WHY DOES INTENSITY OF AVIAN NEST DEFENSE INCREASE DURING THE NESTING CYCLE?

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ABSTRACT.—Theoretical models predict that intensity of avian nest defense should increase with age of the offspring. Empirical observations conforming with this prediction have been taken as support for these models. We here present a new explanation for the observed correlations between offspring age and level of nest defense. We propose that increased intensity of nest-defense behavior is largely a result of the methods used by the researchers who made the observations. We suggest that when an observer repeatedly visits or brings a potential nest predator to a nest, nest-defense behavior of parents is modified by positive reinforcement and loss of fear. We tested this hypothesis by measuring nest-defense behavior of female American Robins (*Turdus migratorius*) and male and female Red-winged Blackbirds (*Agelaius phoeniceus*). The tests were performed at nests visited only once during different stages of the nesting cycle and at a group of nests visited repeatedly from initiation of incubation to fledging. Nest-defense intensity (as measured by call rates, closest approach to the predator, and numbers of dives and strikes) of robins and blackbirds at nests visited once, in most cases, did not increase through the nesting cycle. At nests visited repeatedly through the nesting cycle, intensity of nest defense by both robins and blackbirds, in many cases, increased significantly. In addition to intensity of nest defense increasing at multiple-visit nests, we observed higher proportions of birds at these nests performing nest-defense behaviors than at single-visit nests. *Received 19 March 1985, accepted 20 October 1985.*

MOST studies of nest defense in altricial birds have revealed increases in the intensity of nest defense by parent birds through the nesting cycle (Smith 1950; Erpino 1968; Barash 1975; Curio 1975; D'Arms 1978; Weatherhead 1979, 1982; Andersson et al. 1980; Greig-Smith 1980; Patterson et al. 1980; Biermann and Robertson 1981; East 1981; Blancher and Robertson 1982; Röell and Bossema 1982; Merritt 1984; Shields 1984). Two explanations have been offered for the temporal changes in the intensity of nest defense. The first, and currently most popular, explanation is derived from the theory of parental investment (Trivers 1972). Barash (1975) extended the theory to include parental defense of eggs and young. Whether based on cumulative past parental investment (Trivers 1972, Barash 1975) or future expected benefits minus expected costs (Dawkins and Carlisle 1976, Boucher 1977, Maynard Smith 1977), this hypothesis predicts an increase in nest defense as the young near fledging. In a similar fashion, Andersson et al. (1980) hypothesized that the relative difference between the expected survival of parents and their young decreases as the nestlings grow older, making parents willing to defend older nestlings more aggressively.

The second explanation is based on the hypothesis that older nestlings are more conspicuous to predators. The nest and its contents become more conspicuous as the nesting cycle progresses, necessitating an increase in the intensity of nest defense to counteract the nest's increased conspicuousness to predators (Skutch 1949, Harvey and Greenwood 1978).

We offer a third, alternative explanation for increases in nest defense through the nesting cycle. We propose that the increases are largely the results of the methods used by the researchers who made the observations. We suggest that when an observer repeatedly visits or brings a potential predator to a nest and records the parent birds' responses, the nest-defense behavior is gradually modified by positive reinforcement and loss of fear. Positive reinforcement is involved because the parent birds have been rewarded repeatedly for their nest-defense behavior. After being attacked, the observer or other potential nest predator leaves without harming the nest. A loss of fear is involved because the defending birds gradually

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learn that the observer or other potential nest predator is not dangerous to them; however, they still view the object as a threat to the nest's contents. Both positive reinforcement and loss of fear could explain much of the reported increases in nest-defense behavior.

We examined these explanations by measuring nest-defense behavior in experiments with American Robins (*Turdus migratorius*) and Red-winged Blackbirds (*Agelaius phoeniceus*).

