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ANTI-PREDATOR AGGRESSION IN BIRDS NESTING IN OLD FIELD HABITATS: AN EXPERIMENTAL ANALYSIS

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A variety of parental behaviors which may reduce predator-induced nest loss have evolved in birds. These include construction of elaborate, cryptic, or concealed nests, distraction displays, and nest guarding (Simmons 1955, Ricklefs 1969, Slack 1976, Scott 1977). There is evidence, although anecdotal, that some species will attack nest predators (for examples see Nolan 1959, Zimmerman 1963, Pettingill 1976). This behavior differs from other forms of anti-predator adaptations in that birds are vulnerable to injury when attacking a predator.

In this paper I report on an experiment dealing with the aggressive responses of breeding birds to nest predators in an old-field habitat. The major predators in old fields seem to be snakes, although birds (e.g. Blue Jays, *Cyanocitta cristata*) and small mammals cause some losses (Nolan 1963, Thompson and Nolan 1973, Best 1978, Gottfried and Thompson 1978).

The study attempts to answer the following questions: 1) How prone are nesting birds to attack a nest predator? 2) Are nesting birds able to recognize nest predators, or do they indiscriminately attack any animal near their nests? 3) Do nesting birds respond differently to Blue Jays than to snakes? 4) Does the stage of the nesting cycle influence the intensity of anti-predator aggression?

METHODS AND MATERIALS

The study took place from 24 April to 30 July 1977 in five old fields in and near Cedar Rapids, Iowa. Multiflora rose (*Rosa* sp.) was the dominant woody plant, and goldenrod (*Solidago* sp.) and aster (*Aster* sp.) were the dominant forbs.

The most abundant breeding birds were Field Sparrows (*Spizella pusilla*), Mourning Doves (*Zenaida macroura*), Cardinals (*Cardinalis cardinalis*), American Robins (*Turdus migratorius*), Gray Catbirds (*Dumetella carolinensis*), and Brown Thrashers (*Toxostoma rufum*). Enough data were collected only on the latter four species to warrant analysis here.

A mounted Blue Jay, in a natural pose, and a rubber snake were used. The 1.2 m blue-black snake resembled a blue racer (*Coluber constrictor*). Both models frequently elicited characteristic aggressive responses from the nesting birds and were thus deemed adequate for the experiments. A mounted female House Sparrow (*Passer domesticus*) was used as a control.

I attempted to find nests of cardinals, robins, catbirds, and thrashers before their clutches were complete. Two sets of experiments were undertaken for each active nest. Each nest was tested with the snake, sparrow, and Blue Jay models on consecutive days, three to five days after the last egg was laid and again three to five days after the last egg hatched. All tests were conducted between 16:00 and 19:00 h, and were 5 min in duration. The models were presented in random sequence. The interval between the tests was sufficient to reduce the possibility of habituation, although Thorpe (1951) suggested that habituation to predators is maladaptive.

The jay model was positioned so that it seemed to be peering into the nest cup; it was attached to the vegetation with a clip. The snake model was "draped" on the vegetation with its head directly in the nest cup.

After positioning the model, I retreated to a concealed place 5–10 m away but from which I could see the nest. The vocalizations of the parents were recorded on tape. I timed the interval between a parent bird's approaching the nest and seeing the model and the start of attack behavior, if any. Changes in vocalization and movement patterns indicated when the returning bird saw the model. To rate the relative aggressiveness toward the model, I devised an Aggression Response Index based on frequency of vocalizations, and frequency and manner of attack. The actual scale is presented in Table 1. The value of each of the three variables was summed to give the Aggression Response Index, which could range from 10 (numerous vocalizations, frequent attacks on model, frenzied movement) to 0 (no response to model).

RESULTS

The proportion of nest failure due to predation during the study was low (catbirds = 13%, n = 12; thrashers = 20%, n = 13; cardinals = 33%, n = 11; robins = 37%, n = 12; pooled mean = 26%). The most common evidence of nest predation was the disappearance of all eggs between my visits to the nest. Only twice did I find broken eggs in a nest. Snakes were common in the study areas, and in at least three instances were encountered near active nests.

