

## NEST-DEFENSE BEHAVIOR OF RED-TAILED HAWKS<sup>1</sup>

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**Abstract.** From 1983 to 1986 I visited 26 Red-tailed Hawk (*Buteo jamaicensis*) nests in east-central and southeastern Colorado. I estimated the closest distance that each defending adult approached, and recorded the number of calls that each bird gave and the number of times it dived while I was at the base of the nest tree for a 10-min period and subsequently at the nest for a 5-min period. The age and number of young in the nest, the height of the nest above the ground, and whether one or both adults were present were used as potential predictors of the intensity of nest-defense behavior. Nestling age was a significant predictor of call rate of the closest adult and nest height was a significant predictor of call rate of the farthest adult while I was at the base of the nest tree. Dive rate and closest approach were not significantly related to any measured variable. No independent variable was significantly related to nest-defense intensity while I was at the nest, however, dive rate increased and closest approach decreased when I was at the nest compared to when I was on the ground. These observations are only in part consistent with current theoretical models that predict patterns of nest-defense intensity in altricial birds.

**Key words:** *Buteo jamaicensis*; nest-defense behavior; parental investment; predator-defense behavior; Red-tailed Hawk.

### INTRODUCTION

Several theories have been presented to explain observed patterns in nest-defense behavior in altricial birds. Trivers (1972) and Barash (1975) predicted that parent birds should defend nestlings more aggressively as nestling age (i.e., amount of parental investment) increases. Andersson et al. (1980) and Harvey and Greenwood (1978) hypothesized that nest-defense intensity should increase with nestling age due to decreasing differences between expected future survival of parents and offspring and due to increased conspicuousness to predators of nestlings during the nestling period. Montgomerie and Weatherhead (1988) have also presented a general model for predicting nest-defense intensity in parent birds based on optimizing the difference between costs and benefits of defending nests.

Most studies of nest defense in birds have been conducted on species in the orders Passeriformes (e.g., Barash 1975; Greig-Smith 1980; Knight and Temple 1986a, 1986b) and Charadriiformes (e.g., Kruuk 1964; Lemmetyinen 1971; Kilpi 1987, 1988) and have documented an apparent in-

crease in nest-defense intensity through the nestling period (see Knight and Temple [1986a] and Montgomerie and Weatherhead [1988] for a review of pertinent literature). Knight and Temple (1986a, 1986c), however, suggested that many of these observations were influenced by methodological and design problems. They provided evidence that repeated visits to an individual nest resulted in an increase in nest-defense intensity and suggested that this increase was a result of positive reinforcement and loss of fear in parent birds (but see Coleman 1987, Montgomerie and Weatherhead 1988, Westneat 1989).

Nest-defense behavior in Falconiformes may differ from that observed in other bird orders. Compared to many passerine species, most Falconiformes are relatively long-lived (Newton 1979) and possess the ability to attack and seriously injure potential nest predators. Past experience with potential nest predators (Knight and Temple 1986a), a high probability of future reproduction (Barash 1980), and the ability to inflict injury to potential nest predators (Montgomerie and Weatherhead 1988) may all influence nest-defense behavior in any single breeding attempt. In addition, most Falconiformes do not nest colonially (Newton 1979), unlike many Charadriiformes in which nest-defense behavior has been studied (e.g., Kilpi 1987), and most Falconiformes exhibit reversed sexual size dimorphism (e.g., Mueller and Meyer 1985). Both

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colonial nesting and sexual size dimorphism have been related to nest-defense behavior in birds.

I characterized nest-defense behavior in Red-tailed Hawks (*Buteo jamaicensis*), a member of the order Falconiformes, to compare their nest-defense behavior with that of birds in other orders. I also examined nest-defense intensity patterns through the nestling period, and tested for a relationship between nest-defense intensity and age and number of nestlings in the nest to determine whether observed patterns were consistent with those predicted by theory.