STUDY AREA AND METHODS

Nests of blackbirds and robins were located within the city of Madison, Wisconsin. Some nests were visited every 3 days, whereas others were visited only once. Blackbird nests visited once were located in Nielsen, University Bay, Redwing, and Odana marshes; nests visited repeatedly were located in Kettle Marsh. These areas are open water, cattail (*Typha* spp.) marshes (Bedford et al. 1975). At no time during the study period were humans seen in any of these marshes. All robin nests were located on the University of Wisconsin campus and adjacent neighborhoods.

Nests at which nest defense was measured once during the incubation period were located during the nest-building or egg-laying stages, thereby ensuring that we knew the date of initiation of incubation. Visits to nests during these periods consisted of walking past the nest without pausing. Nests at which nest defense was measured once during the nestling period were nests we found with nestlings. Measurements of tarsus and wing chord immediately after nest-defense trials allowed us to age nestlings on the basis of comparisons with growth curves (S. K. Knight pers. comm.). Because Red-winged Blackbirds are polygynous, only one nest was used in each male's territory, thereby ensuring that the response of a male blackbird was not measured twice.

Blackbird nests where nest defense was measured once were selected randomly from a larger set of known nests. Blackbird nests visited repeatedly were in a different marsh (Kettle Marsh) and were chosen randomly from nests within each male's territory. Robin nests were assigned randomly as single-visit or multiple-visit nests. One-visit nests were at least 100 m from multiple-visit nests. For multiple-visit nests, we began with a larger number of nests, but in our analyses we used only data collected from blackbird ($n = 7$) and robin ($n = 8$) nests that successfully fledged at least one young.

The combined incubation and nestling periods for both robins and blackbirds are between 22 and 24 days (Stokes 1979). We therefore divided the nesting cycle into 6 four-day intervals, beginning with the initiation of incubation. Initiation of incubation for blackbirds and robins was assumed to have begun the day before the last egg was laid. For single-visit nests, 7 blackbird and 8 robin nests were chosen for each of the 6 time intervals. Multiple-visit nests were visited every 3 days, beginning with the initiation of incubation and continuing until fledging.

Nest defense in blackbirds was quantified by measuring the responses of the male and female parents either to an observer (always the same individual) standing by the nest or to a mounted raccoon (*Procyon lotor*) on top of an adjustable aluminum pole, in both cases within 0.5 m of the nest. Responses of individual blackbirds to the human and the raccoon (balanced for order of presentation) were measured on the same day, 1 h apart. A cloth attached to a string covered the raccoon and was removed after the observer had retreated at least outside of the male's territory and the blackbirds had resumed "normal" behavior. The raccoon mount was placed so that the head was level with and facing the nest. During a 3-min period, the types of calls, the total number of calls, dives, and strikes, and the nearest distance the birds approached the potential predator were recorded by two observers (one observer watched the male and the other watched the female). When the potential nest predator was a human, that individual recorded the female's behavior while the distant observer recorded the male's. Closest distances were estimated to the nearest 0.5 m. Dives were any break in horizontal flight that was directed at the predator. Call types recorded were those described by Orians and Christman (1968).

Nest defense in robins was measured by recording the responses of females to a human at the nest. Females were sexed by their lighter head and breast, particularly when compared with mates, and by the fact that only females incubate (Stokes 1979). Call types (Stokes 1979) and number, dives, strikes, and the closest approach to the potential predator at the nest were recorded during a 3-min period. We did not measure nest-defense behavior of male robins or responses of female robins to a mounted raccoon.

Linear regression analysis (Ryan et al. 1976) was used to assess the degree to which either the stage of the nesting cycle or the number of previous visits could be used to predict nest-defense response. We used analysis of variance to test the null hypothesis that regression coefficients did not differ significantly from zero; all tests were one-tailed. Results were considered statistically significant at $P < 0.05$.

