

# PREDATION ON NORTHERN CARDINAL NESTS: DOES CHOICE OF NEST SITE MATTER?<sup>1</sup>

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**Abstract.** The fates of 121 nests of Northern Cardinals (*Cardinalis cardinalis*) in southwestern Ohio were determined in 1991 and 1992. Success rate was only 15%, estimated by the Mayfield method. All failed nests were known or suspected to have been preyed upon. Several hypotheses to explain differences between the location of successful and failed nests were tested. None of those considered explained why the contents of particular nests were taken. We propose that a high incidence of predation by a rich guild of nest predators precludes the existence of predictably safe nest sites for cardinals. Instead, cardinals appear simply to be well-adapted to renest rapidly in response to the near randomness of nest predation. A similar adaptation may characterize many passerines.

**Key words:** *Northern Cardinal*; *Cardinalis cardinalis*; *nesting success*; *nest site selection*; *nest predation*.

## INTRODUCTION

Selection of nest site may be of crucial importance to the reproductive success of birds. Lack (1954) estimated that 75% of all eggs and nestlings lost from open cup nests are taken by predators. Ricklefs (1969) estimated predation percentages in six passerine species and concluded that predation accounted for 55% of egg losses and 66% of nestling losses. Many aspects of the nesting behavior of birds appear to be adaptations to avoid predation of the nest contents. Many birds hide their nests or build them in inaccessible sites (Collias and Collias 1984). In addition, the behavior of parent birds visiting nests is notably stealthy (Skutch 1976, Breitwisch et al. 1989). Active defense against predators also occurs in some species of birds, but defense entails a risk of injury to or death of the parent. Clearly, birds may be advantaged by selecting sites where nests will be unlikely to be found by predators.

Northern Cardinals (*Cardinalis cardinalis*) are multibrooded, and females lay up to five clutches in a season, of which as many as four have been recorded as successfully fledging (Shaver and Roberts 1930, Laskey 1944). The female usually builds the entire nest (Laskey 1944, Burns 1963,

Bent 1968, Kinser 1973) and builds a new nest in a different location on the territory for each nesting attempt. Females also appear to be the sex that selects nest sites (Kinser 1973; however, see Laskey 1944).

Every passerine studied to date displays some intrapopulational variation in nest site selection. Some studies have revealed patterns in this variation associated with the probability of success (see Martin and Roper 1988), while others have not (e.g., Best 1978, Barnard and Markus 1990, Morton et al. 1993; see also Gottfried and Thompson 1978 for an experimental study). We attempted to test predictions of eight hypotheses for the placement of successful versus unsuccessful nests by cardinals. These hypotheses address losses to predators only; losses due to abiotic environmental factors are not considered here. In addition, our assumption is that predators find nests by actively searching for them rather than by simply watching parent birds attend to the needs of eggs or nestlings (Collias and Collias 1984, Martin 1988a).

The "nest concealment" hypothesis predicts that nests that are concealed regardless of the particular plant structure will be more successful than those that are not so concealed. The "nest inaccessibility" hypothesis predicts that nests that are less accessible (but not necessarily better concealed) will be more successful than those that are more accessible. Inaccessible nests in this study are defined as those over water, in thorny vegetation, among cane (*Arundinaria* sp., a woody herb), or at the end of thin branches or twigs (cf.