#### STUDY AREAS AND METHODS

I visited nests of Red-tailed Hawks at the Fort Carson Military Reservation (FCMR) in east-central Colorado in 1984, and at the Piñon Canyon Maneuver Site (PCMS) in southeastern Colorado from 1983 to 1986. The FCMR was located along the eastern edge of the Front Range south of Colorado Springs, Colorado, and elevation ranged from 1,650 to approximately 2,000 m. Major habitats on the semi-arid FCMR included pinyon pine (*Pinus edulis*)-juniper (*Juniperus monosperma*), blue grama (*Bouteloua gracilis*)-western wheatgrass (*Agropyron smithii*), and cottonwood (*Populus* sp.)-willow (*Salix* sp.) plant associations (Costello 1954, U.S. Dept. of the Army 1980a). The PCMS was located along the western rim of the Purgatoire River Canyon in Las Animas County, Colorado and climate and vegetation on the PCMS were similar to that on the FCMR (U.S. Dept. of the Army 1980b). Elevation ranged from 1,300 to 1,700 m. Undocumented visits to Red-tailed Hawk nests at either the FCMR or the PCMS were unlikely, as public access was restricted and human activity during the nesting period was infrequent.

Occupied nests were located each spring from helicopters (White and Sherrod 1973) and by searching potential territories from the ground for nest sites (Craighead and Craighead 1956). Nests were not approached closer than 500 m on foot prior to visits where nest-defense behavior of the adult birds was recorded. The first time that I visited each nest on foot, I recorded the nest-defense behavior of the adults (Knight et al. 1989). I walked directly toward the nest from a distance of at least 500 m and from a direction where I was conspicuous to one or both adults that were at or near the nest. When I reached the base of the nest tree, I recorded the number of calls and dives made by each adult during a 10-

min period and estimated the closest distance that each adult approached.

Closest distance was visually estimated to the nearest meter from 1 to 5 m, to the nearest 5 m from >5 to 50 m, to the nearest 10 m from >50 to 100 m, and to the nearest 25 m at >100 m. A dive was any downward break from horizontal made by a defending adult (Knight et al. 1989). If both adults actively defended the nest, the bird that approached me the closest was designated the near bird. I was able to determine a relative size difference between defending adults at all nests where both adults were present (92% of all nest visits) and I recorded which bird (large or small) defended the nest more aggressively in order to identify individuals when I subsequently climbed to the nest. I also assumed that the larger bird in each pair was the female, because Red-tailed Hawks exhibit an observable degree of sexual size dimorphism (Craighead and Craighead 1956, Snyder and Wiley 1976). Individuals were also distinguished by differences in vocalizations. Red-tailed Hawks nested on cliffs and in trees (Andersen 1984, unpubl. data) on both the FCMR and the PCMS but only data from tree nests were included in the analyses to control for any effect of nest site (tree or cliff) on nest-defense behavior.

After recording the behavior of the adults while I was at the base of the nest tree, I climbed to the nest and recorded the number of calls and dives and the closest distance that each adult bird approached me during a 5-min period. I also recorded the number of young in the nest, measured the length of each nestling's fourth primary feather, and measured the height of the nest above the ground. Nestling age was estimated to the nearest day based on fourth primary measurements (Petersen and Thompson 1977; Bechard et al. 1985; Andersen, unpubl. data). When there was more than one nestling in the nest, I used the average estimated age of all nestlings in analyses. To minimize any influence of weather, nest visits were made only when estimated wind speeds were <20 km/hr and there was no precipitation. I was the sole observer during the study.

I included only the first nest visit to each territory in statistical analyses for trends in nest-defense intensity, to minimize the chance of including individual birds (or pairs) more than once. However, I visited nests at 12 individual territories in more than 1 year on the PCMS to in-

TABLE 1. Nest-defense behavior of Red-tailed Hawks in response to a human at the base of the nest tree and at the nest at 26 nests in east-central and southeastern Colorado.