ATTACK BEHAVIOR OF NESTING BIRDS

The four species differed in their attack behavior although I detected no differences between the pre- and post-hatching periods.

Robins attacked the mounted jay by flying directly at it, attacking with the bill, wings, and feet as they called. The attacks were always vigorous. Robins attacked the snake model by first perching approximately two meters away and then making a series of flights near the snake, approaching more closely on each trip. After striking the snake rapidly with their feet, the birds would fly away.

Cardinals struck the jay mount almost im-

TABLE 1. Scale used to determine the Aggression Response Index.

Number of vocalizations	Aggression	Movement patterns
0 = None	0 = No response	0 = No movement
1 = <20/min	1 = Approach predator (<5 approaches and retreats/min—no attacks)	1 = Little movement (<5 changes in position/min)
2 = 20–40/min	2 = Frequent approaches (>5 approaches and retreats/min—no attacks)	2 = Medium movement (>5 changes in location/min)
3 = >40/min	3 = Few attacks (<5 strikes on predator/min)	3 = Frenzied movement (movements too frequent to count)
	4 = Frequent attacks (>5 strikes on predator/min)	

mediately upon their return. The attacks were aimed primarily at the head and neck of the jay.

Thrashers attacked the jay by perching about one meter away and flying at the model, attacking with both bill and feet. This "rushing" behavior was also used when attacking the snake model. Some individuals, however, positioned themselves within a half meter of the snake and delivered a series of hammering blows with the bill. While attacking the snake, most thrashers raised and extended their wings, possibly to enlarge their apparent size or maintain their balance.

Catbirds attacked the jay in the same way as thrashers. They attacked snakes in two ways. In one, catbirds hopped to within a meter of the snake, then pounced on it with feet and bill. A second form of attack started similarly; however, instead of flying at the snake, the bird extended its body, pecked the snake a few times, and then retreated. After a few seconds, the procedure was repeated. The wings were extended during attacks on both the jay and snake models.

RESPONSE TO THE JAY MODEL BEFORE AND AFTER HATCHING

Cardinals and robins exhibited a high degree of aggression toward the model both before and after their eggs hatched (Fig. 1). However, the Aggression Response Indices of catbirds and thrashers were significantly higher after their eggs hatched than before (Mann-Whitney U-Test; thrashers, $U = 98$, $P < 0.05$; catbirds, $U = 102$, $P < 0.05$).

Birds could be assigned a relatively high Aggression Response Index even though they did not strike the predator model. Because of the potential importance of physical attack in restricting the activities of predators, I examined this variable separately (Fig. 2). Every robin and cardinal tested struck (attacked) the jay model before and after its eggs hatched. Likewise, the proportions of catbirds and thrashers attacking the model before and after their eggs hatched are not significantly different (although catbirds exhibited a 21% increase in the number that attacked the model during the post-hatching period). My data suggest that catbirds and thrashers attack more vigorously after their eggs hatch, but do not attack significantly more frequently.

The interval between seeing a predator model at the nest and starting an attack may shed some light on the motivational state of the parents (Fig. 3). Of the species tested, cardinals attacked the jay model most quickly ($\bar{x} = 9$ s). The mean interval between seeing the model and attacking ranged from 16–30 s in the other species. The time before an attack was initiated was not affected by egg hatching in any of the species tested (Student's t-test, $P < 0.05$).

RESPONSE TO THE SNAKE MODEL BEFORE AND AFTER HATCHING

Robins were the only species to have a significantly higher Aggression Response Index to the snake model after hatching than before (Mann-Whitney $U = 78$, $P < 0.05$). Catbird and thrasher indices were relatively high during both periods (Fig. 1), whereas cardinals exhibited little aggression.