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Collias and Collias 1984). The "nest height" hypothesis predicts that nests placed high or low relative to the frequency distribution of nest heights in the population will be more successful than those of more typical height. The first prediction (high nests are more successful) assumes that nests built high in plant crowns are concealed better than nests built lower, especially as the breeding season progresses and plants leaf out (Nolan 1978), and, in this sense, is a version of the nest concealment hypothesis. Such nests may also be found less frequently by or be less accessible to terrestrial predators than lower nests. The second prediction (low nests are more successful) assumes that aerial predators are of major importance and are less successful in either finding or accessing low nests. The "mid-height" hypothesis predicts that nests placed at mid-height in a tree or shrub will be more successful than those placed either higher or lower in the plant. This hypothesis assumes that nests built higher are more easily seen by aerial predators, while those built closer to the ground are located more easily by mammals and snakes (see Alonso et al. 1991). The "needle in a haystack" hypothesis predicts that nests placed in a common species of plant will be more successful than those that are placed in uncommon plant species (see Martin and Roper 1988). If a predator restricts its search for nests to a few appropriate plant species, then nests in the most common plant species will be more difficult to find because there are more individual plants to search. The "rare site" hypothesis predicts that nests placed in uncommonly used plant species will be more successful than those placed in commonly used plants. If a predator searches plant species commonly used for nesting, then it is best to be atypical and nest elsewhere. This hypothesis differs from the others in that success depends on where other members of the population are nesting (as proposed among species for communities of nesting birds by Martin 1988b). The "edge distance" hypothesis predicts that nests farther from a habitat edge (defined here as where a closed habitat changes obviously to another more open habitat, e.g., forest to field) will be more successful than those placed closer to an edge. The distance to habitat edge is important because some mammalian and avian predators actively search near these edges (Gates and Gysel 1978). Furthermore, Brown-headed Cowbird (*Molothrus ater*) parasitism (which can be viewed as a

form of predation) increases from forest interior to forest edge (Brittingham and Temple 1983). The "distance to human activity" hypothesis predicts that nests placed closer to areas of human activity will be more successful than those that are farther away (Collias and Collias 1984). Human activity may discourage predators from searching near heavily used trails and in other areas frequented by people. We added this hypothesis and tested it in late 1991 and 1992 after finding that successful nests tended to be closer to areas of human activity than unsuccessful nests earlier in 1991.

## STUDY SITE AND METHODS

This study was conducted at the Aullwood Audubon Center and Farm, located about 15 km northwest of Dayton, Ohio (39°52'N and 84°16'W) from April to August 1991 and 1992. The Aullwood property is an 80 ha sanctuary with habitats in the following proportions: 26% croplands and orchards, 17% mature woodlands (dominated by beech, *Fagus* spp.; oaks, *Quercus* spp.; maple, *Acer* spp.; and buckeye, *Aesculus glabra*), 17% secondary growth (e.g., ash, *Fraxinus* spp.; and maple), 16% pasture, 8% meadow, 5% prairie, 5% residential area, 2% pine plantings, 2% wetlands and 2% wet woods (e.g., ash and red maple, *Acer rubrum*) (J. Ritzenhaler, pers. comm.); see Filliater-Lee (1992) for further details on vegetation. Cardinals frequent nearly all habitats on the property and most densely populate secondary growth and edges of wooded areas.

We discovered nests by intensively searching at least every other day and by following the "chipping" vocalizations of adult cardinals (Lemon 1968, Montgomerie and Weatherhead 1988). Nearly all nests were observed daily to record progress. Many nests were observed through 10 × 40 binoculars at a distance of 5–15 m. We recorded nest height and tree or shrub height with a meter stick to 0.1 m where possible and estimated where necessary (nests in dense multiflora rose [*Rosa multiflora*] or higher than several meters). In addition, in late 1991 and in 1992, we estimated distance to the closest area of human activity to 0.5 m. Human activity areas were defined as trails (most are heavily used) and other areas frequented by people. Although some clearings were foci of human activity, distance to the nearest clearing for any particular nest may

have been different from that to the closest area of human activity.

We recorded nest visibility from six vantage points (above, below, and from four horizontal directions [N, S, E, W]) at a distance of 1–2 m using the following classification scheme: “visible” (visible from five or six vantage points), “ambiguous” (visible from three or four), and “not visible” (visible from none to two). Although this division is somewhat subjective, two observers agreed on the visibility of each nest.

The details of placement of each nest in vegetation were recorded in order to address the concealment and inaccessibility hypotheses. In addition to the direct measurements of visibility, we recorded if the nest was built < 10 cm below leaves, very effectively concealing it from above (a nest not so located could still be “not visible” from above at a distance of 1–2 m). As mentioned in the introduction, a nest was also classified in terms of accessibility.

We recorded all measurements only after each nest had failed or succeeded, in order to avoid possible disturbance. We recorded the date of failure or success as the first day the nest was found to be inactive, i.e., when eggs or nestlings disappeared due to predation or when fledglings were found in the vicinity of the nest. Nests discovered inactive after a two day or rarely three or more day gap in observations were considered inactive at the midpoint of the hiatus. We considered any nest fledging at least one young as successful. All nest failure appeared to be due to predation rather than to any other cause, such as violent weather (one nest failed due to uncertain cause).

