (47 no treatment, 6 control, 4 transmitter). We estimated feeding scores from 93 observations (79 no treatment, 10 control, 4 transmitter) from 54 territories (46 no treatment, 5 control, 3 transmitter).
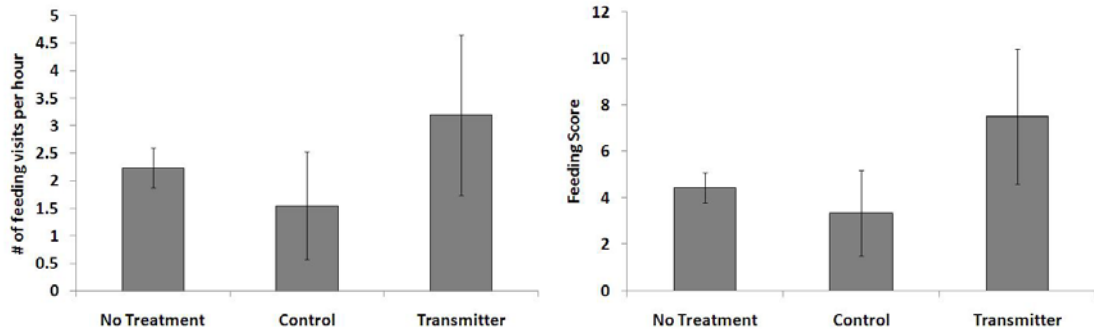
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Chapter 3

A meta-analysis of transmitter effects on avian behavior and ecology

Abstract

Researchers frequently use transmitters and dataloggers to collect data from free-living birds with the assumption that these devices are not harming the birds or producing biased data. Although many studies have investigated the impacts of transmitters on avian behavior and ecology, their conclusions were generally limited to a single species or type of device. To achieve a broader understanding of this topic we combined results from 84 studies into a meta-analysis that we used to explore five questions: 1) Do devices cause an overall effect on birds? 2) Which aspects of avian behavior and ecology are affected? 3) What characteristics of the birds influence effects? 4) What characteristics of the device influence effects? 5) Are effects partially a consequence of capture and restraint? We found a significant negative effect of devices on birds, both overall and for 8 of the 12 specific aspects we analyzed. The most drastic effects were that birds wearing devices expended far more energy and were much less likely to nest than birds without devices. Effects were independent of characteristics of the birds (sex, age, primary method of locomotion, body mass). We also found no evidence that the mass of the device relative to the mass of the bird contributed to effects, although researchers generally avoided using heavy devices. We did find that some methods of attachment increased device-induced behaviors such as preening at the device, whereas other attachment methods were more likely to cause mortality. The observed effects were not a consequence of capture or restraint, which suggests that traditional mark-recapture techniques would not negatively affect birds. Researchers should carefully balance the benefits of using transmitters and other devices against the potential costs to the birds and the reliability of the data obtained.

Introduction

Following wild animals to monitor their activity has long been a challenge for biologists. Several decades ago, however, miniature radio transmitters were developed that allowed biologists to track free-roaming animals (Cochran and Lord 1963;

LeMunyan et al. 1959). Since its initial development, this technique has become an important component of research in animal ecology. Aided by technological advancements that have produced smaller transmitters with greater battery life and signal strength, the pool of suitable species has expanded to ever-smaller animals and made the technology especially useful for studies of birds. More than 190 studies using radio telemetry on birds have been published, and use of this technology is increasing (Fig. 3.1). Growing use of telemetry in avian research makes it increasingly important that we understand how the devices affect the birds. Researchers using radio telemetry assume that birds are unaffected by carrying the transmitters, but if this assumption is wrong, the birds could be harmed and the data collected could lead to erroneous conclusions about the populations studied and the issues addressed. Here we use a meta-analytical approach to investigate the effects of attaching devices to birds.

Clearly, researchers are aware of the potential effects of transmitter attachment; almost 80% of studies we review here (see below) addressed the topic in some fashion. Although there have been several reviews of transmitter effects on birds (e.g., Calvo and Furness 1992; Murray and Fuller 2000; Samuel and Fuller 1994), none have been comprehensive. These reviews have either evaluated transmitter effects qualitatively, or if a quantitative approach was used it relied on "vote counting" (the number of studies reporting negative effects is compared to the number reporting no effects), which ignores effect sizes (Hedges and Olkin 1980). The meta-analytical approach we use here is based upon effect sizes and allows us to explore differences quantitatively, independent of scales of measurement (Gurevitch and Hedges 1993).