For multiple-visit nests the assumption of independence would be violated if we used the responses from all visits to each nest when performing linear regression analysis. Accordingly, for each response variable for each of the 8 nest visits, we randomly selected (with replacement) one nest to provide the datum for the regression analysis. Five independent regression analyses were performed for each response variable. Residuals from the regression anal-

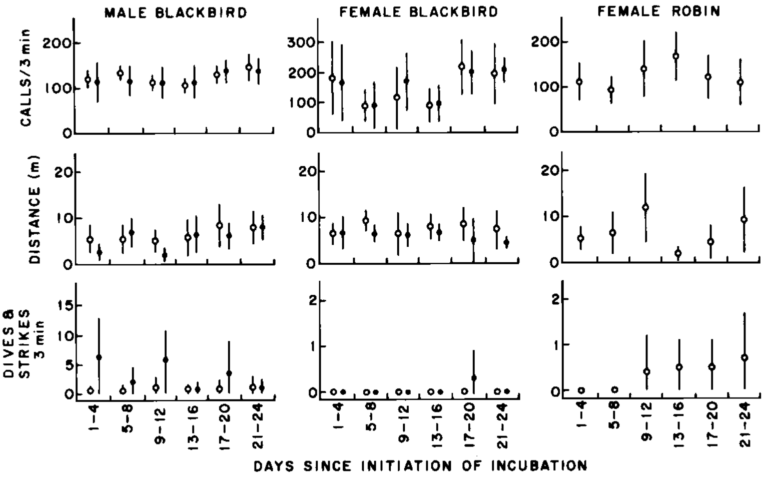

Fig. 1. Mean ± 2 SE of nest-defense responses by blackbirds and robins to a human (open circles) and raccoon (closed circles) at nests visited only once. $n = 7$ nests for blackbirds and $n = 8$ nests for robins.

yses were plotted against the independent variables and the predicted y-values to determine whether data transformations were necessary. The variables were log or square-root transformed when necessary to meet the assumption of linearity. Because existing theory on increases in nest-defense intensity do not necessarily predict a linear increase over time, we also performed ANOVA tests on the data from single-visit nests to see whether there were stepwise increases.

We calculated correlation coefficients between the various nest-defense responses at all nests. Because dives and strikes (when there were strikes) were highly correlated ($P < 0.001$), we used the sum of the dives and strikes in our analyses.

Results

The first hypothesis we examined was that nest-defense intensity was related to the stage of the nesting cycle. To test this hypothesis we analyzed results from only single-visit nests so that stage of the nesting cycle was not confounded with the number of previous visits.

The evidence from single-visit nests only weakly supported this hypothesis and more strongly supported the null hypothesis that intensity of nest defense is independent of stage of the nesting cycle (Fig. 1, Table 1). Nest-defense intensity by both male and female blackbirds did not change through the nesting cycle in the direction predicted by existing theory for 10 of the 11 responses (Table 1). Only for calls by females to the raccoon was the null hypothesis rejected. Indeed, for four variables, our results gave a trend opposite to what existing theory predicted (e.g. as the nesting cycle progressed, male blackbirds increased their distance from the predator model). Coefficients of determination were extremely low for each of the 11 regression equations (Table 1). The greatest amount of variation explained by stage of the nesting cycle was 9% for female calls to the raccoon; in 3 of the 11 regression equations stage of the nesting cycle explained none of the variation.

We found similar trends for the responses of female robins at single-visit nests. For none of the three responses was the null hypothesis that nest-defense intensity was independent of the stage of the nesting cycle rejected (Table 1). As in blackbirds, the coefficients of determination were low. Stage of the nesting cycle explained none of the observed variation in calls or nearest approach and only 1% of the variation in dives and strikes (Table 1).

Results from the ANOVA tests were no different from those of the regression analyses, except that female calls to the raccoon no longer showed a significant increase over time (ANOVA, $P > 0.25$).

The second hypothesis examined was that changes in nest-defense intensity were dependent on the number of previous nest visits by a potential nest predator that does not harm the nest or the defending parents. Our null hypothesis was that nest-defense intensity was independent of number of previous nest visits.