Nests were discovered at various stages in the nesting cycle, and the majority were already at the egg or nestling stage. Such biased discovery can lead to an overestimate of the true nesting success in a population. Therefore, we calculated total nest-days of observation for three stages: (1) nest-building and egg-laying, (2) egg incubation, and (3) nestling periods, and used Mayfield's (1975) calculation for success.

All univariate statistical analyses employed non-parametric tests. Tests of independence ( $G_{adj}$  value reported) were used to ask if associations existed between pairs of variables; all were corrected due to small sample sizes by using Williams' correction (Sokal and Rohlf 1981). Mann-Whitney U Tests ( $z$  value reported) and Median Tests ( $\chi^2$  value reported) were used to compare

central tendencies. Kolmogorov-Smirnov 2-sample tests ( $D_{max}$  value reported) were used to compare shapes of frequency distributions (Siegel and Castellan 1981). Spearman rank correlations ( $r_s$  value reported) were used for tests of monotonic relationship. Results are reported as significant if they are associated with an alpha value of  $P < 0.05$ . All tests were two-tailed. Means  $\pm$  SD are reported for descriptive statistics.

We also conducted a series of eight parametric discriminant function analyses (SAS 1989) of nest site variables to compare successful with failed nests. This series included analyses with as few as two independent variables and as many as seven. The discriminant function analyses do not directly address the predictions of the individual hypotheses but rather search for a combination of variables that is associated with successful nesting.

Data from the two years of the study were pooled for analysis after testing for differences in nest variable distribution between years. Except where noted, no differences were found between years.

## RESULTS

### GENERAL

We found 121 active cardinal nests, 43 in 1991 and 78 in 1992. Cardinals nested in 22 species of plants. Seventy-nine of the 121 nests (65%) were built in the dense shrubs multiflora rose and honeysuckle (*Lonicera* spp.). Eight of the remaining nests (7% of total) were built in red cedar (*Juniperus virginiana*). Only 30 of the 121 nests (25%) were successful.

### SURVIVAL RATE

The mortality rate (Mayfield 1975) for the nest-building/egg-laying period was 0.074 failures per nest-day (14 failures/188.5 nest-days), and the survival rate for this 5-day period was 0.68 ( $= [1 - 0.074]^5$ ). The mortality rate for the egg incubation period (=14 days) was 0.065 failures per nest-day (42 failures/644.5 nest-days), and the survival rate for this period was 0.39. The mortality rate for the nestling period was 0.054 failures per nest-day (17 failures/313 nest-days), and the survival rate for this period (=10 days) was 0.57. In this population, the overall success rate was 15% ( $0.68 \times 0.39 \times 0.57 \times 100\%$ ).

### TIME OF SEASON

Before testing hypotheses for nest success versus failure, we examined the relationship between probability of success and date in the season. We found the first nest of each season at the end of April and the last nest each season in the middle of August. The temporal distributions of nests monitored in the two years had similar means ( $z = 0.88, P > 0.05$ ). Overall, we monitored six nests in April (none of which fledged), 54 nests in May (eight fledged), 34 nests in June (12 fledged), 24 nests in July (eight fledged), and three nests in August (two fledged). We compared "early" and "late" nests, conducting Median tests for seasonal changes where correlations with date of season were inappropriate. Nests "early" in the season were built in April–May, and nests "late" in the season in June–August. The probability of success was greater late in the season ( $\chi^2 = 7.21, df = 1, P < 0.05$ ). Similarly, there was a trend between month of the breeding season and probability of nest success ( $r_s = 0.92, n = 5, P < 0.05$ ), although the sample sizes for April and August were small.

### NEST CONCEALMENT HYPOTHESIS

We classified 55 nests (45%) as visible, 31 (26%) as not visible, and 35 (29%) as ambiguous regarding visibility. We also classified 40 nests (33%) as located < 10 cm below leaves and thus not visible from above. We ranked nest concealment in six categories from most to least visible: (1) nest visible and not located below leaves, (2) nest visible but below leaves, (3) nest ambiguous and not below leaves, (4) nest ambiguous and below leaves, (5) nest not visible but not below leaves, and (6) nest not visible and below leaves.