Our first goal was to determine whether transmitters have any effect on birds. Secondly, we wanted to identify the specific aspects of avian behavior and ecology that were affected by transmitters. The aspects we investigated were nest success, productivity, clutch size, nesting propensity, nest initiation date, nest abandonment, offspring quality, body condition, flying ability, foraging behaviors, device-induced behaviors, energetic expenditure, survival, physical impairment, and device-induced mortality. Although not exhaustive, this list includes most important aspects that might plausibly be affected by transmitters, and for which adequate data were available. Our third objective was to identify characteristics of the birds that contributed to the

transmitter effects. Characteristics considered here were sex, age, mode of locomotion, and body mass.

Our fourth goal was to identify attributes of the transmitters that contributed to their effects. We first assessed the effect of the mass of the transmitters relative to that of the birds on which they were attached. A rule of thumb is that loads weighing less than 5% of an animal's body mass have negligible effects. This "5% rule" has no empirical basis and appears to have originated from a suggestion by Brander and Cochran (1969) regarding transmitter weights. Aldridge and Brigham (1988) did assess the effect of attaching variable loads on bats and found decreased maneuverability as load mass increased. Our objective was to look for a similar effect in birds and determine if there is evidence for a threshold effect that would be consistent with the 5% rule. Lastly, we considered whether the method of transmitter attachment influences transmitter effects, because past studies that compared attachment types produced contradictory results (e.g., Garrettson and Rohwer 1998; Osborne et al. 1997; Small and Rusch 1985).

Finally, we addressed whether any negative effects were attributable only to the transmitter or whether they are partially a result of capture and restraint (Cox and Afton 1998). If birds are affected by capture and restraint, transmitters should appear to have a greater effect in studies that compare birds with transmitters to uncaptured birds than in studies that used procedural controls. Ultimately, the goal of our all our analyses is to provide information that will help researchers design studies that involve attaching devices to birds in a way that will minimize negative effects on either the birds or the research.

Methods

Literature Search

The studies used in this meta-analysis were obtained from a literature search conducted between December 2008 and March 2009. The principal method for identifying relevant studies was searching *ISI Web of Science* and *Google Scholar* using topic words: radio transmitter, transmitter effects/impacts, radio telemetry, radio tagging, device attachment, radio attachment, instrument attachment and load attachment. Because dataloggers and satellite transmitters are similar in shape and methods of attachment to

radio transmitters, and therefore should have comparable effects on birds, we also included them in our study by replacing 'radio' with 'datalogger' or 'satellite' in our literature search. Hereafter we refer to transmitters, dataloggers, etc. as "devices". Finally, we included additional studies found in literature reviews (Calvo and Furness 1992; Godfrey and Bryant 2003; Murray and Fuller 2000; Phillips et al. 2003; Samuel and Fuller 1994) or in the literature cited by published studies.

We identified an initial sample of 192 studies in which devices were attached to birds. For a study to be included in our analysis, however, it had to meet two criteria. First, birds with devices had to be quantitatively compared to birds without devices. Second, we had to be able to estimate effect sizes from the provided information, requiring studies to report sample sizes, direction of the effect, and one of the following statistics: mean and standard deviation, F-statistic, t-statistic, Z-statistic, chi-squared value, or p-value. A total of 84 studies met these criteria.

Data Collection

We used several approaches to obtain data from the 84 studies. If results were divided (among study sites, years, etc.) without a combined analysis, we used the first result provided so only one result for a given analysis was taken from each study. If a study used devices that differed in mass and the effects were analyzed separately we used only the largest mass. If devices with different masses were combined in the analyses, however, we used the mean mass of the devices. We used multiple entries from a given study only if separate analyses were provided for different variables of interest (e.g., attachment type, species, sex). Because the few such studies usually used separate controls for each analysis, the potential lack of independence should have little effect on the results of our meta-analyses (Gurevitch and Hedges 1993). Any time results were provided in a graph we obtained the exact values using *GetData Graph Digitizer 2.24*.

We recorded characteristics of the birds (sex, age, primary mode of locomotion, and body mass) and the devices (% body mass and attachment type) based on certain designations (Table 3.1). We also recorded whether studies compared birds with devices to uncaptured birds or to previously captured procedural controls to determine the effect of capture and restraint. If studies reported results from both procedural control and

uncaptured birds, we only included comparisons to procedural controls. Finally, we categorized foraging behaviors as offspring provisioning or self-provisioning.

