

PREDATION ON THE EGGS AND NESTLINGS OF FLORIDA SCRUB JAYS

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ABSTRACT.—We investigated nest predation in a population of Florida Scrub Jays (*Aphelocoma c. coerulescens*) at Archbold Biological Station, Lake Placid, Florida. Frequency of nest visits by investigators did not influence predation rates. Nest predation increased as the breeding season progressed and occurred most often during daylight hours. When seasonal effects were held constant, nestlings were depredated more often than eggs, and young nestlings were depredated more often than old nestlings. Several lines of evidence indicated that, for Florida Scrub Jays, diurnal snakes and birds were the most important nest predators, while nocturnal mammals were relatively less important. Late in the breeding season, pairs with helpers experienced less nest predation than pairs without helpers. This effect was primarily the result of reduced predation on nestlings. Received 17 June 1991, accepted 13 January 1992.

NEST predation is a primary source of egg and nestling mortality in many species (Martin in press), and is increasingly recognized as a significant process shaping avian life-history characteristics, habitat selection, and community structure (e.g. Slagsvold 1982, Martin 1988a, b, in press). Patterns of nest predation also may interact with habitat fragmentation in ways that have important implications for conservation biology (e.g. Loiselle and Hoppes 1983, Wilcove 1985). However, despite the growing recognition of the importance of nest predation, our understanding of the ecological factors that influence the behavior of specific nest predators and rates of nest predation in natural populations remains limited (Martin 1987, in press).

In this paper we examine the ecological and social factors that may affect predation on eggs and nestlings of the Florida Scrub Jay (*Aphelocoma c. coerulescens*). This jay is restricted to peninsular Florida where it inhabits recently burned oak scrub (Woolfenden and Fitzpatrick 1984). Nests are typically positioned about 1 m above the ground in oak shrubs (Woolfenden 1974). Nesting is from March through June. Most clutches are of three or four eggs, rarely two or five. Incubation begins after the last or penultimate egg is laid. Eggs hatch after approximately 18 days of incubation, and nestlings fledge about 18 days after hatching (Woolfenden and Fitzpatrick 1984).

Florida Scrub Jays exhibit a cooperative breeding system in which about one-half of all breeding pairs are assisted by nonbreeding adults (helpers). For pairs with helpers the modal number of helpers is 1, the mean is 2, and the maximum is 6 (Woolfenden and Fitzpatrick 1990). Helpers assist in feeding young, defending the territory, guarding the nest and mobbing predators. They do not build nests, incubate, or brood. Although breeding pairs assisted by two or more helpers are no more successful than pairs with only a single helper, unassisted pairs produce significantly fewer offspring than pairs with helpers (Woolfenden and Fitzpatrick 1984, Mumme in press). The major way that helpers appear to increase reproductive success is by reducing predation on eggs, nestlings (Woolfenden 1978) and fledglings (McGowan and Woolfenden 1989). Helpers could reduce diurnal predation by serving as sentinels (McGowan and Woolfenden 1989), or by mobbing potential predators (Francis et al. 1989), or both. However, helpers would be ineffective at reducing the frequency of nocturnal predation (Woolfenden and Fitzpatrick 1984).

Based on data collected over a 10-year period (1969-1979), Woolfenden and Fitzpatrick (1984) concluded that predation is the primary cause of nest failure in the Florida Scrub Jay, accounting for 67% of egg loss and 85% of nestling loss. Thus, an evaluation of factors influencing nest predation is critical for a thorough understanding of the breeding biology of this species. In this paper, we provide such an evaluation by focusing on the following questions: (1) Does

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the frequency at which investigators visit nests influence predation rates? (2) What are the effects of habitat and proximity to vehicle trails? (3) How is the frequency of nest predation influenced by season and nest stage? (4) Does nest predation in the Florida Scrub Jay occur primarily during the day or the night? (5) Which predators are primarily responsible? (6) How does the presence of nonbreeding helpers affect the rate of nest predation? In addressing these questions, our study extends earlier analyses (e.g. Woolfenden and Fitzpatrick 1984) and provides several revised interpretations of previously published work on this species.