We found no correlation between nest concealment and the proportion of successful nests ( $r_s = -0.14, n = 6, P > 0.05$ ). Twelve of 45 (27%) category 1 nests, four of 10 (40%) category 2 nests, two of 18 (11%) category 3 nests, four of 17 (24%) category 4 nests, four of 18 (22%) category 5 nests, and four of 13 (31%) category 6 nests were successful. Furthermore, there was no association between "visibility" regardless of leaf cover and probability of success ( $G_{adj} = 1.69, df = 2, P > 0.05$ ) or between leaf cover regardless of visibility and probability of success ( $G_{adj} = 0.83, df = 1, P > 0.05$ ). However, a higher proportion of nests had leaf cover in 1991 than in

1992 ( $G_{adj} = 12.18, df = 1, P < 0.05$ ), and a higher proportion of nests with leaf cover were successful in 1991 than in 1992 ( $G_{adj} = 4.82, df = 1, P < 0.05$ ). Yet, there was no difference between years in the proportion of successful nests for those without leaf cover ( $G_{adj} = 0.11, df = 1, P > 0.05$ ). Similarly, there was no difference in the probability of success whether nests were visible or not from above ( $G_{adj} = 0.017, df = 1, P > 0.05$ ) or visible or not from below ( $G_{adj} = 0.44, df = 1, P > 0.05$ ).

There was no correlation between visibility and date in the season ( $r_s = 0.13, n = 121, P > 0.05$ ) and no association between leaf cover and date in the season ( $G_{adj} = 0.10, df = 1, P > 0.05$ ). There was also no difference in successful vs failed nests in the distance from the nest to the nearest outer edge of the plant's foliage ( $z = 1.39, P > 0.05$ ). The mean distance for all nests was  $0.47 \pm 0.48$  m. However, cardinals built deeper in vegetation in 1992 than in 1991 ( $z = 3.11, P < 0.05$ ).

### NEST HEIGHT HYPOTHESIS

We tested for an association between nest height and success by both a test of central tendency and a distribution test. The mean nest height was  $2.1 \pm 1.6$  m (range: 0.7–12 m). The mean nest height for successful nests was  $2.7 \pm 2.6$  m and for failed nests  $1.9 \pm 1.0$  m ( $z = 0.47, P > 0.05$ ). There was also no difference in the shapes of the frequency distributions ( $D_{max} = 0.156, P > 0.05$ ).

There was a correlation between the height of the nest and date in the season in both years ( $r_s = 0.26, n = 121, P < 0.05$ ). Cardinals built nests higher as the season progressed.

### MID-HEIGHT HYPOTHESIS

The height of each nest in the plant divided by the height of the plant gave the relative height of each nest in the tree or shrub. The mean height of nests was 2.1 m (see above), and the mean height of trees and shrubs in which nests were built was  $3.8 \pm 2.9$  m (range: 1.1–20 m). The mean relative height of nests was  $0.60 \pm 0.20$  (range: 0.13–0.96). Successful nests were located at similar relative heights as failed nests ( $z = 0.92, P > 0.05$ ). Similarly, there was no difference in the shapes of the frequency distributions for relative heights of successful vs. failed nests ( $D_{max} = 0.136, P > 0.05$ ).

We tested for an association between date in the season and the location of the nest in the

plant. Cardinals built nests relatively higher in plants as the season progressed ( $r_s = 0.42$ ,  $n = 121$ ,  $P < 0.05$ ). We tested for a difference in the proportionate height of successful vs. failed nests for both early and late nests. There was no difference for either early nests ( $z = 1.48$ ,  $P > 0.05$ ) or late nests ( $z = 0.71$ ,  $P > 0.05$ ).

Second, we found a correlation between proportionate height and visibility for each half of the season and for the entire season ( $r_s = 0.35$ ,  $n = 121$ ,  $P < 0.05$ ). Relatively higher nests were less visible than lower nests.

Third, we tested for an association between proportionate height and leaf cover for early and late nests. Nests located high in a plant were more likely to be covered by leaves if they were built early in the season ( $G_{adj} = 9.22$ ,  $df = 1$ ,  $P < 0.05$ ), but this was not so for nests built later in the season ( $G_{adj} = 2.43$ ,  $df = 1$ ,  $P > 0.05$ ).