Response variable	Near bird <sup>a</sup>		Far bird	
	Base (n)	Nest (n)	Base (n)	Nest (n)
Mean distance <sup>b</sup>	31.7 (24)	13.9 (25)	62.5 (19)	26.1 (19)
Range	4-100	2-50	8-200	2-75
Mean calls <sup>c</sup>	59.4 (25)	25.2 (25)	32.2 (20)	18.5 (22)
Range	15-116	7-45	0-88	0-39
Mean dives <sup>d</sup>	2.9 (25)	5.7 (25)	1.3 (20)	2.2 (22)
Range	0-12	1-21	0-9	0-9

<sup>a</sup> Near bird = the bird that came closest to the observer during a 10-min period at the base of the nest tree.

<sup>b</sup> The closest distance (m) that the bird approached the observer.

<sup>c</sup> The number of calls given by the bird.

<sup>d</sup> The number of times that the bird dived.

investigate Knight and Temple's (1986a, 1986c) explanation for observed patterns in nest-defense behavior. At four of these nests, individual birds could be identified between years by plumage characteristics (one melanistic individual) or because they were marked with radio transmitters (three individuals). I also visited six nests twice in the same season at the PCMS, at an approximately 2-week interval.

I conducted stepwise multiple regression analyses with nestling age, number of young in the nest, number of defending adults, and the height of the nest above the ground as independent variables. Separate regression analyses were conducted for the closest distance that the adults approached me, the number of calls, and the number of dives in a 10-min period while I was at the base of the nest tree. Age and number of young in the nest were used as a measure of parental investment. Age of the young also reflected the relative difference between expected future survival of parents and young (Andersson et al. 1980). The number of adults defending the nest was included in regression analyses to determine whether there was any increase in nest-defense intensity in the presence of a second bird (Montgomerie and Weatherhead 1988), and the height of the nest above the ground was used as a measure of my proximity to the nest (Greig-Smith 1980) and thus reflected the degree to which I was a threat to the nestlings while I was at the base of the nest tree. Similar analyses were conducted for data collected while I was at the nest.

Of the 12 territories that were visited in more than 1 year, eight were visited in at least three successive years and were used to test for the possible effect of repeated visits on the behavior of adults. Annual adult survival in Red-tailed

Hawks is approximately 0.70 to 0.80 (Luttich et al. 1971, Henny and Wight 1972) and if individual birds occupied the same territory through time (Janes 1984; Andersen, unpubl. data), the probability that the same individual defended the same nest site for three consecutive years was approximately 0.56. I tested for a trend in call rate through time using a multivariate, repeated measures analysis (Hand and Taylor 1987) of adjusted call rates. Adjusted call rate was calculated as the difference between the observed call rate of the near adult and the call rate predicted by regressing observed call rate on nestling age for the first visit to all nests, and was used to control for the observed increase in adult call rate during the nestling period. Multiple regression procedures and other parametric statistics follow Ryan et al. (1976), Snedecor and Cochran (1980), and Hand and Taylor (1987) and non-parametric tests are after Gibbons (1985).

## RESULTS

Red-tailed Hawks aggressively defended their nests in response to a human at the base of the nest tree and at the nest (Table 1). When nests were originally visited, the age of nestlings ranged from 1 to 42 days, and brood size ranged from one to three young. Both adults actively defended the nest in all but two (8%) of the 26 initial nest visits. Birds that aggressively defended the nest while I was at the base of the nest tree also were aggressive when I reached the nest, as measured by the number of calls given and the closest distance that they approached (Table 2).