METHODS

We worked on marked jays that reside on the property of the Archbold Biological Station (ABS), a 2,000-ha research station located 12 km south of Lake Placid, Highlands County, Florida. Since 1969, Woolfenden and colleagues have monitored a subset of the total population of Florida Scrub Jays resident at ABS. Up to 50 groups of Scrub Jays are censused every month and all nests are found each year. Almost all nests are found before or very early in incubation. Through these efforts the age, sex, and breeding histories of many individuals are known.

In 1987, Schaub and Mumme conducted detailed observations on 76 nests with contents owned by 49 groups located in open oak scrub immediately south of the groups monitored by Woolfenden and colleagues. Most nests ($n = 60$) were found before incubation began, and all nests were monitored until they either fledged young or failed. Schaub visited some nests twice daily ($n = 41$) at sunrise (± 30 min) and sunset (± 30 min) and others approximately every third day ($n = 35$). Acts of predation that occurred between the sunrise and sunset nest checks are considered diurnal, and those that occurred between the sunset and sunrise nest checks are considered nocturnal.

To determine seasonal and circadian activity rates of the snakes and mammals that are the probable nest predators, Schaub censused vertebrate tracks during most of the 1987 nesting season. Tracks on a strip of sand 1.1 km long and 1 m wide, which extended along a broad firelane that coursed through the study site, were censused twice daily immediately after the sunrise nest checks and immediately before the sunset nest checks. Tracks made between the sunrise and sunset censuses are considered diurnal, and those made between the sunset and sunrise censuses are considered nocturnal. Terrestrial-predator activity is calculated as the number of tracks per number of hours since the last census. For example, a census showing tracks of five potential predators, which were known to have been made during the preceding 10 h, results

in an activity index value of 0.5. If rain obscured the tracks (21 of 100 mornings and 11 of 91 evenings), no census was made. Sightings of potential avian nest predators also were recorded and used to determine their activity rates. The rate of avian predator activity was calculated as number of visual sightings per hour of field time within the study tract. The activity rates of terrestrial and avian predators were combined into a single index, which was calculated as the number of observations (tracks plus sightings of birds) per observation hour (tracking hours plus field hours).

Data from 552 nesting attempts from the years 1974–1979 and 1981–1987 combined were used to calculate predation rates. The years 1969–1973 were excluded because historical information about the breeders was sparse, and the year 1980 was excluded because of the social disruption caused by a major die-off in fall 1979 (Woolfenden and Fitzpatrick 1991). The number of fledglings produced per group within a breeding season was used to make between-year comparisons. For this measurement of nesting success the years 1974–1987, excluding 1980, were not significantly different (Kruskal-Wallis, $H = 17.33$, $df = 12$, $P = 0.14$). We deleted from our analyses the few nests that failed to reach the incubation stage, or that experienced loss or injury of a breeder.

Daily predation rates were calculated as the number of apparent acts of predation per number of days a nest contained either eggs or nestlings. Losses that occurred at an unknown time between nest visits were considered as having occurred midway between visits.

Calculation of daily rates of predation are based on three different ways of recognizing apparent nest predation: (1) *Individual acts*—losses of all or part of a clutch or brood between consecutive nest visits that cannot be attributed to a cause other than predation. (2) *Ultimate failures*—nests that eventually lose all eggs or nestlings as a result of one or more acts of apparent predation. (3) *Instantaneous failures*—nests that fail as a result of loss of all eggs or nestlings between consecutive nest inspections. Predation rates derived from rates of individual acts of predation thus provide the most liberal estimate of nest predation, while estimates derived from the rate of instantaneous failure provide the most conservative estimate. For Florida Scrub Jays, we think the most liberal method provides the most accurate measure. Starvation of nestlings and subsequent brood reduction is a rare event for Florida Scrub Jays (Woolfenden and Fitzpatrick 1984). In the few cases observed during 1987, one member of a brood became visibly smaller than its siblings early in the nestling period, usually by day 3. Most of these runts survived to day 12. Therefore, we suspect that brood reduction that is the direct result of starvation rarely goes undetected in Florida Scrub Jays. The existence of long-enduring runts suggests that most instances of partial brood loss do in fact represent instances of partial predation, which sup-

TABLE 1. Effect of habitat type on rates of nest predation, as measured by both daily rates of individual acts and overall ultimate nest failures, 1974-1979 and 1981-1987 combined.