#### EDGE DISTANCE HYPOTHESIS

There was no difference in the distance of successful vs. failed nests from the nearest edge of open habitat. Successful nests were a mean  $3.4 \pm 4.2$  m from habitat edge, and failed nests a mean  $4.6 \pm 6.2$  m ( $z = 0.82$ ,  $P > 0.05$ ). Nests in 1991 were a mean  $2.0 \pm 2.2$  m from habitat edge, and those in 1992 were  $5.6 \pm 6.6$  m ( $z = 4.28$ ,  $P < 0.05$ ). In neither year was the probability of success related to the distance from the nest to habitat edge.

#### NEST INACCESSIBILITY HYPOTHESIS

Similar proportions of inaccessible nests (23%) and accessible nests (26%) were successful. There was no association between accessibility of the nest and the probability of success in either year or for the years pooled ( $G_{adj} = 0.10$ ,  $df = 1$ ,  $P > 0.05$ ). However, a higher proportion of inaccessible nests were successful in 1991 than in 1992 ( $G_{adj} = 4.56$ ,  $df = 1$ ,  $P < 0.05$ ). Accessible nests were no more successful in one year than the other ( $G_{adj} = 0.78$ ,  $df = 1$ ,  $P > 0.05$ ).

Furthermore, there was no relationship between the proportion of accessible nests and the date in the season. Forty-nine percent of inaccessible nests and 50% of accessible nests were built early in the season ( $G_{adj} = 0.02$ ,  $df = 1$ ,  $P > 0.05$ ).

#### NEEDLE IN A HAYSTACK AND RARE SITE HYPOTHESES

These hypotheses cannot be tested directly. Cardinal predators likely include snakes, small

mammals, and predatory birds (Kinser 1973), but we do not know whether these predators restrict their search to a few, commonly used plant species. Further, we did not map the vegetation of the Aullwood property and do not know relative abundances of plant species.

However, the three most common species on the study site are multiflora rose, honeysuckle, and ash (J. Ritzenthaler, pers. comm.), and the first two were frequently chosen as nest sites by cardinals. In both 1991 and 1992, 65% of the nests were built in these two species. We tested for an association between plant species and probability of nest success by dividing all nests into two categories: those in the two common shrubs and those in all other species. The probability of success was not associated with species category; 22% of nests in the common shrubs were successful vs. 31% of those in other species ( $G_{adj} = 1.25$ ,  $df = 1$ ,  $P > 0.05$ ).

There was no difference in relative use of common species from early to late in the season ( $G_{adj} = 0.006$ ,  $df = 1$ ,  $P > 0.05$ ). Forty (51%) of 79 nests in common species and 19 (51%) of 37 nests in other species were constructed early in the season.

#### DISTANCE TO HUMAN ACTIVITY HYPOTHESIS

Human activity in the study area is restricted to particular sites, in addition to heavily-used paths. The mean distance of successful nests from human activity areas was  $6.2 \pm 7.3$  m (range: 0–25 m,  $n = 23$ ), and of failed nests was  $8.7 \pm 9.9$  m (range: 0.4–50 m;  $n = 73$ ) ( $z = 1.35$ ,  $P > 0.05$ ). There was no correlation between distance of a nest to human activity and date in the season ( $r_s = -0.14$ ,  $n = 96$ ,  $P > 0.05$ ).

#### MULTIVARIATE ANALYSES

None of the discriminant function analyses yielded a combination of variables associated with successful nesting. In each of the eight analyses, at least 34% of the nests were incorrectly assigned status of successful or failed (and as many as 48% in one analysis). These results thus agreed with those of the univariate analyses.

#### DISCUSSION

None of the eight hypotheses for explaining cardinal nest success was supported by the results of this study. For this population, there seems to be neither a single nor a combined predictor

of nest success among the nest variables measured. Cardinals nonetheless appear to follow a few simple behavioral rules in placing nests: (1) provide some concealment for the nest, (2) build within a few m of the ground, (3) build the nest higher as the season progresses, and (4) build the nest relatively higher in plants as the season progresses. Although nests built later in the season tended to fare better than earlier nests, none of these behavioral rules is specifically associated with an increased probability of nest success. Conner et al. (1986) also failed to find a correlation between probability of cardinal nest success and either nest height or concealment. Similarly, Best (1978) and Morton et al. (1993) found what might be simple behavioral rules followed by nesting Field Sparrows (*Spizella pusilla*) and White-crowned Sparrows (*Zonotrichia leucophrys*), respectively, without effects on the probability of nesting success.

