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THE NEST DEFENSE BEHAVIOR OF EASTERN SCREECH-OWLS: EFFECTS OF NEST STAGE, SEX, NEST TYPE AND PREDATOR LOCATION[1]

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Abstract. The responses of male and female Eastern Screech-Owls (*Otus asio*) to a human approaching the nest were examined. Intensity of nest defense as measured by distance of approach, number of flights and dives, and number of vocalizations was more pronounced during the nestling stage than during the incubation stage. These results generally support both the age-investment and positive-reinforcement hypotheses. In addition, male owls defended nestlings more vigorously than did females. As in many other owls, male screech-owls are smaller than females (reversed sexual dimorphism), and the increased maneuverability of the smaller males may have contributed to this difference. Other factors (e.g., the use of a relatively large predator), however, could also be involved. Males also responded with greater intensity as the human intruder moved closer to the nest, supporting the hypothesis that "well-armed" parents should respond vigorously as a predator gets close to a nest. Such a response informs the potential predator of the direction it must move to reduce the likelihood of injury.

Key words: Eastern Screech-Owl; nest defense; Otus asio; *age-investment; reversed sexual dimorphism.*

INTRODUCTION

Nest defense behavior has been defined as "... behavior that decreases the probability that a predator will harm the contents of the nest but which simultaneously increases the probability of injury or death to the parent" (Montgomerie and Weatherhead 1988). Previous studies have revealed that parent birds typically increase the intensity of such defense during the period from clutch initiation through fledging (Montgomerie and Weatherhead 1988) and, further, that males often defend nests more vigorously than females (Buitron 1983, Regelmann and Curio 1986, Breitwisch 1988, Knight and Temple 1988, Westneat 1989; but see Hobson et al. 1988, Weatherhead 1989).

Most studies of nest defense have been conducted with passerines. Several factors suggest that the nest defense behavior of raptors may differ from that of passerines. For example, raptors are relatively longer-lived than passerines (Andersen 1990) and also have the ability to attack and injure potential nest predators (Montgomerie and Weatherhead 1988). In addition, unlike passerines, the value of young raptors to predators may not increase throughout the nestling period because their ability to defend themselves increases with age (Wallin 1987). Finally, most raptors exhibit reversed sexual dimorphism (Mueller and Meyer 1985, Mueller 1986). Most owls exhibit these characteristics and, as a result, their nest defense behavior might differ from that of passerines.

Much of the information available concerning the nest defense behavior of owls is qualitative, with little or no supporting data (e.g., Mikkola 1983). To date, only two studies have quantified the nest defense behavior of owls (Wiklund and Stigh 1983, Wallin 1987). Our objectives were to examine nest defense behavior of Eastern Screech-Owls (*Otus asio*) and, where possible, to compare their behavior to that of passerines. We specifically sought to (1) examine intensity of nest defense by screech-owls throughout the nesting period, (2) compare nest defense behavior of male and female screech-owls, and (3) examine possible effects of nest type and predator location on nest defense behavior.

METHODS

Nest defense behavior was examined during the breeding seasons of 1990 and 1991 at the Central

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Kentucky Wildlife Management Area, 17 km southeast of Richmond, Madison Co., Kentucky. Screech-owls in central Kentucky begin egg-laying in mid- to late March and young typically leave the nest in mid- to late May (Belthoff 1987). Thus, experiments began in March and continued until fledging of the young.

Screech-owls were captured either by taking them from nest boxes and natural cavities or by luring them into mist nets by broadcasting bounce songs (Cavanagh and Ritchison 1987, Ritchison et al. 1988). Captured owls were fitted with a U.S. Fish and Wildlife Service aluminum band and a radio-transmitter (Wildlife Materials, Inc., Carbondale, IL).

Sex was determined by observing behavior during nesting. Females incubate eggs and brood young (Gehlbach 1986, pers. observ.), while males typically roost in nearby trees (pers. observ.). Nests were not examined prior to hatching because screech-owls disturbed during incubation often abandon the nest (VanCamp and Henny 1975). Date of hatching was determined by placing microphones in the cavities and noting the date when young were first heard. The date on which incubation began was estimated by backdating 26 days, the average duration of incubation (Sherman 1911). After hatching, each nest was inspected twice, once during the first week post-hatching to determine the number of nestlings and a second time about 21 to 28 days post-hatching to determine the number of fledglings.