	Habitat type		
	Open scrub	Overgrown scrub	Pasture
Total nest-days	13,193	2,113	731
Individual acts of predation	244	44	19
Predation rate	0.0185	0.0208	0.0260
$G = 2.25, n = 16,037, P > 0.25$			
Nests that produced young	258	40	12
Nests failing because of predation	112	27	14
Predation rate	0.3027	0.4030	0.5385
$G = 7.59, n = 463, P < 0.025$			

ports our incorporating partial losses into estimates of nest predation rates.

The time period within the nesting season, experience of the breeders, and age of the breeders all affect nesting success in Florida Scrub Jays (Woolfenden and Fitzpatrick 1984). To control for the effect of season, we divided the nesting season into half-month (15-16 day) and month (30-31 day) intervals. To reduce the effects of breeder inexperience and senescence, in analyses of helper contributions we deleted all first breeders and those few breeders older than 11 years.

Because sample sizes and variances were unequal, nonparametric statistics were used to analyze daily rates of predation and predator activity. Categorical data were analyzed via contingency tables using log-likelihood ratio tests (G -test) with Williams' correction (Sokal and Rohlf 1981), or chi-square tests with Yates' correction for continuity (Zar 1984). Some of the following analyses use individual nests rather than nest days as units in order to more closely meet the assumption of independence.

RESULTS

Effects of investigator visitation.—Rates of nest predation in 1987 were not significantly influenced by the two different nest-visitation treatments. Nests visited by investigators twice daily experienced 32 individual acts of apparent predation in 1,155 nest-days (0.028 acts/day), compared to 22 individual acts in 979 nest-days (0.022 acts/day) for nests visited approximately every three days ($G = 0.37, P > 0.9$). Similarly, 19 (46.3%) of the 41 nests visited twice daily ultimately failed due to predation, compared to 17 (48.6%) of the 35 nests visited every three days ($G = 0.38, P > 0.9$).

Effects of habitat and proximity to vehicle trails.—In examining the effects of habitat on the rate of nest predation, three major habitats were ex-

amined: recently burned open scrub (burned within last 20 years), unburned overgrown scrub (not burned for more than 20 years), and cattle pasture with scattered oak shrubs, palmetto clumps and tall pines. Although the daily rate of nest predation (individual acts) is similar for all three habitats, the rate at which nests ultimately failed because of predation differs significantly among habitats, with open scrub exhibiting the lowest rate (Table 1).

We analyzed the effects of proximity to vehicle trails on nest predation by dividing nests into two categories: those within 15 m of a vehicle trail, and those farther away. We consider it unlikely that a potential predator searching for prey from these trails would detect a nest beyond 15 m into the scrub. Analysis shows proximity to trails had no effect on nest predation. Nests within 15 m of vehicle trails experienced 104 individual acts of predation in 6,137 nest-days (0.017 acts/day), compared to 183 individual acts in 9,372 nest-days (0.019 acts/day; $G = 1.23, P > 0.25$). Over the entire breeding cycle 54 of 172 nests (31.4%) within 15 m of a trail ultimately failed because of predation, compared to a similar 85 of 271 (31.4%) of the more distant nests ($G = 0.00, P > 0.9$).

Effects of season, nest stage, and time of day.—All three methods of calculating daily rates indicate that nest predation increased as the season progressed (Fig. 1). Daily rates of predation, calculated by the number of individual acts, the number of ultimate failures, and the number of instantaneous failures were all significantly correlated with the advance of the breeding season ($r_s = 0.96, 1.00, \text{ and } 0.96$, respectively; $n = 7, P < 0.05$ for all).

