Commentary

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PARENTAL NEST DEFENSE ON VIDEOTAPE: MORE REALITY THAN "MYTH"

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Predation is recognized as the primary source of nest mortality in most passerine species (e.g. Ricklefs 1969, Martin 1992a); thus, it is no surprise that parental nest defense has received considerable scientific attention (see below). By nest defense, we refer to any parental behavior that decreases the probability that a predator (or brood parasite) will harm the nest contents and that simultaneously entails some cost to the bird engaged in the behavior—either by increasing the bird's risk of injury or death (Montgomerie and Weatherhead 1988) or by at least increasing its expenditure of time and energy (Buitron 1983).

Bradley and Marzluff (2003) used an innovative combination of approaches to investigate potential nest predation by three species of rodents; in the discussion section of that paper, they made the general assertion that "nest defense by parent birds seems to be more myth than reality." That statement is at odds with a vast scientific literature on the topic that spans several decades (e.g. Skutch 1955, reviews by Montgomerie and Weatherhead 1988, Martin 1992b, Sealy et al. 1998). A simplistic search for the phrase "nest defense" in one online database (Wildlife and Ecology Studies Worldwide) produced a list of >90 papers published on nest defense by birds for 1994–2004 alone. Fifty of those papers deal with nest defense by passerines. Although parental defense is often unsuccessful, especially in passerines, one cannot dismiss its existence or its potential value as a predator deterrent (e.g. Montgomerie and Weatherhead 1988, Martin 1992b).

Given the wealth of observational and experimental evidence of nest defense, one may wonder whether further discussion of Bradley and Marzluff's statement is even warranted. However, the authors supported their dismissal of nest defense with data from a relatively new research tool—miniature video cameras used to continuously monitor active nests. In the last several years, such cameras have provided unprecedented information on nest predators of passerines (e.g. Thompson et al. 1999, Pietz and Granfors 2000a, Granfors et al. 2001, Williams and Wood 2002, Liebezeit and George 2003, Renfrew and Ribic 2003, Stake and Cimprich 2003, Thompson and Burhans 2003, Schaefer 2004). We therefore thought it appropriate to discuss the suitability of this tool for studies of nest defense, and to present some additional data related to nest defense that we acquired with video cameras.

Form and frequency of nest defense.—Bradley and Marzluff (2003) noted that "during 61 video-monitored predation events of passerine nests, F. R. Thompson III (pers. comm.) has rarely observed nest defense, and never successful defense, against bird, mammal, or snake predators at night or day." The authors cited one of our papers (Pietz and Granfors 2000a) to support their contention that "adult passerines will immediately flush without defending their nest when disturbed by predators during nighttime."

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In fact, although we did not explicitly say that in our paper, we have noticed that adult birds usually flush off the nest (during both day and night) shortly before a predator comes into view on videotape. However, in a number of cases, the adult birds fly back into the field of view, apparently trying to drive off the predator. We detected such nest defense (Table 1) on videotapes of 24 of 85 predation events documented during grassland studies in North Dakota and Minnesota (data collected with several collaborators in 1996–2001 and 2003). We documented defense by five species of grassland-nesting passerines against eight species of mammalian, avian, and reptilian predators. Defense occurred during both daytime and nighttime and was directed at mice, thirteen-lined ground squirrels, a Franklin's ground squirrel, a raccoon, a long-tailed weasel, Brown-headed Cowbirds, and plains garter snakes (scientific names in Table 1).

The instances of parental nest defense that we have detected on videotape can be qualitatively informative, but they do not necessarily provide a basis for estimating the frequency of parental nest defense. Several factors make it difficult to accurately quantify the proportion of cases in which nest defense occurred at our video-monitored nests. In our grassland habitats, we placed cameras so close to nests (10–30 cm to prevent vegetation from obscuring nest contents) that the field of view was usually restricted to the nest and a small area immediately around it. Only a small part of larger predators, like badgers (*Taxidea taxus*) and white-tailed deer (*Odocoileus virginianus*), were within the cameras' fields of view (Pietz and Granfors 2000a, b). Thus, we do not know whether the rarity of documented attacks on larger predators (only one case of defense during 24 nest predations by hawks, skunks, badgers, raccoon, canids, and deer) indicates an unwillingness to defend against animals of that size or the high probability that those attacks would be beyond camera view. Nest defense against smaller predators also may occur out of view, but >43% of 46 nest predations by smaller predators (mice or voles, ground squirrels, weasels, snakes, cowbirds) elicited nest defense that was captured on videotape.