Seven pairs of screech-owls (four in 1990 and three in 1991) were tested four times and one pair (1991) was tested three times. Trials were conducted at 12 to 14 day intervals during the approximately eight-week nesting cycle. For pairs tested four times, Trial 1 was conducted during the early incubation stage, Trial 2 during the late incubation stage, Trial 3 during the early nestling stage, and Trial 4 during the late nestling stage. For the pair tested three times, no trial was conducted during the early incubation stage. Two people were involved in each trial, with TMS remaining 10 m from the nest as an observer and the second person approaching the nest as a predator. During each trial, the predator (equipped with helmet and jacket) spent 8 min at a point 8 m in front of the nest tree, 4 min at the base of the nest tree, 4 min at a location about half way between the ground and the cavity (using a ladder), and a final 4 min at the 8 m location.

Trials began when both adults were within approximately 40 m of the nest (estimated using radio-telemetry). To permit observation of screech-owls in the vicinity of nests (within about 10 m), two lanterns (each equipped with a dark red lens) were mounted on poles about 5 m apart and about 5 m in front of the nest tree. Lanterns were set up prior to sunset to minimize disturbance. All trials were conducted within 1 hr of sunset and trials were not conducted during precipitation, fog, or winds over 20 km/hr.

During each trial, we noted the following. (1) Minimum approach distance, which is the closest approach by owls to the predator. (2) Number of flights. All observed flights were noted. Suspected flights, such as a possible change in location as determined by radio-telemetry, were not counted. (3) Number of dives. A dive was defined as any break in horizontal flight directed at the predator (Knight and Temple 1988). (4) Number of hits, which was the number of times an owl struck the predator. (5) Number and type of vocalizations. The vocal repertoire of Eastern Screech-Owls includes bounce songs and whinny songs (Cavanagh and Ritchison 1987, Ritchison et al. 1988, Sproat 1992), bark calls, screeches, and bill-claps (Gehlbach 1986, Voous 1988, Sproat 1992). Vocalizations were recorded by the individual acting as the predator using a Uher 4000 Report Monitor tape recorder with a Dan Gibson parabolic microphone.

In addition to the pairs of screech-owls tested several times during the nesting cycle, six pairs (four in 1990 and two in 1991) were tested only once. Four of these trials were conducted during the incubation period (two each year) and two during the nestling period (both in 1990). Although the limited number of such "non-repetitive" pairs precluded comparisons with pairs tested repetitively, data from these non-repetitive pairs were combined with those from the repetitive pairs to examine the effects of predator location on nest defense behavior.

Paired comparisons (males versus females and egg stage versus nestling stage) were made using Wilcoxon tests (SAS Institute 1989). Multiple comparisons (among predator locations) were made using repeated measures analysis of variance with a least-squares post-hoc test (SAS Institute 1989). Spearman tests (SAS Institute 1989) were used to examine the possible relationship between the intensity of nest defense and the number of eggs and nestlings. All values are presented as mean ± standard error.

TABLE 1. Comparison of the responses of male and female Eastern Screech-Owls during the nestling stage.

Behavior	Males[a]			Females[a]			Wilcoxon	
	n[b]	Mean	SE[c]	n[b]	Mean	SE[c]	z	P
Minimum approach distance (m)	11	3.36	0.93	7	6.70	1.15	2.19	0.0288
Flights	11	2.20	0.51	7	1.07	0.45	1.73	0.0840
Dives	7	0.73	0.25	1	0.20	0.20	2.22	0.0267
Hits	1	0.07	0.07	0	0.00	–	0.93	0.3506
Bounce songs	2	0.60	0.53	0	0.00	–	1.39	0.1644
Whinny songs	10	4.67	1.42	4	1.00	0.63	2.43	0.0149
Bark calls	6	3.40	2.41	2	0.73	0.61	1.49	0.1354
Screech calls	2	0.13	0.09	1	0.20	0.20	0.48	0.6326

[a] Based on results of all trials (n = 15) conducted with eight males and eight females (seven trials during the early nestling stage and eight during the late nestling stage).
[b] Number of individuals responding during the 15 trials.
[c] Standard error.

RESULTS

RESPONSES DURING INCUBATION

All female screech-owls (seven for Trial 1 and eight for Trial 2) were incubating at the start of the trials. Two females left nest cavities during the trials, and only one approached the predator. During Trial 1, no males (n = 7) approached nest sites. Two of eight males approached the nest during Trial 2, both to within 5 m. Males made only two flights during the 15 trials while females made only one. Neither males nor females made any dives or hits. Few vocalizations were uttered during Trials 1 and 2. Females uttered only whinny songs (one by one female during Trial 1 and 15 by one female during Trial 2), while males uttered bounce songs (one by one male during Trial 1 and 12 by two males during Trial 2), whinny songs (one by one male during Trial 1), and bark calls (one by one male during Trial 1). No significant changes (Wilcoxon, $P > 0.05$) in behavior were observed between Trials 1 and 2 for either males or females.

