A Safe Nest?
Nest Predation and Nest Sites
New perspectives on old patterns

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Identifying causes of general patterns of habitat selection, species coexistence, and life-history traits are central issues in evolutionary ecology. Many organisms have been studied to address these issues, but no group has had a greater influence on current perspectives than birds (Konishi et al. 1989).

Rapid advances came a few decades ago with work by Lack (1948, 1954), Hutchinson (1957, 1959), and MacArthur (1958, 1972) and his associates (Cody and Diamond 1975). These investigators argued that competition and food limitation were the major underlying influences of habitat selection, species coexistence, and life-history traits among birds (reviewed in Martin 1986, 1987). In recent years, the ubiquity and importance of competition and food limitation have been debated (Salt 1983, Wiens 1989).

Nonetheless, although the competition paradigm has been challenged, alternative explanations are rarely explored for birds. New hypotheses need to be developed and examined, and they need to be directed at old and long-standing patterns that have been interpreted in the conventional perspectives of competition and food limitation.

In this article, I focus on nest predation as a process and nest sites as a resource. Predation is considered an important process in many systems (e.g., aquatic systems), but it has been neglected as an evolutionary process in avian systems (Martin 1988c, 1992b, Sih et al. 1985). This neglect of nest predation as an evolutionary force is surprising because population studies indicate that nest predation is pervasive; nest predation has been observed to be the primary source of nest losses across a wide diversity of species, habitats, and geographic locations, accounting for 80% of nest losses on average (Martin 1992a, 1993, Ricklefs 1969). Natural selection should favor birds that choose habitats, communities, and life-history traits that reduce the negative effects of nest predation given the importance of reproductive success to fitness. I will show how nest predation and nest sites can provide viable alternative hypotheses for long-standing patterns of habitat selection, species coexistence, and life-history traits that traditionally have been attributed to food limitation and competition.

Habitat selection and species coexistence

More than three decades ago, MacArthur (1958) published a study, widely cited in general biology textbooks, showing that five coexisting warbler species differed in their foraging locations and methods (Figure 1a). This partitioning of resources among coexisting species is an old and well-studied pattern that has long been considered necessary for coexistence (reviewed in Schoener 1974, 1986). MacArthur and others also showed...
Birds are often inconspicuous in their nests in the sites they choose for nesting. This female orange-crowned warbler (center of photo) has nested in a site without woody vegetation.

that numbers of coexisting bird species increase with vegetation density and spatial heterogeneity (Karr and Roth 1971, MacArthur et al. 1962, Willson 1974), a pattern that exists in many other animal foraging systems, including lizards, mammals, freshwater fish, and marine intertidal organisms.

These two well-documented patterns generate two questions: Why is foliage density important to choice of habitats? Why do increasing numbers of species coexist in habitats with more foliage and greater structural heterogeneity? Historically, these questions have been explained in terms of food limitation and competition: birds were thought to choose habitats with greater foliage density because more foliage provided more food, and more species were thought to coexist in habitats with greater structural heterogeneity because there were more types of foraging sites to partition to minimize competition (MacArthur 1958, 1972, MacArthur et al. 1962; see Martin 1986). Yet, evidence of competition and food limitation was indirect or absent, and other processes were not examined.

Habitat selection. Dense foliage and increased structural heterogeneity can affect habitat choice by reducing risk of predation in aquatic systems (e.g., Sih et al. 1985, Werner and Hall 1988). Birds may similarly choose habitats with dense vegetation to reduce the probability of nest predation. Foliage next to the nest can reduce the probability of predation by concealing the nest. Indeed, predation rates were lower at nests with greater concealment in 29 of 36 studies (Martin 1992a). At a larger spatial scale, foliage in the patch (5-meter radius circle) surrounding the nest may also influence predation risk; dense and complex vegetation may impede the ability of mobile predators to locate sedentary prey (e.g., nests), even when the prey are poorly concealed. The latter result is expected primarily if predators are searching vegetation randomly. However, bird species (and sedentary organisms) usually specialize on individual plant species for nesting and, thus, do not use vegetation randomly. In such cases, predators waste time and effort if vegetation is searched randomly. Instead, predators should only search substrate types that represent potential sites for encountering prey.

As a result, predation risk and patch choice may be influenced by numbers of potential prey sites rather than foliage density per se, thereby creating two mechanistic hypotheses. The total-foliage hypothesis states that predation risk decreases with increases in total vegetation in the nest patch because greater foliage density inhibits transmission of visual, chemical, or auditory cues by prey. The potential-prey-site hypothesis states that increases in the density of plants of the type used by prey reduces the probability of predation because it increases the number of potential prey sites that must be searched and can cause the predator to give up before finding the occupied site.