Predators took relatively more nestlings than eggs (Fig. 2). The overall daily rate of egg pre-

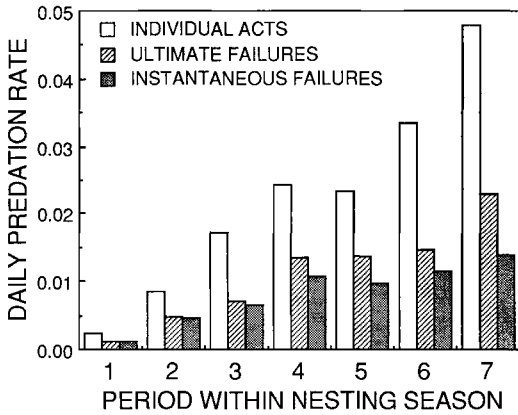


Fig. 1. Daily predation rates on nests of Florida Scrub Jays calculated three different ways (1974–1979 and 1981–1987 combined). Half-month periods within nesting season are: (1) 9–24 March, (2) 25 March–8 April, (3) 9–23 April, (4) 24 April–8 May, (5) 9–23 May, (6) 24 May–7 June, and (7) 8–23 June.

dation of 0.0072 (66 individual acts in 9,204 nest days) was significantly lower than the overall daily rate of nestling predation of 0.0285 (212 individual acts in 7,428 nest days; $G = 117.06$, $P < 0.001$). Furthermore, the rate of predation on nestlings was higher than that on eggs during six of the seven half-month periods of the nesting season (Wilcoxon $T = 1$, $n = 7$, $P = 0.028$). Similar results were obtained in analyses controlling for age and experience of breeders (Schaub 1990).

Young nestlings (day 8 or younger) were taken by predators more often than older nestlings

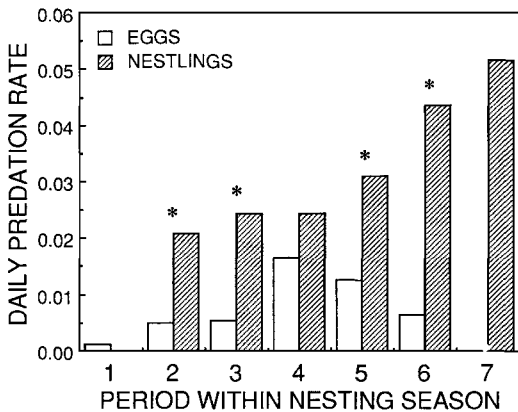


Fig. 2. Daily predation rates (individual acts) on eggs and nestlings of Florida Scrub Jays (1974–1979 and 1981–1987 combined). Asterisks indicate a log-likelihood ratio $P < 0.05$. Half-month periods within nesting season as in Figure 1.

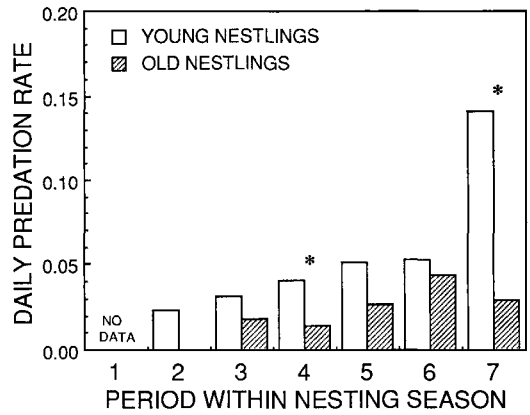


Fig. 3. Daily predation rates (individual acts) on young (day 8 or younger) and old (day 9 or older) nestlings of Florida Scrub Jays (1974–1979 and 1981–1987 combined). Asterisks indicate a log-likelihood ratio $P < 0.05$. Half-month periods within nesting season as in Figure 1.

(Fig. 3). The overall daily rate of predation on the younger nestlings (0.0404, 115 individual acts in 2,847 nest days) was significantly greater than for older nestlings (0.0214, 40 individual acts in 1,869 nest days; $G = 13.53$, $P < 0.001$). Predation rates on younger nestlings consistently exceeded that on older nestlings during all six half-month periods for which data were available (Wilcoxon $T = 0$, $n = 6$, $P = 0.032$) and were significant for two periods (log-likelihood ratio $P < 0.05$).