The number of times the near bird called while I was at the base of the nest tree increased with the age of young in the nest ( $F_{1,23} = 7.44$ ,  $P < 0.025$ ,  $R^2 = 0.24$ ) (Fig. 1). When a single unag-

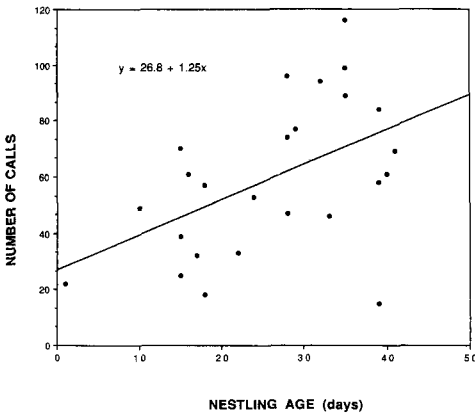


FIGURE 1. The number of calls given by the closest defending Red-tailed Hawk in response to a human at the base of the nest tree vs. the age of the young in the nest. Data are from first visits to 25 of 26 nests studied in east-central and southeastern Colorado.

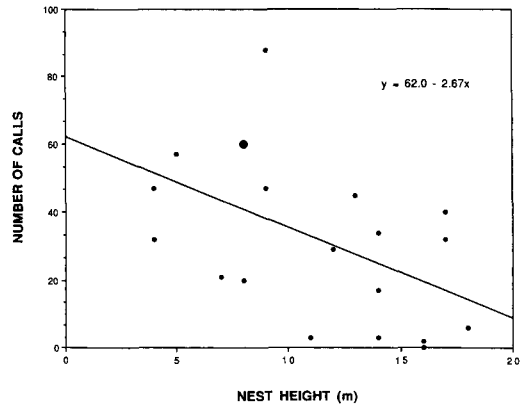


FIGURE 2. The number of calls given by the farthest defending Red-tailed Hawk in response to a human at the base of the nest tree vs. the height of the nest above the ground. Data are from first visits to 20 of 26 nests studied in east-central and southeastern Colorado.

gressive bird that called infrequently, did not dive, and remained > 100 m away was removed from the regression, nestling age was an even more highly significant predictor of call rate ( $F_{1,22} = 14.68, P < 0.005, R^2 = 0.40$ ). For the far bird, only the height of the nest above the ground was a significant predictor for any response variable ( $F_{1,18} = 6.16, P < 0.025, R^2 = 0.26$ ) (Fig. 2). Call rate of the far bird decreased as nest height increased. Because nest-defense intensity may not increase linearly through the nestling period, I also tested for differences in response variables between the first half (nestlings 0–23 days old) and the second half (>23–45 days old) of the nestling period. Only call rate of the near bird ( $t = -3.57, df = 23, P = 0.002$ ) differed significantly between the first and second half of the nestling period, with higher call rates in the second half of the nestling period when I was at the base of the nest tree.

Neither the nearest distance that either adult approached nor the frequency with which either

TABLE 2. Pearson's product-moment correlation coefficients and levels of significance for nest-defense behavior of individual Red-tailed Hawks while I was at the base of the nest tree vs. at the nest.

Response variable	Near bird (n)	Far bird (n)
Closest distance (m)	0.061 (23)	0.850** (17)
Number of calls	0.459* (24)	0.641** (20)
Number of dives	0.220 (24)	0.351 (20)

\*  $P < 0.05$ .  
 \*\*  $P < 0.001$ .

adult dived when I was at the base of the nest tree were significantly related to nestling age, the number of young in the nest, or the height of the nest above the ground. The distance that individuals approached was highly variable, and most birds dived very few times. Only a few birds dived repeatedly. Similarly, whether one or both adults defended the nest did not appear to influence nest-defense intensity. Although both adults defended most nests (92%) that I visited, the presence or absence of a second adult did not appear to influence the behavior of the first adult when I was at the base of the nest tree or at the nest.

No independent variable was significantly related to nest-defense intensity of either adult while I was at the nest. In all cases when both adults defended the nest, the female defended more aggressively than the male. When I was at the nest, the female approached closer ( $S = 12, n = 14, P = 0.013$ ), dived more frequently (paired  $t = 3.61, df = 21, P = 0.001$ ), and, in general, called more frequently (paired  $t = 1.70, df = 21, P = 0.100$ ) than the male. Similarly, when I was at the base of the nest tree, the female approached closer ( $S = 16, n = 16, P = 0.000$ ), dived more frequently (paired  $t = 2.27, df = 19, P = 0.035$ ), and called more frequently (paired  $t = 3.86, df = 20, P = 0.001$ ) than the male.