Statistical Analyses

For each study that met the criterion for inclusion we calculated the correlation coefficient *r* for each measured variable from one of the required statistics mentioned above along with either the sample size or degrees of freedom using the *MetaCalc Statistical Calculator* within the program *MetaWin* (Rosenberg et al. 2000). We then entered the correlation coefficients and sample sizes into *MetaWin* and used the program to calculate the effect size, Fisher's z-transformation, and its variance for all variables from each study. We appointed positive or negative directionality to the differences between birds with and without devices in each analysis, since each aspect of behavior or ecology had a clear direction that was beneficial. Therefore, negative effect size values are in the direction considered detrimental.

For each analysis, we used a random-effects model in *MetaWin* (Rosenberg et al. 2000) because it accounts for a random component of variation in effect sizes between studies and is generally considered more appropriate for ecological data than a more restrictive fixed-effects model (Gurevitch and Hedges 1993). Categorical characteristics of the bird or device could only be analyzed if they have two or more categories, and each category contained two or more studies (required to calculated mean effect size). We calculated 95% confidence intervals of the mean by bootstrapping with 999 iterations and considered the mean effect sizes significant if the confidence intervals did not overlap zero. We estimated probability values from randomization tests with 999 iterations and used those values to detect differences among group effect sizes (described by *Q*) in the categorical characteristics and to determine whether the slopes (*b*) of continuous characteristics plotted against effect sizes were different than zero. We report effect sizes and confidence intervals that are transformed from Fisher's z-transformation to Cohen's *d* (using the *MetaCalc Statistical Calculator* within the program *MetaWin* (Rosenberg et al. 2000)), because Cohen clearly defined how to interpret 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 (Cohen 1988).

Since the tendency for studies with insignificant results to go unpublished could lead to a reporting bias known as the file-drawer effect (Sterling 1959), we addressed this problem by calculating Rosenthal's fail-safe numbers (Rosenthal 1979) with alpha equal to 0.05 in the program *MetaWin* (Rosenberg et al. 2000). This value is the number of unpublished studies with a mean effect size of zero required to reduce the combined significance to the nominated alpha value. For example, a fail-safe number of 100 would mean 100 studies with no effect must have gone unpublished to eliminate the significance of the results. If this number is large relative to the number of included studies it suggests the conclusions are relatively robust, even if some publication bias exists. We present fail-safe numbers only for marginal results where the outcome would change with a few unpublished studies showing no effect. The potential for an opposing publication bias to exist (if researchers preferentially publish results showing no impact of device attachment) cannot be investigated and will therefore not be discussed.

In our first summary analysis we determined whether devices cause an overall effect by combining all aspects of behavior and ecology into a universal meta-analysis. If studies investigated more than one aspect, we only included the one with the most robust sample size to avoid introducing nonindependence. We then ran a summary analysis for each independent aspect to determine which were affected. Next, we conducted a summary analysis for each of the categorical and continuous characteristics of the bird and device to determine their influence on device effects. Finally, we determined the role of capture and restraint by running a summary analysis for each aspect using the categorical model of whether a study compared birds with devices to uncaptured birds or procedural controls.

The potential importance of attachment type led us to also investigate its influence on the frequency of nest abandonment, physical impairment, and device-induced mortality. We could not analyze this with a meta-analytical approach because the consequences of interest had discrete (but ordinal) outcomes, thus preventing the calculation of effect sizes. Studies received a '2' if they reported at least one occurrence of a consequence, '1' if they reported no occurrence, and '0' if they did not address the topic. We included the '0' category because the frequency of non-reporting studies could be related to the frequency of a consequence if the topic is primarily addressed when it

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occurs or if researchers purposely omit negative findings. Data were gathered from all 192 studies because even those not meeting the criteria for inclusion in the meta-analysis frequently reported deaths, physical harm, and nest abandonment. We compiled singly ordered contingency tables for each variable and then compared the proportion of studies in each response category for each attachment type with a Kruskal-Wallis test in the program *StatXact*. The null hypothesis of no attachment effect was assessed by estimating exact p-values with a Monte Carlo procedure.