Dawn and dusk nest checks allowed 32 individual acts of predation at 41 nests to be categorized as either diurnal ($n = 23$) or nocturnal ($n = 9$). Thus, diurnal predation occurred more than twice as often as nocturnal predation, and the difference is significant ($X^2 = 5.28$, $df = 1$, $P < 0.025$). Because some acts of predation categorized as nocturnal may have occurred in the dim light shortly before the early morning nest checks or after the evening nest checks, the true frequency of diurnal predation may have been even higher.

Activity of potential nest predators.—Track censuses revealed that most of the potential mammal nest predators were active at night, and most of the potential snake nest predators were active during the day. In 1987, 1,814 of 1,846 (98.3%) mammal tracks were made between the evening and morning track censuses, compared to just 31 of 544 (5.7%) snake tracks ($G = 1,996$, $P < 0.0001$). Furthermore, some of the few snake tracks counted during the morning censuses may

TABLE 2. Rates of individual acts of predation (1974–1979 and 1981–1987 combined) and rates of potential nest-predator activity (1987).

Half-month periods	Acts of predation ^a	Predator activity ^b				
		All predators	Nocturnal mammals	Diurnal birds	Diurnal snakes	Diurnal snakes and birds
9–24 March	2/870 0.0023	259/565 0.46	196/263 0.75	32/223 0.15	23/79 0.29	55/302 0.18
25 March–8 April	30/3,556 0.0084	280/555 0.50	175/213 0.82	31/225 0.14	67/117 0.57	98/342 0.29
9–23 April	85/4,951 0.0172	630/584 1.08	464/202 2.30	62/224 0.28	95/158 0.60	157/382 0.41
24 April–8 May	87/2,067 0.0243	458/559 0.82	292/194 1.51	76/200 0.38	84/163 0.52	160/363 0.44
9–23 May	48/2,067 0.0232	339/418 0.81	222/141 1.57	35/176 0.20	80/101 0.79	115/277 0.42
24 May–7 June	44/1,312 0.0335	474/434 1.09	309/152 2.03	36/132 0.27	93/150 0.62	129/282 0.46
8–23 June	21/439 0.0478	242/245 0.99	136/81 1.68	20/78 0.26	71/85 0.84	91/163 0.56
r_s with period in season		0.68	0.61	0.39	0.86	0.96
P		> 0.05	> 0.05	> 0.10	< 0.025	= 0.0025
r_s with predation rate		0.71	0.57	0.54	0.71	1.00
P		= 0.05	> 0.10	> 0.10	= 0.05	< 0.005

^a Individual acts of predation per number of nest-days.

^b For mammals and snakes tracks/tracking hour; for birds sightings/field hour, and rates for both.

have been made during the brief periods of light before the morning censuses or, more likely, after the evening censuses. Most of the mammal tracks (>80%) were made by raccoons (*Procyon lotor*).

When all track counts and avian predator sightings were combined to form an index of the activity of all potentially important nest predators, no significant correlation exists with the advance of the nesting season, but one does exist with the rate of nest predation as measured with individual acts (Table 2). Neither an index of nocturnal mammal predator activity nor an index of diurnal avian predator activity is significantly correlated with the advance of the nesting season or the rate of individual acts of nest predation. Diurnal snake activity, however, is significantly and positively correlated with both the advance of the nesting season and with the rate of nest predation (individual acts). Because most nest predation is diurnal, the activities of diurnal snakes and birds are combined into a single index of potential diurnal predator activity. The activity rate of diurnal snakes and birds was significantly correlated with the advance of the nesting season and was perfectly correlated with the rate of individual acts of nest predation (Fig. 4).

Effects of helpers.—In general, the presence of

helpers had little effect on rates of individual acts of nest predation (Fig. 5). However, during the final month of the breeding season, pairs without helpers experienced significantly higher rates of nest predation than pairs with helpers (Fig. 5A). This apparent effect of helpers on late-season nest predation was attributable to a significantly reduced rate of predation on nests with nestlings, but not nests with eggs (Figs. 5B and 5C).