By using wide-angle lenses or setting cameras farther from nests, researchers can obtain video images with larger fields of view (e.g. Brown et al. 1998, Thompson and Burhans 2003, Schaefer 2004). However, those images generally show less detail and thus make it more difficult to identify small predators. At night, the benefit of an increased field of view also depends on the proportion of the view that is illuminated by an infrared light source.

Even with a relatively large field of view, most camera systems used for monitoring nests are unlikely to document parental activities that prevent a predator from discovering the nest. Distraction displays, injury-feigning, alarm-calling, and mobbing generally occur away from the nest and can redirect a predator (e.g. Buitron 1983, Montgomerie and Weatherhead 1988) long before it is close enough to the nest to be detected on camera.

Aside from those difficulties in documenting nest defense, there is a more pedestrian reason we hesitate to assess rates of nest defense from our videotapes. To date, we have reviewed only a small fraction of ~1,800 tapes obtained at >160 passerine nests. By recording continuously at a tape speed of four images per second, we obtained one tape every 24 h from the time a camera was deployed at a nest until the nest either failed or fledged young. To meet our initial research objectives, we reviewed in detail any tape with evidence of egg or nestling losses. It is possible that tapes we have not reviewed completely contain cases of successful nest defense during which no losses occurred. Because detailed tape reviews are very time-consuming, many predation studies may lack the resources to check all tapes for nonpredation events.

Despite those caveats, it is probably reasonable to use camera data to estimate a minimum frequency of parental defense at our grassland nests. During our studies, parental defense was detected at 26% of 81 camera-monitored nests that were affected by predator visits. The apparent lack of defense noted in another study (i.e. F. R. Thompson III pers. comm. *in* Bradley and Marzluff 2003) may reflect behavioral differences associated with other nesting species in different habitats responding to different predators. It is also possible that methodological differences (e.g. in camera systems, tape reviews) produced the disparity in our assessments of nest defense. In either case, the frequency of parental defense noted in our grassland studies should not be extrapolated to other nesting

TABLE 1. Parental defense documented at camera-monitored passerine nests in North Dakota and Minnesota.

Defense by [a]	Defense against	Nest stage	Age [b]	Date	Time [c]	Nest fate [d]
Bobolink [1] (*Dolichonyx oryzivorus*)	Brown-headed Cowbird (*Molothrus ater*)	Incubation	5	9 June 1999	1318	
Bobolink [1]	Brown-headed Cowbird	Nestling	1	15 June 1999	1203	Fledged
Bobolink [2]	Mouse	Nestling	4	4–5 July 1997	2356, 0130, 0455	
Bobolink [2]	Franklin's ground squirrel (*Spermophilus franklinii*)	Nestling	5	5 July 1997	1738	Force fledged [e]
Chestnut-collared Longspur (*Calcarius ornatus*)	Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)	Nestling	4	14–15 June 1997	1155, 0919	Depredated
Clay-colored Sparrow (*Spizella pallida*)	Jumping mouse (*Zapus* sp.)	Incubation	6	27 July 1996	0022, 0216	Depredated
Clay-colored Sparrow [3]	Mouse (probably *Zapus* sp.)	Incubation	6	13 June 1999	2148	
Clay-colored Sparrow	Vole or mouse	Incubation	6	26–27 June 1999	2001, 0130	Depredated
Clay-colored Sparrow	Brown-headed Cowbird	Incubation	≥6	7 June 2000	0509	Abandoned
Clay-colored Sparrow	Jumping mouse	Incubation	7	7 July 1996	1914	Depredated
Clay-colored Sparrow	Raccoon (*Procyon lotor*)	Incubation	7	30 June 1999	2026	Depredated
Clay-colored Sparrow	Franklin's ground squirrel	Nestling	1	27 July 1997	1419	Depredated
Clay-colored Sparrow	Long-tailed weasel (*Mustela frenata*)	Nestling	2	19 July 2003	2234	Fledged
Clay-colored Sparrow	Thirteen-lined ground squirrel	Nestling	3	7 June 1999	1646, 1709	Depredated [f]
Clay-colored Sparrow	Perpetrator not in view	Nestling	5	20 July 1999	0532	Fledged
Clay-colored Sparrow	Perpetrator not in view	Nestling	7	26 July 1997	1005	Fledged
Clay-colored Sparrow	Plains garter snake (*Thamnophis radix*)	Nestling	8	8 August 1998	1332	Force fledged [e]
Clay-colored Sparrow [3]	Perpetrator not in view	Nestling	8	25 June 1999	0344	Fledged
Savannah Sparrow (*Passerculus sandwichensis*)	Thirteen-lined ground squirrel	Hatching	0	26 July 1998	1503	Depredated
Savannah Sparrow	Thirteen-lined ground squirrel	Nestling	2	10 July 1999	1144, 1306, 1342	Depredated
Savannah Sparrow	Plains garter snake	Nestling	2	14 July 2001	2013	Depredated [f]
Savannah Sparrow	Thirteen-lined ground squirrel	Nestling	4	14 June 1997	1155	Depredated
Savannah Sparrow	Vole or mouse	Nestling	4	9 June 1999	0012	Depredated
Vesper Sparrow (*Pooecetes gramineus*)	Deer mouse (*Peromyscus maniculatus*)	Nestling	7	6 June 1998	0158, 0211, 0401	Depredated