For blackbirds at multiple-visit nests, regres-

TABLE 1. Contribution of stage of the nesting cycle in explaining variance in predator-elicited responses of Red-winged Blackbirds and American Robins to potential nest predators at nests visited once.

Species and sex and response variable	Regression coefficient (B)[a]	Coefficient of determination (r^2)[b]	Results of analysis of variance[c]	
			F	*P*
Red-winged Blackbird males				
Calls/3 min to human	2.71	0.00	1.14	>0.25
Calls/3 min to raccoon	0.05	0.02	1.90	>0.10
Closest approach (m) to human	0.60	0.03	2.07	>0.10
Closest approach (m) to raccoon	0.48	0.08	4.37	<0.05
Dives and strikes/3 min to human	0.03	0.00	0.03	>0.25
Dives and strikes/3 min to raccoon	−0.78	0.03	2.10	>0.10
Red-winged Blackbird females				
Calls/3 min to human	18.00	0.03	2.19	>0.10
Calls/3 min to raccoon	0.24	0.09	4.44	<0.05
Closest approach (m) to human	0.09	0.00	0.08	>0.25
Closest approach (m) to raccoon	−0.09	0.01	1.51	>0.10
Dives and strikes/3 min to human[d]				—
Dives and strikes/3 min to raccoon	0.08	0.00	0.77	>0.25
American Robin females				
Calls/3 min to human	4.25	0.00	0.64	>0.25
Closest approach (m) to human	−0.05	0.00	0.10	>0.25
Dives and strikes/3 min to human	0.09	0.01	1.44	>0.10

[a] In all cases $n = 42$ for Red-winged Blackbirds and $n = 48$ for American Robins.
[b] Adjusted for degrees of freedom.
[c] Analysis of variance tested whether the regression coefficients were significantly different from zero.
[d] No dives or strikes.

sion coefficients for each of the 12 responses differed significantly from 0 in at least 1 of the 5 regression analyses performed on each response variable. For 7 of the response variables all regression analyses were significant (Table 2, Fig. 2). For all 12 variables, the results were uniformly in the direction predicted by our alternative hypothesis. These results indicate that blackbirds called more often, dove and struck more often, and approached potential nest predators closer as the number of previous nest visits increased. Coefficients of determination were consistently much higher for number of previous visits than for stage of the nesting cycle (Tables 1 and 2).

Nest-defense intensity by robins at multiple-visit nests also increased in response to the number of previous visits. As with blackbirds, the number of calls, dives, and strikes increased with repeated visits, while closest distance approached by robins decreased (Table 2). For all response variables, coefficients of determination were much higher for number of previous visits than for stage of nesting cycle (Tables 1 and 2). For example, stage of the nesting cycle explained none of the variation in closest distance robins approached the human intruder, whereas number of previous nest visits explained as much as 44% of the variation.

Although all blackbirds and robins called while defending their nests, there were marked differences in the proportion of birds that dove at or hit the potential predator at single- and multiple-visit nests. For nests with nestlings 9–12 days old, very few parents at single-visit nests either dove at or hit the potential predator, whereas at multiple-visit nests over half of the parents did (Table 3). Additionally, there were many more dives and strikes by parents at multiple-visit nests than by parents at single-visit nests. For example, when young were between 9 and 12 days old, there were 1,244 dives and strikes by parents at multiple-visit nests but only 21 dives and no strikes by parents at single-visit nests.

Differences in predator-elicited responses by birds at nests visited once and nests visited repeatedly could be due to multiple-visit nests having parents that were inherently more aggressive than parents at nests visited only once. Blackbirds in Kettle Marsh, where nests were visited repeatedly, may be more aggressive toward humans and raccoons than blackbirds in the marshes where we measured nest defense

TABLE 2. Contribution of stage of the nesting cycle in explaining variance in predator-elicited responses of Red-winged Blackbirds and American Robins to potential nest predators at nests visited every 3 days.