RESPONSES DURING THE NESTLING STAGE

Six males approached the predator during both Trials 3 and 4 (n = 8 for Trial 3 and n = 7 for Trial 4), with mean minimum approach distances of 3.6 ± 1.8 m and 3.1 ± 1.2 m, respectively. Three females approached the predator during both Trials 3 (n = 8) and 4 (n = 7), with mean minimum approach distances of 6.5 ± 1.6 m and 7.0 ± 2.1 m, respectively. Approaching males averaged about two flights and less than one dive per trial (Table 1). Vocal responses of male screech-owls consisted mainly of whinny songs during Trial 3 and whinny songs and bark calls during Trial 4 (Fig. 1). Approaching females averaged about one flight per trial, made only one dive, and uttered few vocalizations during the nestling stage (Table 1). No significant changes (Wilcoxon, $P > 0.05$) were observed between Trials 3 and 4 for either males or females.

The responses of male screech-owls were more pronounced than those of females during the nestling stage (Table 1). The responses of males were significantly greater for three measures (minimum approach distance, number of dives, and number of whinny songs), and approached significance for one additional measure (number of flights).

COMPARISON OF RESPONSES

Male owls responded with greater intensity during the nestling stage than during incubation, making significantly more flights (z = 3.05, P = 0.0023) and dives (z = 2.92, P = 0.0036) and uttering significantly more whinny songs (z = 3.43, P = 0.0006) and bark calls (z = 2.16, P = 0.0309). Female screech-owls exhibited little change in behavior, with only the number of flights increasing significantly (z = 2.46, P = 0.0139) during the nestling stages.

NEST DEFENSE AND NUMBER OF EGGS AND NESTLINGS

The mean clutch size for screech-owls in this study was 3.2 ± 0.9 (n = 8, range = 2–5). The mean number of nestlings was 2.9 ± 1.1 (n = 8, range = 1–5). No significant correlations were found between any measure of nest defense and either clutch size or number of nestlings (Spearman, $P > 0.05$).

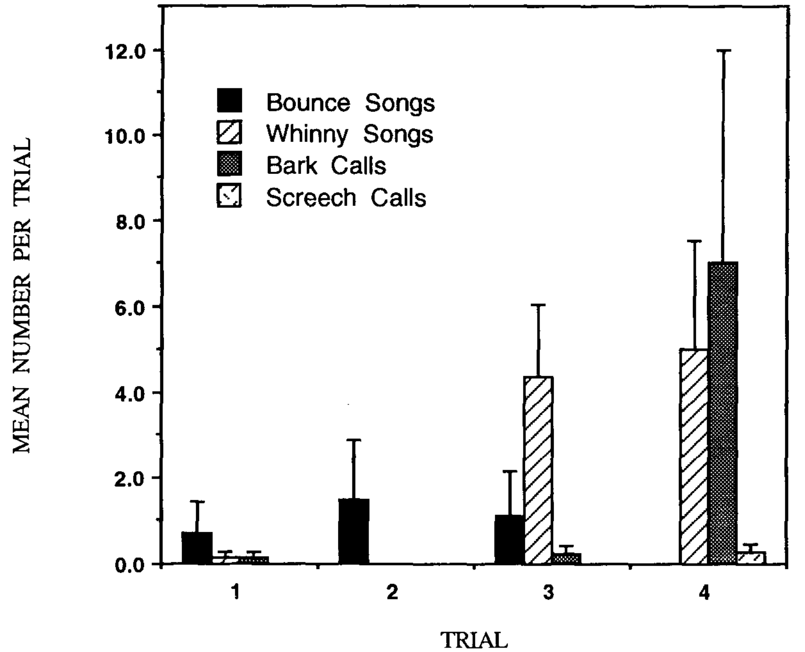

FIGURE 1. Number (±SE) of vocalizations given by male Eastern Screech-Owls during nest defense trials. Trial 1 = early incubation, Trial 2 = late incubation, Trial 3 = early nestling, and Trial 4 = late nestling.