The proportion of robins attacking the snake during the two periods was significantly different ($\chi^2 = 8.51$, $P < 0.05$). No robins attacked the model prior to egg-hatching, but 80% attacked after their eggs hatched (Fig. 2). Greater proportions of catbirds and thrashers also attacked the snake after their eggs hatched (catbird = 6% higher, thrasher = 15% higher), although these differences are not significant for either species. Cardinals never attacked the model, although occasionally they came within a meter of it.

I found no significant differences be-

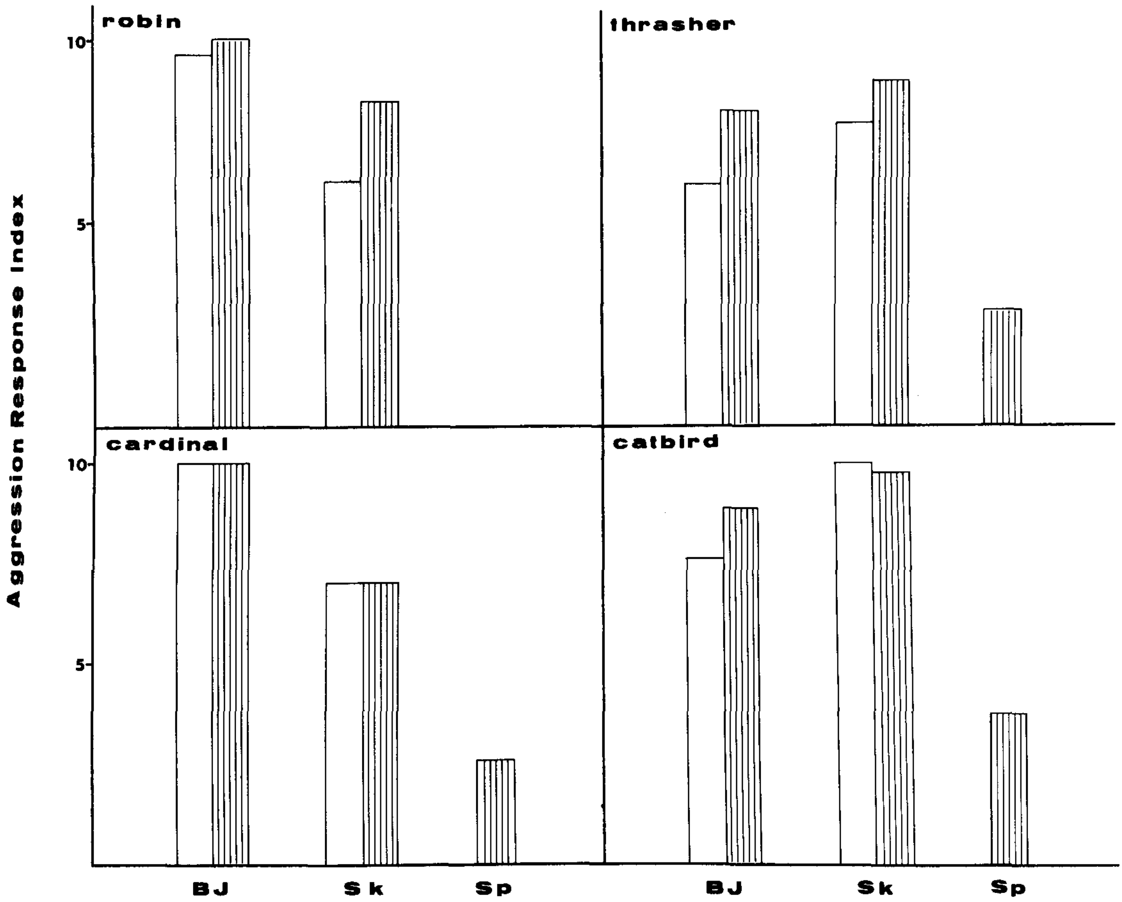

FIGURE 1. Aggression Response Indices of four species in response to Blue Jay (BJ), snake (Sk), and sparrow (Sp) models. Clear histograms represent pre-hatching period experiments, striped histograms represent post-hatching experiments.

tween the pre- and post-hatching periods in the interval between the birds' returning to the nest and attacking the snake model (Fig. 3).