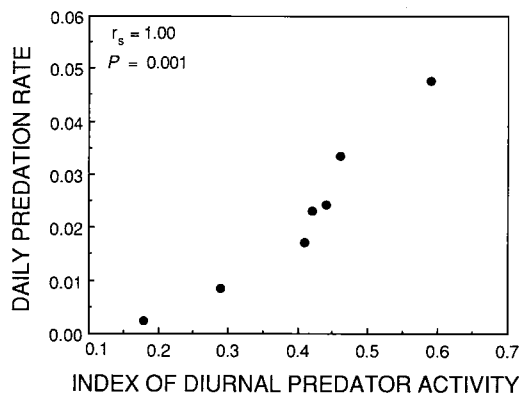


Fig. 4. Relationship between an index of diurnal predator activity and daily predation rates (individual acts) during seven half-month periods of nesting season shown in Table 2.

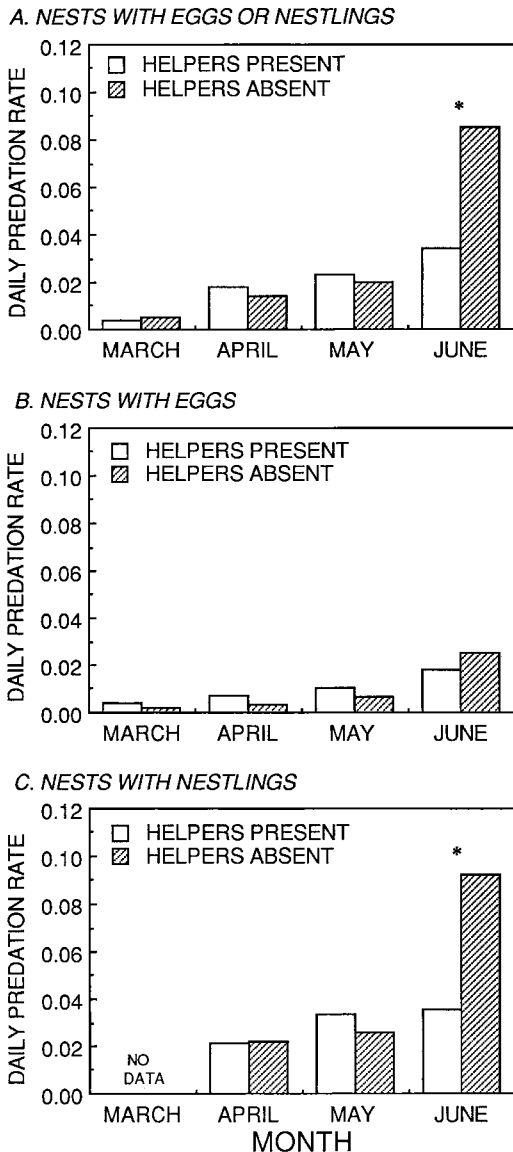


Fig. 5. Daily predation rates (individual acts) on nests with (A) eggs or nestlings, (B) eggs, and (C) nestlings for Florida Scrub Jay pairs with helpers present and helpers absent (1974–1979 and 1981–1987 combined). Nests belonging to novice and senescent breeders excluded from analysis. Asterisks indicate a log-likelihood ratio $P < 0.05$.

DISCUSSION

Identifying the predators.—The eggs and nestlings of Florida Scrub Jays are potential food for many possible predators. The continuing 22-year study of Scrub Jays at Archbold Biological Station (Woolfenden and Fitzpatrick 1990) has

implicated several species. One snake, the eastern coachwhip (*Masticophis flagellum*) is known to take nestlings (Westcott 1970), and it and the eastern indigo snake (*Drymarchon corais*) are known to take fledglings (Webber 1980, Mumme 1987). Convincing evidence of nest predation, including direct observations, also exist for the Red-tailed Hawk (*Buteo jamaicensis*), Eastern Screech-Owl (*Otus asio*), Great Horned Owl (*Bubo virginianus*), and bobcat (*Lynx rufus*), as well as for the Northern Harrier (*Circus cyaneus*), a northern migrant which may be present through late spring. Despite the enormous number of hours of field observations, the relative importance of these and other potential Scrub Jay nest predators (e.g. Swallow-tailed Kites, *Elanoides forficatus*; Fish Crows, *Corvus ossifragus*; Blue Jays, *Cyanocitta cristata*; and raccoons) has been unclear (Schaub 1990).