Proximity of the investigator to the nest influenced intensity of nest-defense behavior. Individual birds approached closer when I was at the nest vs. at the base of the nest tree (near adult:

sign test,  $S = 17$ ,  $n = 20$ ,  $P = 0.0026$ ; far adult:  $S = 16$ ,  $n = 16$ ,  $P = 0.0000$ ) and dived more frequently (near adult: paired  $t = -5.36$ ,  $df = 23$ ,  $P = 0.0000$ ; far adult: paired  $t = -3.16$ ,  $df = 18$ ,  $P = 0.0055$ ). However, call rate did not change when I was at the base of the nest tree vs. at the nest site for either the near (paired  $t = 1.16$ ,  $df = 23$ ,  $P = 0.26$ ) or the far adult (paired  $t = 1.26$ ,  $df = 19$ ,  $P = 0.22$ ).

There were no differences (paired  $t$ -tests, all  $P$ 's  $> 0.50$ ) between visits in call or dive rates or in the closest distance that the near adult approached at the six nests I visited twice during the same season on the PCMS in 1986. For the eight nests that were visited in three successive years, call rate (adjusted) did not vary linearly ( $F_{1,17} = 0.655$ ,  $P > 0.40$ ) or quadratically ( $F_{1,7} = 1.970$ ,  $P > 0.20$ ) with repeated visits to the nest.

Individual birds could be identified between years at four territories. These individuals exhibited similar nest-defense intensity between years. Dive rate (paired  $t = 0.400$ ,  $df = 3$ ,  $P = 0.72$ ), call rate (paired  $t = 0.36$ ,  $df = 3$ ,  $P = 0.740$ ), and the closest distance that they approached (paired  $t = -2.65$ ,  $df = 2$ ,  $P = 0.120$ ) while I was at the base of the nest tree varied little between years. When I was at the nest, there were no significant differences between years in dive rate (paired  $t = 0.93$ ,  $df = 3$ ,  $P = 0.420$ ), call rate (paired  $t = -1.10$ ,  $df = 3$ ,  $P = 0.350$ ), or closest approach (paired  $t = -1.89$ ,  $df = 3$ ,  $P = 0.160$ ).

## DISCUSSION

The intensity of nest-defense behavior of Red-tailed Hawks, as measured by call rate, appeared to increase through the nestling period. Although there was considerable variation among birds, there was a significant correlation between call rate of near adults and nestling age (Fig. 1) and call rate of far adults and height of nests above ground (Fig. 2). Calling may serve both to distract a potential predator and to make the nestlings less conspicuous in the nest (Greig-Smith 1980, Knight and Temple 1986b). Especially in the case of potential human predators, distraction (including calling) may pose a serious risk, as humans have been a significant source of mortality in Red-tailed Hawks in North America in the past (Henny and Wight 1972, Keran 1981).

Calling, however, involves relatively little cost to the adults and is a less aggressive nest-defense behavior compared to diving at and closely approaching a potential nest predator (Greig-Smith 1980, Montgomerie and Weatherhead 1988).

These behaviors have a higher risk of injury (and thus cost) to the parent bird. However, neither dive rate nor closest approach were related to age of the nestlings in the nest, as predicted by theory (Trivers 1972, Barash 1975, Andersson et al. 1980). Similarly, most birds approached closely and dived infrequently, although dive rate increased and closest approach decreased when I was at the nest vs. when I was at the base of the nest tree.