Variables related to nest site not measured in this study include the density and homogeneity of vegetation within a several m radius of the nest. Martin and Roper (1988) found that successful Hermit Thrush (*Catharus guttatus*) nests tended to be surrounded by similar vegetation as that in which the nest was placed. Kelly (1993) showed the same for Dusky Flycatchers (*Empidonax oberholseri*). Conner et al. (1986) found that more successful pairs of cardinals had territories with higher foliage density and patchiness at 2 m height (mean nest height was 1.6 m) than less successful pairs.

Cardinals in this population are subject to a high incidence of nest predation, similar to that found by Kinser (1973) and Best and Stauffer (1980). The conventional argument is that the high incidence of nest predation characteristic for passerines should select strongly for choice of less vulnerable nest sites (Best and Stauffer 1980, Martin and Roper 1988, Li and Martin 1991). For example, in a study of nesting success in riparian bird communities, Best and Stauffer (1980) found that species characterized by more "general" choice of nesting sites suffered higher nest predation rates than species with more restricted choice of sites. They interpreted the high incidence of predation as the consequence of generality in choice. We argue here for the opposite interpretation of causality: a high incidence of predation may be the cause of generality in choice of nest sites.

We propose that the usual strong-selection ar-

gument can be inverted: a rich guild of nest predators may—by its very diversity—eliminate predictably safe nest sites. This does not preclude the possibility that the simple behavioral rules suggested above for cardinals are an evolutionary response to selection for safe sites. Our proposal does, however, predict that such rules will be of only limited benefit in predator-rich communities. Predators search in different ways, and a safe site with respect to one predator may make the nest more vulnerable to a different predator. For instance, depredations by terrestrial predators should favor nests placed higher in vegetation, while predation by birds such as crows may well favor lower-placed nests. Although heavy predation pressure independent of predator diversity should also make avoidance of nest predation difficult, we suggest that the latter is the more important variable because diversity of predatory tactics forecloses options. As portrayed in Figure 1, this population of cardinals is then proposed to occupy a point in the foreground of the "selection landscape."

Cardinal nesting behavior in general appears to fit this scenario. Parents are weak defenders of eggs and nestlings against predators (Nealen and Breitwisch, unpubl. manuscript). Rather than risk injury or death in defense of the nest, cardinals are instead well-adapted for rapid re-nesting following predation. Nest intervals are as short as four days from nest loss to initiation of the next clutch (Scott et al. 1987), and the cardinal breeding season is long, from mid-April to mid-August. This allows as many as six nesting attempts in a single season (TSF, RB, PMN, unpubl. data).

There also appears to be a rich guild of predators on cardinal (and other passerine) eggs and/or nestlings in southwestern Ohio. These likely include Blue Racers (*Coluber constrictor*), Rat Snakes (*Elaphe obsoleta*), Milk Snakes (*Lampropeltis dolia*), Gray and Red Squirrels (*Sciurus carolinensis* and *Tamiasciurus hudsonicus*), Eastern Chipmunks (*Tamias striatus*), Blue Jays (*Cyanocitta cristata*), and American Crows (*Corvus brachyrhynchos*) (cf. Kinser 1973, Nolan 1978). A pattern of predation characterized by empty, undisturbed nests was common, and this observation does not exclude any of the above predators (I. Lovette, pers. comm.). As a group, snakes, small mammals, and birds also accounted for the majority of failed cardinal nests in another study (Best and Stauffer 1980).