NEST DEFENSE AND NEST TYPE

Screech-owls used both nest boxes ($n = 4$) and natural cavities ($n = 4$) and the behavior of owls using these two types of sites did not differ significantly (Wilcoxon, $P > 0.05$ for all variables) during the incubation stage. During the nestling stage, males using nest boxes approached significantly ($z = 1.97$, $P = 0.0484$) closer to the predator and made significantly ($z = 2.16$, $P = 0.0309$) more flights than males using natural cavities. Although only approaching significance ($z = 1.88$, $P = 0.0608$), males using nest boxes also made more dives. No significant differences were observed in the behavior of female screech-owls using the two types of nest sites. However, two variables approached significance, i.e., females using nest boxes approached closer ($z = 1.67$, $P = 0.0952$) to the predator and gave more ($z = 1.74$, $P = 0.0815$) whinny songs.

NEST DEFENSE AND PREDATOR LOCATION

Males performed significantly ($F = 5.86$, df = 3, 140, $P = 0.0008$) more dives when the predator was closest to the nest (stop 3). Males also performed more flights ($F = 2.58$, df = 3, 140, $P = 0.059$) when the predator was closest, a difference that approached significance. The single hit was also performed by a male when the predator was at the closest stop. In contrast, the behavior of female screech-owls did not vary significantly (ANOVA, $P > 0.05$ for all variables) with predator location.

DISCUSSION

VARIATION IN BEHAVIOR DURING NESTING

The intensity of nest defense by adult Eastern Screech-Owls increased during the nesting period, with males and, to a lesser degree, females exhibiting greater responses during the nestling period than during incubation. Similar results have been reported for several species of birds (reviewed by Montgomerie and Weatherhead 1988), including other raptors (Wallin 1987, Ferrer 1990, Wiklund 1990, Andersen 1990). Factors that may contribute to an increased intensity of nest defense during the nestling period include declining renesting potential (Barash 1975, Weatherhead 1979), increasing nest conspicuousness and value of the young to predators (Harvey and Greenwood 1978), the increasing value of the young to parents (Andersson et al.

1980), and positive reinforcement (Knight and Temple 1986a, 1986b).

The breeding cycle of Eastern Screech-Owls in central Kentucky lasts approximately four months, with egg-laying beginning in mid-March and young owls leaving parental territories beginning in mid-July (Belthoff 1987, Belthoff and Ritchison 1989). As a result of this long breeding cycle, screech-owls have limited renesting potential (Johnsgard 1988, pers. observ.), with opportunities for renesting probably limited to pairs that lose nests early in the incubation period (pers. observ.). This suggests that changes observed in the intensity of nest defense by screech-owls during the nesting period were probably not related to changes in renesting potential.

The increasing conspicuousness of nests (e.g., begging calls of nestlings may become louder and adults may make more trips to and from the nest as feeding rates increase) and the increasing mass of nestlings (and, therefore, increasing value to predators) may require an increase in the intensity of nest defense by parent birds during the nestling period (Harvey and Greenwood 1978, Greig-Smith 1980). These factors seem unlikely to apply to Eastern Screech-Owls. Newton (1979) suggested that most predation in raptors occurs during incubation or early in the nestling stage. Predation rates may decline during the nesting period because nest sites may become less conspicuous as trees leaf out (Montgomerie and Weatherhead 1988). In central Kentucky, leaf out typically begins in April and screech-owl eggs usually hatch in mid- to late April. Another factor influencing predation rates is nest height. Nilsson (1984) found a negative relationship between nest height and predation rate for several species of cavity-nesting birds, with very few high nests (higher that 4.1 m) lost to predators. Belthoff and Ritchison (1990) examined nest site selection by Eastern Screech-owls and reported a mean cavity height of 6.5 m. Nests located in high cavities may be less vulnerable because ground-based predators may be less likely to either hear the begging calls of young or observe adults visiting the nest site. Finally, the growth of young screech-owls or other young raptors may not increase their value to predators. As young raptors grow older their ability to defend themselves improves and, thus, their value to potential predators may decline (Wallin 1987).

Andersson et al. (1980) suggested that parent birds should increase levels of nest defense during the nesting period because chances of the young surviving increase with age and, thus, they become increasingly valuable. This may be particularly true for Eastern Screech-Owls because the chances of nest predation may decline after hatching (Gehlbach 1986) and, in addition, young raptors are better able to defend themselves as they grow older (Wallin 1987). In agreement with Andersson et al.'s (1980) age-investment hypothesis, Eastern Screech-Owls took relatively low risks during incubation and relatively greater risks during the nestling period.