In predatory birds, published reports of nest-defense behavior are primarily anecdotal (e.g., Brown and Amadon 1968, Olsen and Olsen 1980), although nest-defense behavior has been quantified in three species of Falconiformes, Merlins (*Falco columbarius*) (Fox and Donald 1980), Rough-legged Hawks (*Buteo lagopus*) (Andersson and Wiklund 1987), and Red-tailed Hawks (Knight et al. 1989), and in two species of predatory Strigiformes, Snowy Owls (*Nyctea scandiaca*) (Wiklund and Stigh 1983) and Tawny Owls (*Strix aluco*) (Wallin 1987). Unlike Rough-legged Hawks (Andersson and Wiklund 1987) and Snowy Owls (Wiklund and Stigh 1983), female Red-tailed Hawks defended nests more aggressively than males. Several authors (Storer 1966, Reynolds 1972, Snyder and Wiley 1976, Andersson and Norberg 1981, Cade 1982) have suggested that larger females are more effective in deterring potential nest predators than smaller males, although Mueller and Meyer (1985) found no support for this hypothesis in published accounts of nest-defense behavior in raptors.

Red-tailed Hawks are different from most birds in which nest-defense behavior has been studied in several ways. First, Red-tailed Hawks are relatively long-lived and have the opportunity to learn from encounters with potential nest predators (including humans) through several breeding seasons and in the period from fledging to first breeding. Intensity of nest-defense behavior may be influenced by the number and outcome of previous encounters with humans. Second, most nest predation and failure in raptors occurs early in the nestling period, or during incubation (Newton 1979; Andersen, unpubl. data). Diving at, and closely approaching, potential nest predators late in the nestling period, when young can flee or hide, may not be an appropriate or effective deterrent (Buitron 1983, Kilpi 1988, Montgomerie and Weatherhead 1988). Third, Red-tailed Hawks do not readily renest if a nest fails, and survival from hatching to fledging is high (Andersen, unpubl. data). Thus, during a single

breeding season, as nestlings grow older, their relative value to parents may not increase dramatically and related nest-defense intensity may remain constant. Fourth, adult survival and probability of nesting in subsequent years is higher in Red-tailed Hawks than in many passerines, and expected future reproduction can influence nest-defense behavior (Barash 1980). High-risk behavior (e.g., diving at and closely approaching a potential nest predator) may be avoided because failure of a single breeding attempt does not influence lifetime reproductive performance to the degree that potential injury or mortality does (Newton 1979). Finally, it is unlikely that nestling visibility increases nest-defense intensity with nestling age in Red-tailed Hawks. Red-tailed Hawk nestlings begin to stand up in the nest at approximately 14 days of age (Moritsch 1983). After this period, it is not likely that visibility of nestlings in the nest to terrestrial predators increases. Uneaten prey remains in the nest, which might also attract potential nest predators, are also less frequent in the nest later in the nestling period (Andersen, unpubl. data).

Knight and Temple (1986a, 1986c) suggested that many observed increases in parental nest-defense intensity result from methodological problems and positive reinforcement of aggressive behavior and subsequent loss of fear in parent birds. In Red-tailed Hawks, nest-defense intensity as reflected by call rate, increased through the nestling period without reinforcement by repeated investigator presence. In contrast, dive rate and closest approach did not change through the nestling period at either nests that were visited once or repeatedly in the same season. When I did visit nests twice in a single season and visited nests in the same territories in different seasons, intensity of nest-defense behavior of the near (most aggressive) adult did not increase significantly.

Nest-defense behavior of Red-tailed Hawks is in part similar to nest-defense behavior in other bird species although relatively high-risk behaviors (e.g., diving at and closely approaching a potential nest predator) do not seem to increase through the nestling period as predicted by theory. Rather, these behaviors were highly variable among individuals with no clear trend through time. Current theoretical models, tested primarily with observations of nest-defense behavior in short-lived birds, or with data collected at repeat visits to individual nests, predict that these rel-

atively high-risk behaviors should increase in intensity through the nestling period. Further study of nest-defense behavior in long-lived species may explain some of these inconsistencies and result in modification of existing theories.

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