PREDATOR COMPARISONS

Before their eggs hatched, robins and cardinals showed significantly higher Aggression Response Indices toward the jay than they did toward the snake (robins, $U = 80$, $P < 0.05$; cardinals, $U = 100$, $P < 0.05$). Most cardinals and robins attacked the jay but none attacked the snake.

During the post-hatching period robins attacked both predators, while cardinals continued to attack only the jay. Nevertheless, robins had a significantly lower Aggression Response Index toward the snake than toward the jay ($U = 60$, $P < 0.05$), due to the cautious manner in which the snake was attacked.

Robins attacked the jay significantly sooner than the snake on returning to their nests ($t = 4.0$, $P < 0.05$). The mean interval between recognition and attack with the jay was 23.5 s, and 143.5 s with the snake.

In contrast, the catbirds and thrashers responded more aggressively to the snake than to the jay model during the pre-hatching period. Differences in the Aggression Response Index and proportion of birds attacking the model were significant in catbirds. Both species reacted more aggressively after their eggs hatched than before. Hence, the differences in the responses to the two types of predators were smaller during this period.

RESPONSES OF BREEDING BIRDS TO CONTROL

The Aggression Response Indices of cardinals, catbirds, and thrashers in response to the sparrow model were significantly lower than those in response to both predator models (Fig. 1). A bird returning to its nest fitted with the sparrow model usually appeared agitated (frequent approaches and vocalizations). After less than 20 s the par-