Results

Effect of device attachment

The universal analysis assessing any effect showed that birds are significantly impacted by devices ($\bar{x}$ = -0.27, 95% CI = -0.37 to -0.17, n = 84). When specific aspects of avian behavior and ecology were analyzed separately we saw a negative (detrimental) mean effect size for every aspect except flying ability, and 8 of the 12 values were significantly different from zero (Table 3.2). The fail-safe value for productivity (9) was lower than the number of studies, however, suggesting that the negative effect could be attributable to the file-drawer effect. Device attachment had a "small" effect on most aspects, except that birds with transmitters had drastically increased energetic expenditure and were much less likely to nest (Table 3.2). We detected no difference between foraging behaviors related to provisioning offspring and those of self-provisioning (Q_1 = 1.23, p = 0.34, n = 38), indicating that birds do not sacrifice self-feeding in favor of current reproduction or offspring feeding in favor of self-preservation.

Influence of bird characteristics

We found little evidence that characteristics of the bird influence its response to the device. In fact, birds were similarly affected for every aspect examined regardless of age, mode of locomotion, and body mass (Table 3.3). The only characteristic having any influence was sex, with birds increasing the frequency of device-induced behaviors in studies using both sexes ($\bar{x}$ = -0.83, 95% CI = -1.08 to -0.38, n = 4), but not in studies using only females ($\bar{x}$ = -0.18, 95% CI = -0.39 to 0.06, n = 9), only males ($\bar{x}$ = 0.25, 95% CI = -0.03 to 0.55, n = 2), or an unknown sex ($\bar{x}$ = -0.62, 95% CI = -3.86 to -0.21, n = 3; p = 0.05; Table 3.3). If effects on these behaviors differ between sexes, we would have

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expected studies using both sexes to produce an effect size between studies using only males or females. The lack of an ecological explanation for this finding, along with its marginal significance, suggests that a bird's sex has little impact on device-induce behaviors.

Influence of device characteristics

The type of attachment influenced the degree of effects for both nest success ($p = 0.05$) and device-induced behaviors ($p = 0.03$; Table 3.3). Birds with anchor attachment had the lowest nest success ($\bar{x} = -0.75$, 95% CI = -1.14 to -0.41, $n = 3$) followed by harness attachment ($\bar{x} = -0.33$, 95% CI = -0.99 to -0.08, $n = 5$), but glued devices caused no decrease in nest success ($\bar{x} = 0.21$, 95% CI = -0.08 to 0.55, $n = 4$). This influence on nest success, however, could be an artifact of the file-drawer effect since the fail-safe number (12) is equal to the number of studies in the analysis. Birds performed the most device-induced behaviors when wearing breast-mounted devices ($\bar{x} = -1.05$, 95% CI = -1.10 to -0.89, $n = 2$) followed by those attached with a harness ($\bar{x} = -0.51$, 95% CI = -1.16 to -0.18, $n = 7$); whereas, neither glued ($\bar{x} = -0.34$, 95% CI = -0.46 to 0.10, $n = 2$) nor implanted devices ($\bar{x} = 0.08$, 95% CI = -0.12 to 0.40, $n = 5$) caused an increase in device-induced behavior. The method of attachment had no influence on the degree of effects for the other aspects analyzed in the meta-analysis (Table 3.3).

Attachment type did not influence the proportion of studies reporting physically impairment ($X^2 = 12.83$, $df = 7$, $p = 0.7$) or nest abandonment ($X^2 = 7.64$, $df = 7$, $p = 0.35$), but we did observe that the proportion of studies reporting device-induced mortality differed among attachment types ($X^2 = 29.37$, $df = 8$, $p < 0.001$). When we compared the percentage of studies reporting on mortality that had a bird die, we found that mortality was most common in studies using anchors (100%, $n = 2$), followed by implants (57%, $n = 23$), then harnesses (52%, $n = 27$), then collars (50%, $n = 6$), and finally glue (31%, $n = 13$). No mortality was reported in studies using tailmounts (0%, $n = 3$).

The effect of device attachment did not increase with increasing percent body mass for most aspects of behavior or ecology (Table 3.3). Birds wearing proportionally heavier devices, however, did initiate nests later than those wearing lighter devices ($p = .03$; Table 3.3), but the very small fail-safe number (0) indicates little effect of

proportional device mass on nest initiation date. Surprisingly, two variables showed amelioration of effects with increasing percent body mass, as birds with proportionally heavier devices had higher nest success ($p = 0.04$) and survival ($p = .05$; Table 3.3).