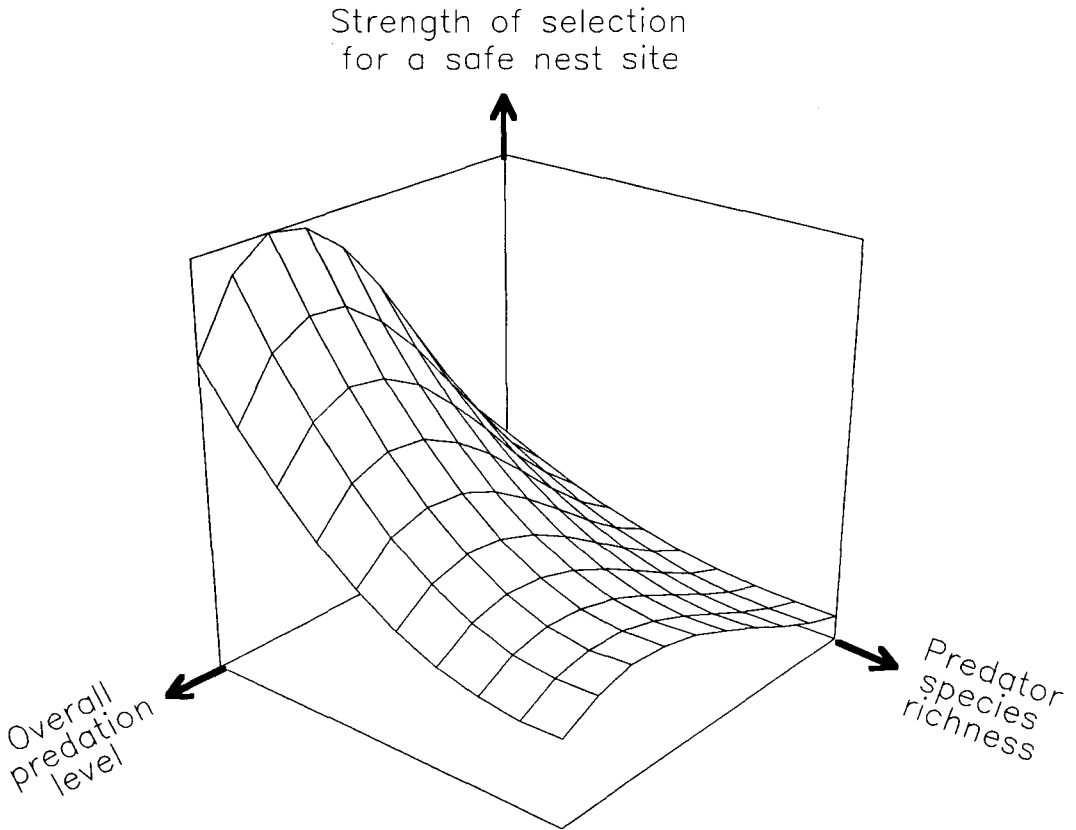


FIGURE 1. Strength of selection for a safe nest site is shown on the vertical axis as a function of both predator species richness and overall intensity of predation.

It is worth noting that the general design of nest predation studies probably favors finding some relationship between at least one variable related to nest site and probability of success. Most such studies include an array of variables, and as the number increases, it clearly becomes more likely that one or more will display a relationship with probability of nest success by chance alone (see Knopf and Sedgwick 1992). Consistency across years in the variables associated with success would be more persuasive than data gathered in a single breeding season.

It would also be instructive to have more information on the studies of nest predation that have *not* revealed patterns in nest site selection and success. When this occurs, the study is always subject to the criticism that the meaningful variables were simply not examined. Indeed, no revealed pattern may well increase the probability of the study not even being published (or

submitted for publication). Although the criticism of incorrect variables is an alternative interpretation of our own results, we contend that it is useful to put forward a novel interpretation.

We doubt that cardinals are unusual in being subject to a rich guild of nest predators. Further, their weak defense of offspring against predators is typical of many passerines (Nealen and Breitwisch, unpubl. manuscript; P. M. Nealen, unpubl. data). Finally, short relaying intervals following nest failure are also common in passerines (Scott et al. 1987 and references therein). Therefore, we predict that future research will show that many passerines nesting in predator-rich habitats display the same suite of aspects of nesting behavior as cardinals: simple behavioral rules for nest placement, weak defense of offspring, and rapid renesting following failure. We also predict that studies of nest sites and predation will frequently either fail to reveal interpretable

patterns or display "statistically significant" but biologically insignificant patterns of nest site selection and the success or failure of nests.

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