Species and sex and response variable	Regression coefficient (B)[a]	Coefficient of determination (r^2)[b]	Results of analysis of variance[c]	
			F	P
Red-winged Blackbird males				
Calls/3 min to human	0.11-0.20	0.26-0.74	3.46-20.52	$0.0025 < P < 0.25$
Calls/3 min to raccoon	0.11-0.20	0.46-0.64	7.00-13.32	$0.01 < P < 0.05$
Closest approach (m) to human	−2.98 to −1.49	0.48-0.53	7.40-8.88	$0.01 < P < 0.05$
Closest approach (m) to raccoon	−0.74 to −0.53	0.26-0.43	3.50-6.35	$0.025 < P < 0.25$
Dives and strikes/3 min to human	0.32-2.34	0.70-0.78	16.97-25.50	$0.001 < P < 0.01$
Dives and strikes/3 min to raccoon	6.91-16.40	0.16-0.55	2.31-7.02	$0.025 < P < 0.25$
Red-winged Blackbird females				
Calls/3 min to human	0.25-38.52	0.49-0.58	7.73-10.50	$0.01 < P < 0.05$
Calls/3 min to raccoon	0.17-32.85	0.40-0.51	5.71-8.29	$0.025 < P < 0.10$
Closest approach (m) to human	−0.28 to −0.25	0.49-0.53	7.73-8.88	$0.01 < P < 0.05$
Closest approach (m) to raccoon	−0.38 to −0.28	0.20-0.41	2.80-5.86	$0.05 < P < 0.25$
Dives and strikes/3 min to human	1.61-1.94	0.65-0.68	14.21-15.52	$0.005 < P < 0.01$
Dives and strikes/3 min to raccoon	2.37-14.67	0.52-0.74	8.47-20.70	$0.0025 < P < 0.05$
American Robin females				
Calls/3 min to human	0.24-4.32	0.34-0.71	4.58-17.72	$0.0025 < P < 0.10$
Closest approach (m) to human	−1.97 to −1.61	0.39-0.44	5.57-6.50	$0.025 < P < 0.10$
Dives and strikes/3 min to human	1.71-1.75	0.39-0.75	5.57-22.09	$0.001 < P < 0.10$

[a] For each response variable on each of the 8 nest visits, we randomly selected (with replacement) one nest to provide data for the regression analyses. Range of values presented from 5 independent regression analyses performed for each response variable.

[b] Adjusted for degrees of freedom.

[c] Analysis of variance tested whether the regression coefficients were significantly different from zero.

only once. This could be due to proximity and natural exposure to humans or raccoons. Such an explanation is unlikely for robin nests because they were assigned randomly to treatments. We examined this possibility for both blackbirds and robins by comparing the initial responses among nests visited once and nests visited repeatedly. There were no significant differences (Mann-Whitney *U*-test, all P values > 0.10) in any of these comparisons.

DISCUSSION

Our evidence suggests that stage of the nesting cycle has only a weak influence on nest-defense intensity. Our results strongly support the hypothesis that increased intensity in nest-defense behavior through the nesting cycle occurs when an observer repeatedly visits or places a potential nest predator at a nest and then leaves or withdraws the stimulus without harming the birds.

Even though nests were not harmed, parent birds still viewed us or the predator model as a potential threat. The continued nest defense, however, implies that parents lose fear of the predator, because the proximity and intensity of their nest-defense behavior increased. Conversely, if parents or their nests were harmed (negative reinforcement), then a decline would be expected in the intensity of particular components (e.g. dives and strikes) of nest-defense behavior, depending upon the frequency and outcome of these previous encounters (e.g. Knight 1984, Knight and Temple in press a).