Effect of capture and restraint

Birds carrying devices showed a greater decrease in foraging behaviors when compared to uncaptured birds ($\bar{x} = -0.59$, 95% CI = -0.89 to -0.30, $n = 12$) than when compared to procedural controls ($\bar{x} = -0.02$, 95% CI = -0.26 to 0.22, $n = 24$; $Q = 10.69$, $p = 0.002$; Table 3.4), suggesting that birds decrease their foraging behaviors following capture and restraint. On the other hand, birds did not alter any other aspects of their behavior or ecology in response to capture and restraint (Table 3.4), suggesting that the negative effects described above are primarily due to device attachment.

Discussion

This study provides cumulative evidence that transmitters and other devices do cause negative impacts on birds and that most aspects of avian behavior and ecology are negatively affected to some degree. The most considerable impacts were that birds with transmitters had drastically increased energetic expenditure and were much less likely to nest. Researchers may be comforted, however, that four of twelve aspects were unaffected and six were affected only to a "small" degree, motivating little concern over generalizing estimations of these aspects from birds with devices to untagged populations.

Nest abandonment, physical impairment, and death were commonly reported in studies using devices. Our analyses suggest that although attachment type does not affect the frequency of nest abandonment or physical impairment, certain attachments are more likely to cause death. The two types with the highest percent of reported mortalities, suture and implant, require anesthesia, which highlights the risk of this procedure. Machin and Caulkett (2000) showed that anesthetizing with propofol instead of isoflurane minimizes impacts on the bird's health and decreases the probability of nest abandonment. Harnesses and collars have the next highest mortality rates and deaths were commonly a consequence of birds becoming entangled with vegetation (36% of reported harness deaths and 33% of collar deaths). Researchers can minimize this risk by

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using adjustable harnesses and collars (Dwyer 1972) to custom fit each bird and by adding a weak link that allows the device to detach from the bird if entangled (Karl and Clout 1987). Unfortunately the glue and tailmount attachments, which have the lowest reported frequency of mortality, have low retention rates on many species (Woolnough et al. 2004). If long-term attachment is not required, however, they should be preferentially used.

Considering the widespread acceptance of the "5% rule" of device attachment, it is surprising that we detected little impact of proportional device mass. In fact, no aspect was negatively affected independent of the file-drawer effect and nest success and survival actually showed benefits to increasing percent body mass. This counterintuitive result cannot be explained by a life-history response where birds perceive the device as decreasing their probability of survival and therefore place extra effort into current reproduction (Trivers 1972), as that would produce the observed increase in nest success but a decrease in survival. This trend is therefore best explained by non-random sampling. Perhaps it is proportional surface area rather than proportional mass that is most important in determining a device's effects, especially for flying and swimming birds that experience drag (Gessaman and Nagy 1988a; Obrecht et al. 1988). Researchers can minimize drag by reshaping the device, modifying its antenna, or placing it in the most caudal position (Bannasch et al. 1994; Obrecht et al. 1988; Wilson et al. 2004).

Regrettably, this meta-analysis is insufficient to properly address the "5% rule" of device attachment because its near-universal acceptance prevented studies from attaching larger devices. Indeed, only 10% of the reviewed studies exceeded this recommendation and the heaviest proportional mass used was 10%. This did not provide the variability to search for a threshold (whether 5% or a higher value) above which effects increase dramatically. Although it is possible that a device's effect increases linearly with increasing proportional mass, our results reject this idea for relatively small devices. This topic needs further clarification by attaching a range of proportional device masses greatly exceeding 5%, although this important research may be prohibited due to permitting and animal care restrictions.

The findings of this study have strong implications for using devices on sensitive, rare, or endangered birds. Although many of the aspects investigated were minimally

affected, the mean effect on almost every one was negative. The cumulative impact could be much greater than is indicated by looking at these individually. For example, the reductions in nest success, productivity, nesting propensity, and foraging behavior could combine to decrease reproductive potential. Similarly, reduced foraging behaviors, body condition, flying ability, and survival along with increased device-induced behaviors and energetic expenditure could decrease the probability that an individual endures to the following year. The combined effects on reproduction and survival would cause a drastic decline in the fitness of device carrying birds. Device attachment could also have indirect effects on the fitness of an unmarked mate if it compensates for the decreased parental investment of the marked bird (Paredes et al. 2005), as this increase in current brood investment would decrease future reproductive potential (Trivers 1972). Our results show little effect of capture and restraint, suggesting that negative effects are solely attributable to the device. This makes it unlikely that traditional mark-recapture approaches would have similar consequences and implies that managers should carefully balance the benefits of gaining data from transmitters and other devices with the potential costs to the viability of the species.