I tested the response of predators to numbers of unoccupied and occupied sites using artificial nests baited with quail (Coturnix coturnix) eggs (Martin 1988b). I put out seven nests per patch and varied the number of egg-containing nests in each patch (one, three, or seven of the seven nests contained eggs). Each of the three experimental treatments was represented by ten patches. Predation rates for any nest in a patch decreased with increases in the number of nests that were unoccupied (Martin 1988b). Such results show that predators can respond to numbers of unoccupied and occupied prey sites, at least in an artificial setting.

Potential prey sites are represented in a natural setting by plants of the species and size used for nesting. Nest predation should decrease with increased number of these plants under one of the simplest situations of the potential-prey-site hypothesis. Under the total-foliage hypothesis, predation should decrease with increases in numbers of total stems rather than the subset of stems of the type used for nesting. These predictions were tested on study sites in high-elevation snowmelt drainages in Arizona (Martin 1988a) by counting the number of stems in a 5-meter-radius circle surrounding nests. Analyses of hermit thrushes (Catharus guttatus) and MacGillivray’s warblers (Oporornis tolmiei) support the potential-prey-site hypothesis; nest predation was reduced when the nest patch contained more potential nest sites (Fig-
The total foliage hypothesis was rejected for both species; predation rates were not reduced at nests surrounded by more total vegetation stems (Figure 2; also Martin and Roper 1988).

Predation risk is not necessarily always high in small patches (few potential prey sites); if birds only used large patches, then predators should ignore small patches in the same way they ignore unused substrate types, and any bird that used a small patch would escape predation. Of course, predators would learn to explore small patches as numbers of prey using them increased, and predation rates would quickly escalate because of the low search time in small patches. This arms race should ultimately level off with birds using patches in proportion to their relative abundance and the amount of time it takes the predator to search them. Thus, some birds (con-specifics or a different species) should use small patches; in Arizona, green-tailed towhees (Pipilo chlorurus) choose small patches of firs, whereas hermit thrushes and MacGillivray's warblers mostly choose large patches.

If birds select nesting patches that reduce predation risk, then they should choose patches with greater numbers of potential nest sites in situations in which these are the patches with the least risk of predation (e.g., hermit thrush and MacGillivray's warbler). Patches used for nesting were compared to unused patches centered on a stem of the same type used for the nest (nonuse patches). These comparisons showed that patches used for nesting by MacGillivray's warblers and hermit thrushes did indeed have more potential prey sites, but not more total vegetation, than nonuse patches (Martin and Roper 1988). Such choices minimize predation risk given the patterns of predation found for these two species (i.e., Figure 2). Moreover, some species, such as the hermit thrush, do not forage in vegetation of the type used for nesting, so abundance of foraging sites can be eliminated as a basis for these nest patch choices (see Martin and Roper 1988). Thus, birds choose nest sites and patches with reduced risk of nest predation.

Predation risk can increase with prey density (Martin 1988c), but such effects could be offset by greater numbers of potential prey sites, given that the latter apparently reduce predation risk. Consequently, numbers of individuals and species may increase with foliage density due to increasing numbers of potential nest sites (Martin 1988a), rather than the historical argument of greater numbers of foraging sites (e.g., MacArthur 1972, MacArthur et al. 1962).

I tested this possibility by reanalyzing a classic study by Willson (1974); she showed that bird species numbers increased with the addition of shrub and tree layers, but she questioned the importance of foraging substrates to this result. I reanalyzed her data by classifying species based on nesting versus foraging sites and found that more of the species that were added with shrub and tree foliage layers were species that nested in those layers than species that foraged in them (Martin 1988a). Moreover, examination of the correlation between number of species and density of foliage in these above-ground layers showed that almost 20% more of the variation in species numbers was explained based on nesting preferences than on foraging preferences.

Similar results were obtained for my sites in Arizona (Martin 1988a). Thus, availability of nest sites with low risk of predation provides a strong alternative explanation for the long-standing relationship between bird species numbers and foliage profiles. Of course, such effects do not eliminate the possibility that food limitation and competition are also operating, but the results challenge the priority of the latter processes and show that they certainly are not the only explanations for these patterns.