Andersson et al. (1980:538) also predicted that "... the optimal level of parental defense increases during any well-defined stage of the breeding cycle, for example the incubation and nestling periods. ..." Eastern Screech-Owls exhibited little or no nest defense during the incubation period, and no significant changes in behavior were observed between the early incubation and late incubation trials. In addition, disturbance of screech-owls during the incubation period often causes nest abandonment (VanCamp and Henny 1975). Similarly, Wallin (1987) found no evidence of nest defense by adult Tawny Owls (*Strix aluco*) during the incubation period. In contrast, nest defense during incubation has been reported in several passerine species (Bjerke et al. 1985, Knight and Temple 1986b, Breitwisch 1988, Hobson et al. 1988, Weatherhead 1989, Westneat 1989, Rytkonen et al. 1990). Interspecific differences in behavior may be due in part to differences in average lifespan. The probability of survival until the next breeding season is lower for shorter-lived species than for longer-lived species and, therefore, the cost of nest defense (i.e., loss of future reproductive success due to injury or death) is greater for long-lived species (Montgomerie and Weatherhead 1988). Thus, relatively long-lived species like Eastern Screech-Owls and Tawny Owls may be less willing to take risks defending eggs. Andersen (1990) suggested that Red-tailed Hawks (*Buteo jamaicensis*) may avoid high risk behavior during nest defense because adult survival and probability of renesting in subsequent years are high compared to many passerines.

Eastern Screech-Owls also exhibited no changes in behavior between the early nestling and late nestling stages. Similarly, Andersen (1990) found that while the calling rates of Red-tailed Hawks increased during the nestling stage, other measures of defense (dive rate and closest approach) were not correlated with the age of nestlings. In contrast, the intensity of nest defense has been found to increase throughout the nestling stage, peaking at the time young leave the nest, in a variety of passerines (Bjerke et al. 1985, Weatherhead 1989, Rytkonen et al. 1990). The failure of Eastern Screech-Owls and Red-tailed Hawks to increase levels of nest defense during the nestling stage may be due to the increasing ability of young raptors to either defend themselves or flee from predators as they get older. Andersen (1990) suggested that defending older nestlings who could hide or flee might be an inappropriate response for adult Red-tailed Hawks. Similarly, Wallin (1987) suggested that young Tawny Owls were better able to defend themselves as they grew older. In addition, as young raptors or other relatively large species increase in size, the chances that a predator will take the entire brood may decrease.

Knight and Temple (1986a, 1986b) suggested that increased levels of nest defense during the nesting period may be due to positive reinforcement. Recent studies, however, suggest that such reinforcement appeared to have little or no effect on levels of nest defense by Northern Mockingbirds (*Mimus polyglottos*; Breitwisch 1988), Song Sparrows (*Melospiza melodia*; Weatherhead 1989), Mourning Doves (*Zenaida macroura*; Westmoreland 1989), Indigo Buntings (*Passerina cyanea*; Westneat 1989), and Willow Tits (*Parus montanus*; Rytkonen et al. 1990). Contrary to the predictions of this hypothesis, screech-owls in our study exhibited no significant changes in behavior between trials conducted during the same breeding stage (i.e., during the incubation stage or nestling stage). If birds are rewarded for heightened aggressiveness, then a continuous increase in response levels might be evident between successive trials. However, these results are only suggestive, and our limited sample of pairs tested only once does not permit a direct test of the positive reinforcement hypothesis. Thus, both the age-investment hypothesis and the positive reinforcement hypothesis are supported by our results.

SEX DIFFERENCES IN NEST DEFENSE BEHAVIOR

Male screech-owls defended nestlings more vigorously than did females. Several factors may contribute to such sexual differences, including differences in risk perception (Montgomerie and Weatherhead 1988). Nest defense may be more risky for females than males if females are weakened by the rigors of nesting (Reid and Montgomerie 1985, Montgomerie and Weatherhead 1988). Although Wallin (1987) found that the physical condition of female Tawny Owls influenced the intensity of nest defense, even the lightest females showed high defense levels. Further, although the body mass of female owls typically declines during brooding, such losses may be adaptive by permitting females to serve a passive storage role. Mass loss therefore may not be a true indicator of condition (Korpimaki 1990). Thus, the possible effects of nesting on the condition of female birds, including female screech-owls, and how such effects might influence the intensity of nest defense remain unclear. However, females are the primary nest defenders in several species (e.g., Wallin 1987, Andersen 1990, Ferrer 1990), suggesting that, at least in those species, the rigors of nesting do not weaken females sufficiently to preclude nest defense.