Our study, however, has produced several lines of evidence indicating that mammalian predators are relatively less important than are snakes and birds. First, twice-daily nest checks and track censuses indicate that, although at least two-thirds of the predation on Florida Scrub Jay nests occurs during daylight hours, potential mammalian predators are overwhelmingly nocturnal in their activity patterns. Second, results from radio-tracking studies conducted at ABS indicate that potential mammalian predators such as bobcats and raccoons commonly use vehicle trails as avenues for travel (Worley 1980, Wassmer et al. 1988). If bobcats and raccoons were important as predators upon jay nests, proximity of nests to the trails might correlate with increased nest predation (Best 1978, Kerppe and Herzog 1978). However, we found that the rate of Scrub Jay nest predation is not affected by proximity to vehicle trails. In fact, jays regularly place their nests at the edges of clearings, including trail edges (Woolfenden 1974). Finally, seasonal activity rates of potential mammalian predators were not significantly correlated with nest predation rates (Table 2). Therefore, we conclude that although bobcats, raccoons, and other mammals undoubtedly depredate some jay nests, they appear to be less important nest predators than snakes and birds.

The snakes we observed most frequently in Scrub Jay habitat at ABS were the eastern indigo, eastern coachwhip, and southern black racer (*Coluber constrictor*), although virtually all the racers we saw were too small to pose a significant threat. Florida pine snakes (*Pituophis*

melanoleucus) also were observed, but less frequently. All of these species are primarily diurnal (Ernst and Barbour 1989), and 94% of the snake tracks we recorded were made during daylight. We suspect that the coachwhip, a large, locally common snake that easily traverses shrubbery and is strictly diurnal (Ernst and Barbour 1989), is the most frequent snake predator of the jays.

As shown in Table 2, an index of diurnal predator activity is strongly correlated with nest predation rates. Because it combines data obtained from both visual sightings and track counts, and includes several species of birds and snakes that vary in conspicuousness, this index is at best only a crude measure of relative predator activity and should be viewed with caution. Nonetheless, the correlation between the index of diurnal predator activity and nest predation is striking (Fig. 4). Activity of the snakes alone shows a significant correlation both with the progression of the jay nesting season and with jay nest-predation rates. However, activity of the diurnal bird nest predators does not correlate significantly with either of these features of jay nesting. Because snakes are ectotherms, their activity would be expected to increase over the course of the March–June Scrub Jay breeding season. Thus, the positive correlations among snake activity, date within the nesting season, and nest predation rates (Table 2, Figs. 1 and 4) suggest that, although diurnal snakes and birds are frequent nest predators, snakes are relatively more important in our system.

Factors influencing nest predation.—Predators may use visual, auditory, or olfactory cues provided by researchers to locate bird nests. Therefore, in studies of nesting success, it is important to determine the effect that investigator visitation has on the rate of nest predation (Best 1978, Gottfried and Thompson 1978, Wray et al. 1982, Westmoreland and Best 1985, Martin and Roper 1988). We addressed this problem in 1987 by visiting samples of nests on two schedules. All nests were checked in the same manner, during one season, and mostly by the same person. Predation rates did not differ significantly between nests visited twice daily and those visited every third day. Although nest visits at three-day intervals may influence predation rates (Westmoreland and Best 1985), we conclude that within the strictures of our experiment, the frequency of investigator visits had no influence on the rate of nest predation.

Nest mortality usually is greater on nests with eggs than on nests with nestlings (Martin in press). However, our data show that Florida Scrub Jay nests experience significantly greater predation when they have young than when they have eggs, and this trend is consistent throughout the nesting season (Fig. 2). Adult jays visit nests more frequently when tending young than when incubating eggs (Schaub 1990). Nestling jays beg frequently and loudly, and move about in the nest. Increased activity may make nests with young easier to locate by certain predators and may contribute to the higher predation rates (Hammond and Forward 1956, Young 1963, Horn 1968, Knight and Temple 1986). Furthermore, this study has implicated snakes as the primary nest predator. Because many snakes locate prey by olfaction, in addition to vision (Ashton and Ashton 1981), increased olfactory cues emitted by nestlings might further facilitate their detection.