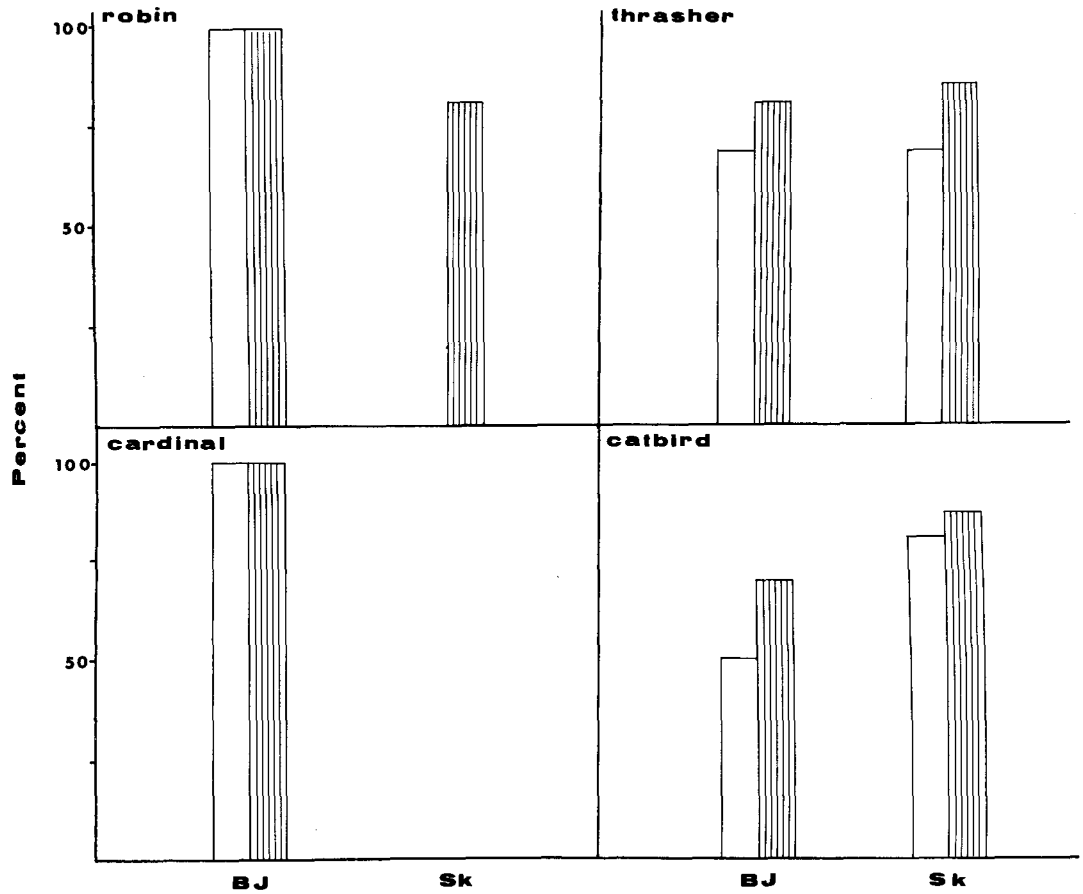

FIGURE 2. Proportion of individuals attacking the jay (BJ) and snake (Sk) models. Marked as in Figure 1.

ent usually became calm and remained 2–5 m from the nest.

The single attack on the sparrow model may have resulted from a slight deviation in my method. Inclement weather forced me to test a thrasher nest containing two nestlings with both the jay and sparrow models on the same day. The sparrow was presented 30 min after the cessation of the jay experiment. Hence, the thrasher's behavior toward the sparrow may have been influenced by the prior presence of the jay model.

THE EFFECT OF CLUTCH SIZE

The relationship between clutch size and the intensity of anti-predator behavior was tested with a Spearman Rank Correlation Test (Siegel 1956). Positive correlations were found between the size of the clutch and the intensity of aggression toward the snake model in cardinals, robins, and thrashers. I found no such correlations in the jay experiments as the parents were highly aggressive regardless of the size of the clutch (Table 2).

TABLE 2. The relationship between clutch size and the intensity of anti-predator aggression.*

					r_s**	
Species	n	$\bar{x}$ clutch size	range	SE	Blue Jay	Snake
American Robin	12	3.6	3–4	0.23	−.24	.81***
Cardinal	11	2.7	2–4	0.39	.33	.82***
Gray Catbird	12	3.3	2–4	0.25	.36	.07
Brown Thrasher	13	2.8	1–4	0.12	.13	.78***

* Pooled data from pre- and post-hatching experiments.
** Spearman Correlation Coefficient.
*** Significant at $P < 0.05$.