Species from other taxa could be similarly affected by device attachment (particularly species that are small and fly) and a comparable meta-analysis would be incredibly useful in determining the universal nature of device-induced effects. Researchers using transmitters and other devices should supply the necessary information for inclusion in a meta-analysis (see methods) to ensure that this is possible.

Tables and Figures

Table 3.1. Description of designations for each categorical characteristic of the bird or device. Although species in the 'walking' category fly during migration, studies of those species primarily used non-migrating individuals.

Characteristic	Category	Description
Attachment Type	Harness	Backpacks and harnesses
	Collar	Collars, necklaces, and pendants
	Glue	Glue and tape, whether alone or in combination with sutures, cable ties, or Velcro
	Anchor	Any method of anchoring subcutaneously
	Implant	Implanted anywhere in the body
	Breast-mounted	Attached to the breast
	Tailmount	Attached to tail
Locomotion	Walk	Shorebirds, galliforms, and rails
	Swim	Penguins
	Various	Waterfowl
	Fly	All other birds
Sex	Male	Devices on males only
	Female	Devices on females only
	Both	Devices on males and females
	Unknown	Devices on unknown sex
Age	Adult	Reproductively mature
	Juvenile	Non-reproductively mature

Table 3.2. The number of studies (*n*), estimates of Cohen's *d,* and 95% confidence intervals for each aspect of avian ecology. Confidence intervals were obtained by bootstrapping with 999 iterations and are considered significant if they not overlapping zero.

Aspect	*n*	Cohen's *d*	95% confidence interval
Nest Success	16	-0.33	-0.59 to -0.09
Productivity	14	-0.22	-0.48 to -0.01
Clutch Size	14	-0.17	-0.31 to 0.00
Nesting Propensity	5	-0.57	-0.81 to -0.30
Nest Initiation Date	9	-0.12	-0.36 to 0.12
Offspring Quality	8	-0.42	-0.95 to 0.02
Body Condition	35	-0.38	-0.63 to -0.17
Flying Ability	7	0.27	-0.52 to 1.12
Foraging Behaviors	38	-0.26	-0.46 to -0.10
Device-induced Behaviors	18	-0.37	-0.37 to -0.12
Energetic Expenditure	13	-0.96	-1.74 to -0.32
Survival	38	-0.18	-0.28 to -0.10

Table 3.3. The impact of characteristics of the bird and device on aspects of behavior or ecology. The value reported for categorical characteristics is the variation in effect size explained by the model (Q), with number of categories and number of studies in parentheses. The value reported for continuous characteristics is the slope (b) $\pm$ 1 standard error, with the number of studies included in parentheses. Significant ($\alpha < 0.05$) results are designated by a single asterisk if the number of studies is similar to Rosenthal's fail-safe number and by two asterisks if Rosenthal's fail-safe number is much higher. Aspects without an entry could not be calculated because there were not two or more categories containing two or more studies.

	Nest Success	Productivity	Clutch Size	Nesting Propensity	Nest Initiation Date	Offspring Quality	Body Condition	Flying Ability	Foraging Behaviors	Device-induced Behaviors	Energetic Expenditure	Survival
Bird Characteristics												
Sex	1.62 (3, 15)	2.58 (3, 14)	2.92 (2, 14)	---	---	---	1.39 (4, 35)	---	5.24 (4, 38)	8.50** (4, 18)	0.19 (3, 12)	4.09 (4, 38)
Age	---	---	---	---	---	---	2.75 (3, 35)	---	0.02 (2, 38)	---	2.19 (2, 13)	0.62 (2, 37)
Locomotion	3.66 (3, 15)	0.97 (2, 13)	2.93 (3, 14)	0.50 (2, 5)	---	0.19 (2, 8)	2.83 (4, 35)	0.22 (2, 7)	0.60 (4, 38)	1.37 (4, 18)	3.35 (4, 13)	0.59 (3, 38)
Body Mass	0.00±0.00 (16)	0.00±0.00 (14)	0.00±0.00 (14)	0.00±0.00 (5)	0.00±0.00 (9)	0.00±0.00 (8)	0.00±0.00 (35)	0.00±0.00 (7)	0.00±0.00 (38)	0.00±0.00 (18)	0.00±0.00 (13)	0.00±0.00 (38)
Device Characteristics												
Attachment Type	8.46* (3, 12)	0.98 (3, 11)	1.19 (3, 11)	---	0.02 (2, 5)	1.01 (2, 5)	1.32 (3, 30)	0.17 (2, 5)	5.98 (5, 33)	9.9** (4, 16)	3.27 (3, 12)	2.68 (5, 34)
% Body Mass	0.07±0.03** (16)	-0.03±0.06 (14)	0.01±0.05 (14)	-0.08±0.09 (5)	-0.14±0.09* (9)	-0.01±0.21 (8)	0.03±0.03 (35)	0.00±0.00 (7)	0.00±0.03 (38)	-0.07±0.07 (18)	-0.11±0.07 (13)	0.02±0.02** (38)