We are not the first to propose that increased intensity of responses to predators might be the result of repeated presentations and withdrawals of potential predators. Verplanck (*in* Hinde 1954) suggested that the withdrawal of an owl that is being mobbed might reinforce distraction behavior. Gramza (1967) proposed that withdrawal of a human intruder might positively reinforce distraction behavior in nesting Common Nighthawks (*Chordeiles minor*). Buitron (1983: 232) declared, "Studies showing an increase in parental defense with the age of the young have generally involved the same predator, human or model, throughout the breeding season. In some cases the same pairs were repeatedly tested, often every day, and increased familiarity with a particular

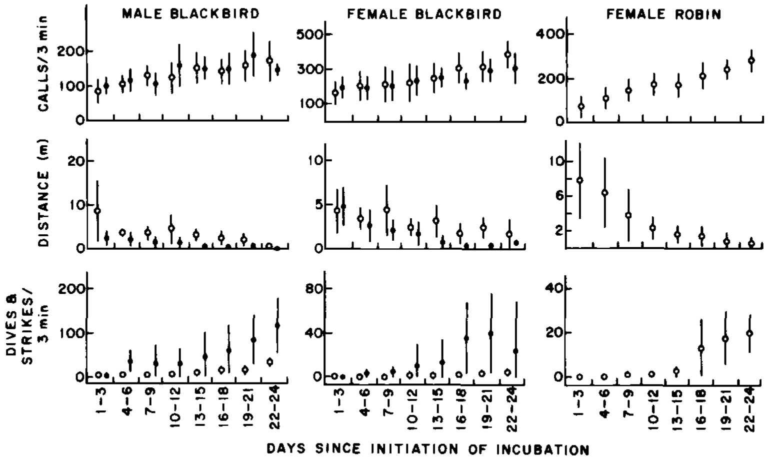

Fig. 2. Mean ± 2 SE of nest-defense responses by blackbirds and robins to a human (open circles) and raccoon (closed circles) at nests visited every three days. $n = 7$ nests for blackbirds and $n = 8$ nests for robins.

predator and situations may have affected the response. While habituation to predators would be disadvantageous, the repeated withdrawal of the human or model predator with no injury to young or adults may reinforce the vigor of the response." American Goldfinches (*Carduelis tristis*) showed significant increases in call rates from the incubation to the nestling period at nests visited every 3 days (Knight and Temple in press b). At nests visited only once during the incubation or nestling periods, however, there were no significant differences in call rates either to humans or to models of a Blue Jay (*Cyanocitta cristata*) or an American Kestrel (*Falco sparverius*).

The large amount of variation around the calculated mean values in our work indicates substantial individual variation in nest-defense behavior (Figs. 1, 2). Despite small sample sizes and the large variations in nest-defense responses, we found striking differences in adult behavior at single- vs. multiple-visit nests. We measured nest defense only during the incubation and nestling stages of the nesting cycle. We would not be surprised to find significant differences through a nesting cycle that included additional stages, such as nest building, egg-laying, and postfledging. Birds respond to the presence of a predator differently during the early part of the nesting cycle, as is evidenced by their greater tendency to desert during the nest-building and egg-laying stages (Skutch 1976). Likewise, parents might defend fledged young less intensely than eggs or nestlings because fledged young are dispersed and can defend themselves (e.g. by flying or hiding).

Intensity of nest defense has been shown to be positively correlated with nest success (e.g. Greig-Smith 1980, Blancher and Robertson 1982, Knight and Temple in press b). Various com-

TABLE 3. Comparisons of predator-elicited responses of Red-winged Blackbirds and American Robins at nests visited once and at nests visited every 3 days.