In populations with biased sex ratios the less abundant sex should take fewer risks in nest defense because the lifetime costs in fitness would be higher than for the abundant sex (Montgomerie and Weatherhead 1988). VanCamp and Henny (1975) reported data suggesting that screech-owl populations in the northeastern United States exhibit a balanced sex ratio. Similarly, Duley (1979) reported a balanced sex ratio for Eastern Screech-Owls in Tennessee. Although not conclusive, such data suggest that differences in the nest defense behavior of male and female screech-owls are not the result of a biased sex ratio.

Differences in the ability of males and females to raise offspring unaided may also contribute to sexual differences in nest defense behavior. A parent whose mate would be unable to raise a brood on its own should take less risk in nest defense (Montgomerie and Weatherhead 1988). Male Eastern Screech-Owls do not incubate eggs or brood young (Bent 1938; Voous 1988, pers. observ.). Further, nestling screech-owls cannot thermoregulate until 14–16 days post-hatching (Lohrer 1985), suggesting that female screech-owls must brood young for about two weeks after hatching. Thus, male screech-owls would probably not be able to raise young unaided until about halfway through the four-week nestling period. This may have contributed to the low levels of nest defense exhibited by female screech-owls during the incubation and early brooding periods. However, the ability of males and females to raise offspring unaided would seem to be similar during the late nestling stage. Despite this, the responses of male screech-owls remained greater than those of females. Similar observations have been reported for Great Tits (*Parus major*; Regelmann and Curio 1986). Such results suggest that factors other than the ability to raise offspring unaided are responsible for differences in the nest defense behavior of males and females.

Like many raptors, Eastern Screech-Owls exhibit reversed sexual dimorphism (Henny and VanCamp 1979), and this difference in relative size could influence the nest defense behavior of males and females. Flights and dives were important components of the nest defense behavior of screech-owls, and the smaller size and, perhaps, greater maneuverability of males may reduce the risk involved in performing such behaviors. Such differences in maneuverability may also contribute to sexual differences in the nest defense behavior of Snowy Owls (*Nyctea scandiaca*; Wiklund and Stigh 1983) and Rough-legged Hawks (*Buteo lagopus*; Andersson and Wiklund 1987). However, the larger size of many female raptors may predispose them to nest defense (Andersson and Norberg 1981). Results in support of this hypothesis have been reported (Wallin 1987, Andersen 1990, Ferrer 1990). Several factors may contribute to interspecific differences in the behavior of male and female raptors. For example, Montgomerie and Weatherhead (1988) suggested that responding to a relatively small predator may be less risky for a larger parent while responding to a relatively large predator may be less risky for a smaller, more maneuverable parent. Habitat characteristics could also be a factor. Larger parents may respond to a potential predator with flights and dives in open habitats, while smaller, more maneuverable parents may respond in habitats with more obstructions (e.g., woodlots or forests). The location of a predator relative to a nest site could also influence response levels. Smaller, more maneuverable parents may use flights and dives to distract approaching predators, while larger parents may use flights, dives, and even hits to deter predators in the immediate vicinity of a nest. Thus, our choices of study site (woodlots) and methodology (using a relatively large predator, humans, that did not go all the way to the nest cavity) may help explain the greater response of male screech-owls. Clearly, additional studies are needed to determine how predator size, habitat characteristics, and predator location influence the responses of males and females in species exhibiting sexual size dimorphism.

NEST DEFENSE AND NEST TYPE

The increased intensity of nest defense exhibited by screech-owls using nest boxes may have been due in part to the greater visibility of such nest sites. Montgomerie and Weatherhead (1988) suggested that crypticity could influence the intensity of nest defense behavior, with individuals in cryptic nests responding less than those with more exposed nests. In support of this hypothesis, Ricklefs (1977) reported that Panamanian birds exhibiting the most vigorous defense were those with conspicuous nests. Similarly, American Robins (*Turdus migratorius*) with exposed nests responded to potential predators with significantly more swoops and hits than those with cryptic nests (McLean et al. 1986).

NEST DEFENSE AND PREDATOR LOCATION

Montgomerie and Weatherhead (1988:183) suggested that "well armed" (raptorial) parents should respond vigorously as a predator gets close to the nest because such a response informs the predator of a willingness to attack. If the intensity of response increases as a potential predator moves closer to the nest, then the direction that the predator must move to reduce the likelihood of injury should be clear (Montgomerie and Weatherhead 1988). In support of this hypothesis, we found that the intensity of response by male screech-owls increased as the predator moved closer to the nest.

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