Table 3.4. The effect of capture and restraint on each aspect of behavior or ecology, as calculated by contrasting studies comparing birds with devices to procedural controls with those using uncaptured individuals. The values reported are sample sizes (n), the variation in effect size explained by the model (Q), and randomized probability value (p). Aspects without an entry could not be calculated because there were less than two studies from one of the categories.

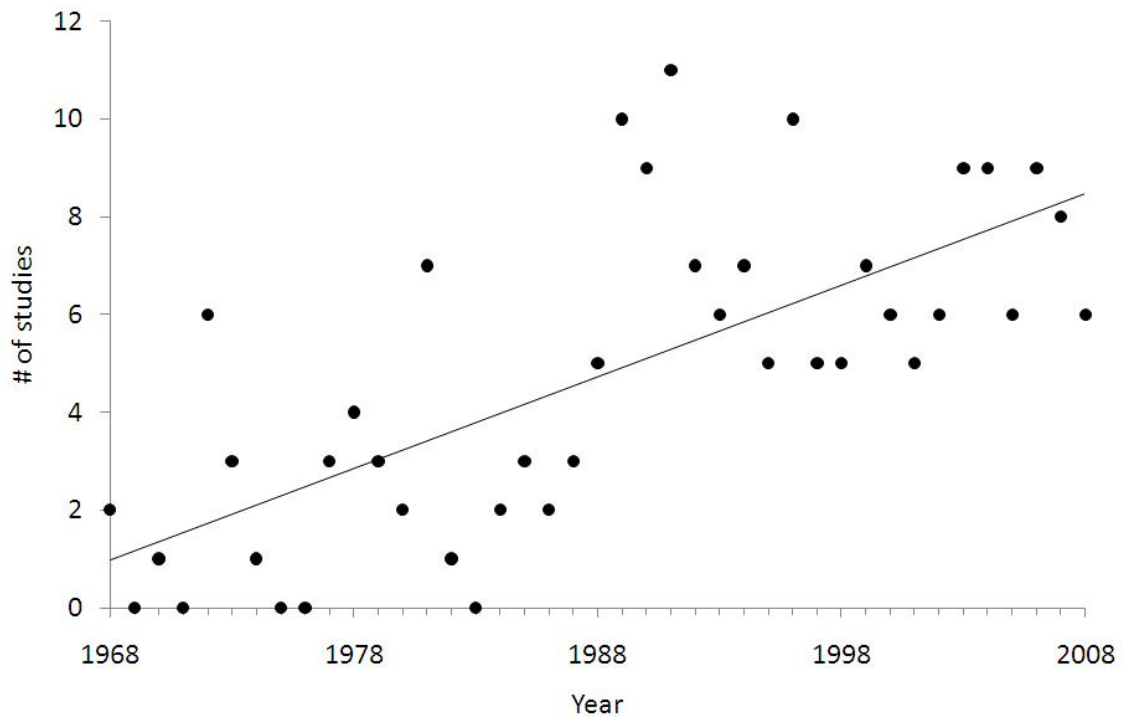| Aspect	n	Q	p
Nest Success	16	0.27	0.62
Productivity	14	0.20	0.72
Clutch Size	14	0.13	0.79
Nesting Propensity	---	---	---
Nest Initiation Date	9	0.16	0.76
Offspring Quality	8	0.35	0.57
Body Condition	35	2.78	0.13
Flying Ability	---	---	---
Foraging Behaviors	36	10.69	0.002
Device-induced Behaviors	18	0.03	0.89
Energetic Expenditure	13	0.42	0.56
Survival	38	0.08	0.80

Figure 3.1. Number of reviewed studies using transmitters or dataloggers per year.

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