[a] Rows with the same numerical superscript in the first column refer to the same nest.
[b] Number of days since onset of incubation (for eggs) or since hatch (for nestlings).
[c] Central Daylight Savings time.
[d] Nest fate is classified as "fledged" only if ≥1 nestling left the nest alive.
[e] At least one nestling left nest during or immediately after predator visit to nest.
[f] Nest defense was recorded after all nestlings had been removed by predator.

species, predator communities, or habitat types. On the other hand, for grassland-nesting passerines of the north-central United States, our data suggest that parental nest defense is relatively common.

Rewards and risks of nest defense.—Some instances of nest defense that we documented were at least partially successful (i.e. some nest contents survived the attack). Among the 21 nests at which we videotaped nest defense, at least 5 successfully fledged young (Table 1). In one of those cases, described in Granfors et al. (2001), a female Bobolink vigorously chased and pecked a female Brown-headed Cowbird that was removing young from the Bobolink's nest. The Brown-headed Cowbird managed to remove three of four nestlings, but one nestling survived to fledge (Table 1, row 2). In another case, a Clay-colored Sparrow apparently thwarted predation by a long-tailed weasel once at the egg stage and again at the nestling stage. Although nest defense was not documented at the egg stage, the weasel's abrupt retreat from the nest, without removing any of the three Clay-colored Sparrow eggs, suggested that parental defense may have occurred outside the camera's field of view. Five days later, parental defense was documented at that nest (Table 1, row 13) as a weasel removed one 2-day-old nestling and injured another (which subsequently died). There were no further attacks on the nest, however, and the third nestling survived and fledged. That case of defense was especially remarkable, given the ability of weasels to kill adult birds (e.g. Keith 1961). It may be difficult to measure the relative value of rewards and risks involved in parental nest defense; however, it is clear that nest defense sometimes pays off.

The risks of nest defense were also documented on videotape, in that some nest predators killed parents as well as their young. In one case, an adult Savannah Sparrow was killed by a short-tailed or least weasel (*Mustela erminea* or *M. nivalis*). More surprisingly, after unsuccessfully defending her nestlings from ground squirrel attacks over a 2-day period (Table 1, row 5), a female Chestnut-collared Longspur was caught, killed, and removed from her nest by a thirteen-lined ground squirrel (fig. 2B in Pietz and Granfors 2000a). It was not clear whether those birds were killed because they attempted to stand their ground or were simply caught off guard. However, the potential danger to a bird that attempts to defend its nest is evident. Given that such relatively small predators are a threat to adult passerines, it is not surprising that parent birds frequently flush from the nest at the first indication of something approaching. In many cases, they probably do not know what is approaching the nest, and are less vulnerable assessing the situation on the wing or from a perch. Most of the parental defense we detected on videotape consisted of attacks launched several seconds after the adult had flushed from the nest.

Conclusions.—Most video nest-monitors are poorly suited to quantify the full range of behaviors that parent birds use to defend their nests. Nevertheless, those cameras can provide glimpses of behaviors that we are rarely able to observe directly, and may provide minimum estimates of the frequency of nest defense. Our videotaped data on grassland passerines suggest that nest defense can be quite common. Comparing data among video studies might help elucidate the factors that contribute to variability in the occurrence and detection of parental nest defense.

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