		Proportion of parents that dove or struck[a]		Total number of dives and strikes[a]	
Species and sex of parent	Potential predator	Single-visit nests	Multiple-visit nests	Single-visit nests	Multiple-visit nests
Male blackbird	Human	2/7	7/7	8	151
	Raccoon	2/7	7/7	7	586
Female blackbird	Human	0/7	3/7	0	15
	Raccoon	0/7	4/7	0	302
Female robin	Human	1/8	8/8	6	190

[a] Responses during nest visits when nestlings were 9-12 days old.

ponents of nest-defense behavior, such as calls, may function in ways that minimize a predator's ability to locate and destroy a nest (e.g. Greig-Smith 1980, Knight and Temple in press b). This suggests that nest-defense behavior is adaptive. The existing theory on nest defense assumes that the reproductive value of the nest contents increases with age, that the nest contents become more conspicuous with increasing age, that nest defense incurs a cost (i.e. is risky or energetically expensive), and that the level of nest defense performed is a measure of either parental investment or the conspicuousness of the young (Skutch 1949, Barash 1975, Harvey and Greenwood 1978, Andersson et al. 1980). Of these assumptions, the first two are axiomatic. The value and conspicuousness of nests inevitably increases with age. Because our results suggest that existing theory does not adequately explain patterns of nest-defense intensity, close scrutiny of the last two assumptions would be instructive.

Previous nest-defense studies.—Each of 12 previous studies that examined nest defense of altricial birds in response to a human intruder reported increases in nest-defense intensity through the nesting cycle (Smith 1950; Erpino 1968; Barash 1975; Searcy 1979; Weatherhead 1979, 1982; Andersson et al. 1980; Greig-Smith 1980; East 1981; Blancher and Robertson 1982; Merritt 1984; Shields 1984). In each study individual nests were visited more than once; in at least eight of the studies nests were visited at 1-3-day intervals. Additionally, because parent birds may learn to recognize individuals (e.g. the researcher) from previous visits (Buitron 1983, Merritt 1984, Knight and Temple in press a), nest defense can be even more intense to familiar individuals than to novel intruders (Knight and Temple in press a). We know of no published studies where observers visited nests repeatedly and failed to obtain an increase in nest defense.

Nest-defense studies that measured parent responses of altricial birds through the nesting cycle to either a taxidermic mount (Curio 1975, Gottfried 1979, Patterson et al. 1980, Biermann and Robertson 1981, Shields 1984) or a living animal (D'Arms 1978, Röell and Bossema 1982, Regelmann and Curio 1983, Curio et al. 1984) have obtained results far less consistent than studies using a human as the stimulus. Several of these presented potential predators to naive birds (i.e. birds that had not previously seen the particular model). Curio (1975: 29) stated that "As in many birds, response strength (calls per minute) exhibits a marked increase during the breeding cycle." Later, however, (p. 31) he stated that ". . . differences between stages (of the nesting cycle) become generally significant only if covering the data of at least three subsequent ones." Regelmann and Curio (1983) and Curio et al. (1984) found that nest-defense intensity of Great Tits (*Parus major*), as measured by time (latency of approach) and distance approached, increased with nestling age; they did not report data for the incubation period. Additionally, they reported inconsistencies in their data based on such factors as year and study area and attributed the large amount of unexplained variation in their response variables to individual variation among the parents. D'Arms (1978) found no differences between the incubation and nestling stages in male Red-winged Blackbird nest defense to avian predators. Female Red-winged Blackbirds with nestlings were more aggressive than females with eggs. Gottfried (1979) measured nest-defense response of Northern Cardinals (*Cardinalis cardinalis*), American Robins, Gray Catbirds (*Dumetella carolinensis*), and Brown Thrashers (*Toxostoma rufum*) to predator models and concluded: "My data do not clearly tell if the intensity of aggression toward nest predators changes during the nesting cycle." Patterson et al. (1980) found that White-crowned Sparrows (*Zonotrichia leucophrys*) were no more aggressive to a mounted Scrub Jay (*Aphelocoma coerulescens*) during the nestling period than during the incubation period. They did report significant increases in nest defense to models of an American Kestrel and a Dark-eyed Junco (*Junco hyemalis*) and to a live terrestrial garter snake (*Thamnophis elegans*). During May and June, Biermann and Robertson (1981) reported that female Red-winged Blackbirds responded no more aggressively to a rubber snake in their nests during the nestling than the incubation period. During July, however, blackbirds were more aggressive when they had nestlings than when they had eggs. Finally, Röell and Bossema (1982) reported a statistically nonsignificant trend for a higher proportion of naive Black-billed magpies (*Pica pica*) to attack a live avian predator at nests during the nestling stage than during incubation.