Our results also indicate that when seasonal effects are controlled, younger nestlings experience a greater rate of predation than do older nestlings (Fig. 3). This difference may reflect the decreased susceptibility of older nestlings to certain predators (e.g. Blue Jays, small snakes) and increased parental defense of nests with older nestlings (Montgomerie and Weatherhead 1988). Another possibility is that the more susceptible nests are found when nestlings are young.

Rates of nest predation have been found to decrease with nestling age in relatively few species (e.g. Holcomb 1972). However, several of the studies reporting nest-predation rates increasing with nestling age did not control for the effect of season (e.g. Young 1963, Best 1978, Woolfenden and Fitzpatrick 1984). Thus, the increased mortality on older nestlings observed in these studies may occur because older nestlings tend to be present later in the breeding season when predation rates are higher.

Nests ultimately failed because of predation more often in shrubby pastures and overgrown scrub than in open, recently burned scrub. Fitzpatrick and Woolfenden (1986) reported similar results. However, the daily rate of individual acts of predation does not differ significantly among the three habitats (Table 1). It appears that individual acts of nest predation are more likely to lead to complete nest failure in pasture and overgrown scrub than in recently burned scrub. It is unknown whether this is due to

among-habitat differences in the behavior of predators, among-habitat differences in nest defense by jays, or both.

Effects of helpers.—Florida Scrub Jay pairs assisted by helpers had a significantly lower rate of nest predation than pairs without helpers only during the last month of the breeding season, and only for nests with nestlings (Fig. 5). Our analysis, which controlled for age and experience of breeders, thus suggests that helpers were effective at reducing predation rates only when the predation pressure was at its greatest intensity (Fig. 1).

How could the presence of nonbreeding helpers reduce predation on nestlings? Although Florida Scrub Jays are almost certainly incapable of defending their nests against attacks by nocturnal predators (Woolfenden and Fitzpatrick 1984), our study has shown that most nest predation is attributable to diurnal snakes and birds. Helpers could reduce the frequency of successful attacks by these diurnal predators by serving as sentinels near nests and by mobbing potential predators once they have been detected (Francis et al. 1989, McGowan and Woolfenden 1989, Mumme in press).

The finding that helpers did not significantly reduce the rate of predation on eggs is not surprising; nonbreeders normally do not participate in reproductive activities until after hatching. In fact, breeders usually chase potential helpers away from the immediate vicinity of the nest during laying and incubation (Stallcup and Woolfenden 1978). Furthermore, nonbreeders have been seen to remove eggs from the nests of the pairs with which they are associated (Woolfenden 1974). Although the results of Woolfenden and Fitzpatrick (1984) suggest that the presence of helpers reduces predation on eggs, our analysis—which employed a more extensive data set and controlled for the potentially confounding effects of season, breeder experience, and senescence—shows no such effect.

Woolfenden and Fitzpatrick (1984:204) reported that helpers significantly enhance survival of eggs and nestlings only during the season's first nesting attempt. For seasonal re-nests, helpers had no significant influence on the survival rates. Our analysis differs from theirs in at least one important respect; we investigated seasonal influences by examining nest predation in monthly and half-monthly intervals, regardless of whether a particular nest was a first

nest or a re-nest. Our analysis indicates that helpers reduced nest predation only during the final month of the nesting season. We propose that the results of Woolfenden and Fitzpatrick (1984), suggesting that helpers enhance reproduction of the first attempts, may have been confounded by correlated differences in breeder experience. Pairs without helpers are frequently inexperienced breeders that do not begin nesting until late in the season, when nest predation rates are high and success rates are low (Woolfenden and Fitzpatrick 1984:216). Thus, the higher survival observed in seasonal first nests produced by pairs with helpers may be attributed to breeder experience rather than to the effects of helpers per se. In contrast, the analysis reported in this paper examined helper effects while controlling for age and experience of breeders.

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