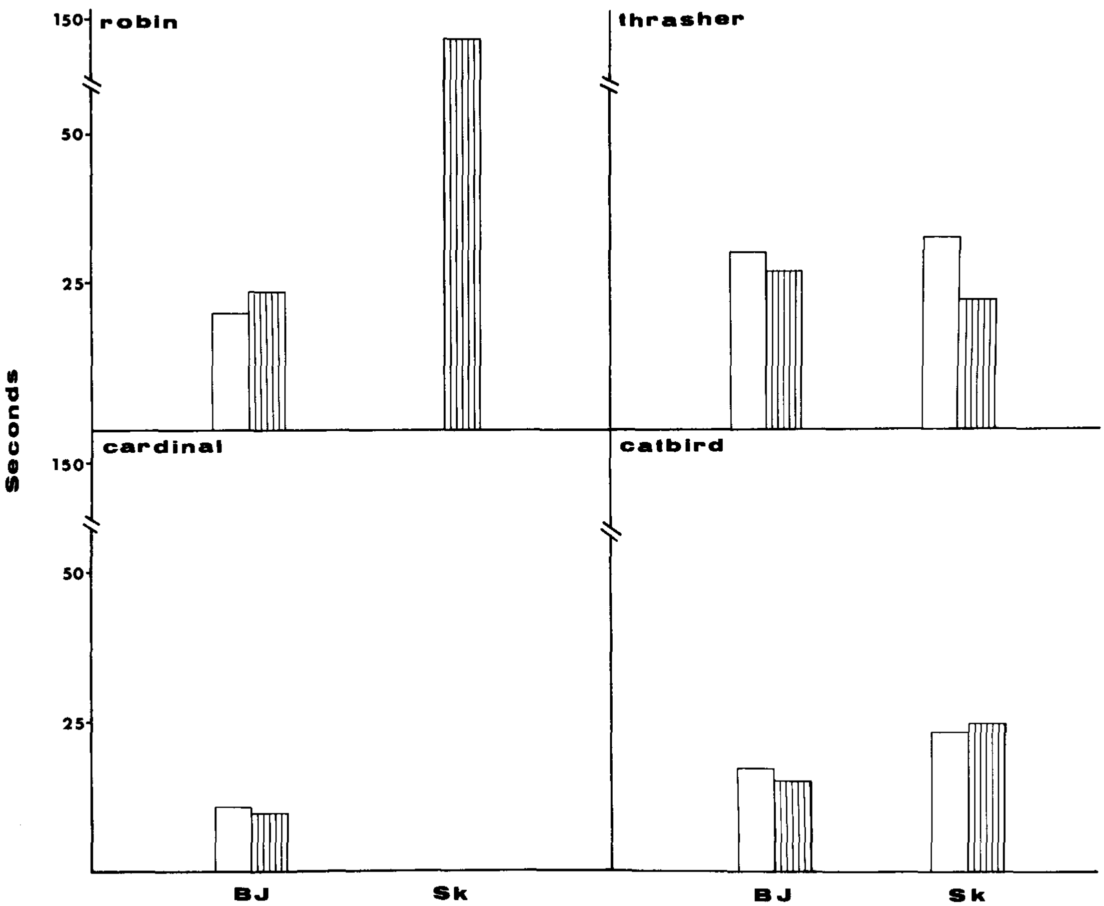

FIGURE 3. Mean time interval between returning to the nest and initiation of attack behavior. Marked as in Figure 1.

DISCUSSION

How prone are nesting birds to attack a nest predator? My data suggest that nesting birds commonly attack models of known nest predators, with a few qualifications which will be discussed later. Overall, over 70% of all individuals tested attacked the jay model, and more than 50% attacked the snake. All four species of birds differed in their reactions to the two predators.

My data do not clearly tell if the intensity of aggression toward nest predators changes during the nesting cycle. Unlike the other three species, cardinals were equally aggressive toward the jay model during the pre- and post-hatching periods. It is evident, however, that species which modified their behavior during the post-hatching period did so toward only one type of predator. Robins attacked snakes only during the post-hatching period, although their response to the jay was the same during the two periods. Both catbirds and thrashers were significantly more aggressive toward the jay model after their eggs hatched than before (only slight differences were detected in their behavior toward the snake during these periods).

TO ATTACK OR NOT

Whenever a predator appears at the nest, a parent must decide whether or not to defend the nest and, if preyed upon, whether to attempt to renest immediately. The first alternative may, at best, lead to the survival of the nest, at worst, to the death of the parent in addition to the likelihood of destruction of the nest (Ricklefs 1977). According to the current hypothesis of parental care, the alternative should be chosen on the basis of which will maximize the production of offspring at a minimum cost (see Trivers 1972, 1974, Barash 1975, Dawkins and Carlisle 1976, Maynard Smith 1977, Boucher 1977).

An older bird, near the end of its reproductive stage and hence with less capacity for renesting after nest loss, may be more likely to attack a predator than a younger bird. Another, perhaps less attractive, hypothesis is that younger birds may be more successful in repelling a nest predator and thus more likely to react that way.

In species with variable clutch sizes, as the clutch increases, the benefits of defense will exceed those of renesting. If the nest is not defended and lost, the size of the future clutch may well be smaller than the abandoned one. The intensity of attacks on the snake model was positively correlated with clutch size in three of the four species tested. However, no relationship was found in the jay experiments. The explanation may be that the relationship is mediated by the size of the potential risk involved. Snakes may be perceived as more likely than jays to inflict serious injury or death to the parent. The weighing of risks involved in attacking a predator against the benefits accrued from such an act has been suggested to influence the intensity of anti-predator behavior in birds (Kruuk 1964, Curio 1975) and mammals (Owings and Coss 1977).

I further suggest that the vigor with which a bird defends its nest may depend on the time of the breeding season. As the breeding season progresses, nest defense behavior should become accentuated, owing to the reduced possibility of successfully renesting.