Röell and Bossema (1982) also measured the responses of magpies and Common Jackdaws

(*Corvus monedula*) to weekly presentations of the predator. None of the eight pairs of magpies showed consistent changes in responses through the nesting cycle, although jackdaws did show increased scolding. Shields (1984) measured nest defense in Barn Swallows (*Hirundo rustica*) to a predator model at nests and found that intensity of mobbing was significantly greater during the nestling stage than during the incubation stage. He placed the predator model near nests at intervals that varied from twice weekly to twice during the breeding season.

Two possible explanations exist for the contradictory findings of the studies with models or live predators other than man. First, because researchers have to place the predator at the nest and then withdraw before measuring nest defense, they have, in effect, presented themselves first as a potential predator (Kruuk 1964: 75–76). Unless the researcher is hidden from the parents' view, is a sufficient distance away from the nest, or allows the parents to habituate to the observer's presence, at least part of the nest-defense behavior measured may be attributed to the researcher's presence. Curio (1975: 26–27), for example, found that Pied Flycatchers (*Ficedula hypoleuca*) continued calling for some time after a potential predator was removed from the area. In only 2 of the 9 studies listed above was it apparent that the observer was concealed. In one study the parent birds were captured and banded before measuring nest defense. In this and four other studies it was not stated whether the observers were visible, whether the birds were allowed to return to "normal" behavior before observations began, or how far the observers were from the nest. In one study there were at least three observers present during the trials. We suggest that the inconsistent findings in these studies may be attributed to the presence of the researcher, particularly if the researcher visited the nest repeatedly through the nesting cycle.

Second, studies using models or live predators as stimuli to study nest-defense behavior have chosen species that occur naturally in nesting areas and that are suspected of being frequent nest predators. We have demonstrated that nest-defense intensity increases after "successful" defenses of the nest (i.e. the researcher withdraws or removes the predator model). Therefore, the frequency and outcome of previous encounters between parents and free-ranging predators probably would influence the response to the predator model (Pugesek 1983, Smith et al. 1984). This is particularly important because many of the species used as predators can be successfully driven off by parents (Biermann and Robertson 1981, Röell and Bossema 1982), thereby providing parents with positive reinforcement.

Our results provide a mechanism for Pugesek's (1983) observations that older California Gulls (*Larus californicus*) attack human intruders more often than middle-aged and young parents do. Older birds may defend their nests more aggressively because they have had more previous "successful" nest-defense interactions with human intruders. In studies where nest-defense intensity and nest success were correlated (e.g. Andersson et al. 1980, Greig-Smith 1980, Blancher and Robertson 1982, Knight and Temple in press b), it would be interesting to know whether the birds that nested successfully were the older birds.

We know of only one study that quantified nest-defense behavior of an altricial bird to free-ranging wild nest predators. Buitron (1983) measured Black-billed Magpie nest-defense behavior to a number of avian and mammalian predators of magpie adults, nestlings, or eggs. Magpies responded to a variety of live predators with similar intensity and frequency regardless of the stage of the nesting cycle.

It is clear that caution must be used in accepting various explanations for increases in nest-defense intensity. Many previous studies that attempted to test hypotheses explaining changes in nest-defense intensity lacked adequate controls, which made it difficult to attribute changes in nest defense to a particular cause. Future nest-defense studies should employ designs that minimize several of the potentially confounding variables we have discussed.

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