Markgren (1960) and Lemmetyinen (1971, 1972) have shown that terns will attack the model of the kind of nest predator that causes the greatest losses. However, in the present study, all four species did not attack the snake model: robins and cardinals were more likely to attack the jay than the snake, while catbirds and thrashers exhibited the reverse behavior. Since catbirds and thrashers tend to nest lower than robins and cardinals (Rothstein, pers. comm.), snakes may pose a greater threat to their nests. Another possible explanation is that a jay may be less likely to attempt to prey upon a guarded nest of a catbird (see Slack 1976 and Scott 1977 on guarding) than an unguarded robin or cardinal nest. Because of the low selection pressures (i.e. few jays attempt to prey upon their nests), catbirds and thrashers may have been less likely to respond aggressively toward the jay mount.

THE INFLUENCE OF ANTI-PREDATOR AGGRESSION ON NEST SURVIVAL

Does the propensity with which members of a species attack nest predators influence the species' overall nesting success? Some evidence appears to support this idea. The magnitude of nest losses through predation from lowest to highest was catbird-thrasher-cardinal-robin. The two species with the lowest losses were also the only two that equally attacked both types of predators. Robins may experience the greatest nest losses due to the exposed nature of their nests.

The probability that a nest will be depredated may be related not only to its detection by predators (Gottfried and Thompson 1978), but also to the vigor of its defense by the parents. Perhaps because of nest guarding by some species and the high level of aggression by all species tested, avian predators successfully prey upon relatively few nests in certain old fields.

SUMMARY

I studied the likelihood of breeding birds defending their nests against models of known nest predators. In a series of experiments, nesting birds were found to respond differently to models of jays, snakes, and sparrows. Catbirds and thrashers were more aggressive toward the snake model than the mounted jay, while cardinals and robins behaved oppositely. The intensity of anti-predator aggression differed during stages of the breeding cycle. Catbirds and thrashers were more aggressive toward the jay model after hatching than before, while robins attacked the snake model only during the post-hatching period.

The intensity of anti-snake behavior was positively correlated with clutch size in three of the four species tested.

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RECENT PUBLICATIONS

Working Bibliography of the Bald Eagle.—Jeffrey Lincer, William Clark, and Maurice N. LeFranc, Jr. 1979. N.W.F. Scientific & Technical Series 2, Raptor Information Center, National Wildlife Federation, Washington, D.C. 268 p. Paper cover. $9.00 (plus $.85 handling charge per order). Available: N.W.F., 1412 16th Street, N.W., Washington, D.C. 20036. The core of this book is a list of 2,000 citations of publications about the Bald Eagle. References on a given topic can be found easily thıough a permuted list of keywords. An introductory chapter reports the status of the species and tabulates current research on it. A well-prepared and useful research tool.

Eleonora's Falcon/Adaptations to Prey and Habitat in a Social Raptor.—Hartmut Walter. 1979. University of Chicago Press. 410 p. $35.00. Eleonora's Falcon breeds in colonies of up to 200 pairs on small rocky islands in the Mediterranean. Uniquely, it breeds in autumn and feeds its chicks on southbound migrating passerines. Furthermore, the falcons often hunt in groups, each colony responding in a different manner to the migration patterns in its airspace. Walter chiefly examines the habits, ecology, and adaptations of this intriguing and hitherto little-known raptor. He also considers the effects of human activities on the species and compares this falcon with other birds of prey. Tables, diagrams, photographs, list of references, and index. This multi-faceted study is a vivid case history on the interrelations between ecology and behavior in the evolution and maintenance of a species.

Hawks and Owls of North America.—Donald S. Heintzelman. 1979. Universe Books, New York. 216 p. $18.50. Here is a book for general readers about hawks (and their allies) and owls. It describes briefly the appearance and habits of all North American species and discusses the ecology, migration, fossil history, and conservation of raptors. The author tends to emphasize his own work with species in Pennsylvania and New Jersey. His text is elementary but informative, making the book suitable for novices and school libraries. Photographs, selected bibliography, and index.