Coexistence of species. Nest predation may also affect the types of species that successfully coexist, based on similarity of their nest sites. When different species use the same site for nesting, then density of potential prey sites is held constant but prey density for that site is increased by coexistence (Figure 3b). If predation risk increases with cumulative prey density, then predation risk should increase for all species using similar nest sites and thus exert negative selection on coexistence (Martin 1988c; also see Holt 1977, 1984). If these species use different nesting sites, then the predator must search more substrates, thereby reducing search efficiency and reducing the cost of coexistence (Figure 3a). When nest site differences are sufficiently large to make searching both sites too costly to the predator, then coexistence should not affect predation rates. Such effects can favor coexistence of species that use different nest sites (Martin 1988b,c). These nest site differences can occur in two
A red squirrel (Tamiasciurus hudsonicus) robs a bird nest. This photo was taken by an automated camera.

Spatial dimensions: vertical (i.e., among vegetation layers) and horizontal (i.e., among substrates or microhabitats in the same vegetation layer).

I used artificial nests to experimentally test the prediction that predation favors nest site differences among coexisting species (Martin 1988b). Nests were placed in positions that simulated nesting locations of four species occurring on the study sites in Arizona. Nests were divided among the sites of these four species in one treatment to simulate coexistence of four species that use different nest sites (Figure 3a). In a second treatment, nests were placed at the same total density but were placed in only one of the four sites to simulate all four species using the same site (Figure 3b). Predation rates were predicted to increase when cumulative density of nests increased in a particular nest site due to overlapping use by coexisting species (Martin 1988c). Indeed, nest predation rates were much greater when the simulated species used the same site than when they used different nest sites (Figure 4). Thus, these experiments indicate that nest predators exhibit behaviors that can favor nest site differences among coexisting species.

Examination of nest site use by birds on my Arizona sites indicated that they do in fact differ in where they place their nests in vertical and horizontal nesting space. The 12 species on the Arizona sites were dispersed vertically, with four species nesting in the ground, three species nesting in the shrub layer, two species nesting in the subcanopy, and three species in the canopy. Data from other avian communities also showed that birds were, moreover, dispersed vertically based on their nesting sites than on their foraging sites (Martin 1988c).

Species within a vegetation layer differed in nest substrates and microhabitats along a short moisture gradient in the Arizona snow-melt drainages (Figure 1b). Each of the four ground-nesting species places nests at the base of different plant species (Figure 5) that occur at different abundances along the moisture gradient (Figure 1b). The three shrub-nesting species overlap in substrate use (all use small firs), but they chose these firs in different microhabitats along the moisture gradient; green-tailed towhees chose small firs in drier sites where New Mexican locust was more abundant, whereas MacGillivray’s warblers chose small firs in patches with more maple, and hermit thrushes chose small firs in patches with more small firs than the other two species. These differences in nest site use among coexisting species are greater than for foraging sites because birds specialize (use a site more than 60% of the time) on nest sites that differ among species (e.g., Figure 5), whereas birds are much less specialized and overlap more based on foraging sites (Figure 1a).

If nest predation favors this use of different nest sites by coexisting species (or favors coexistence of species that already use different sites based on their evolutionary histories), predation rates should be greater for species that use nest sites that are similar to those used by other species. Indeed, predation rates were greater for guilds (shrub nesters) and species within a guild that placed a greater proportion of their nests in sites that were similar to other coexisting species. The cost of using nest sites that are similar to other coexisting species is clearly shown by MacGillivray’s warblers. They place their nests in small firs or short maple thickets. Small firs are also used as nest sites by hermit thrushes and green-tailed towhees, whereas MacGillivray’s warbler is the only species that uses the short maple thickets on these sites. As a result, cumulative nest density in small firs is slightly more than four times as great as in the maple. If predators respond to cumulative densities, predation rates should be greater for MacGillivray’s warblers in small firs than those in maple. Indeed, daily mortality rates were significantly greater in firs than in maple (Figure 6), and total percentage of nests lost to predation was substantially greater in firs (78.3%) than in maple (39.0%).

Moreover, experiments with artificial nests showed that this trend could be reversed by increasing the cumulative density of nests in maple compared with small firs; when nests in maple were four times as dense as nests in small firs, daily mortality rates of nests in maple were much higher than for nests in small firs (compare striped bar of maple with open bar of fir in Figure 4). Such results show that differences in predation rates between these substrates are from differences in density of nests rather than differences in the substrates.

In summary, artificial and real nests show that risk of nest predation increases with overlap in nest site use among coexisting species and thereby provides a strong alternative hypothesis to food-based competition for resource partitioning among coexisting species. Indeed, partitioning of microhabitats among coexisting species is much greater when based on nest sites (Figures 1b and 5) than on foraging sites (Figure 1a). Moreover, the results show a direct fitness cost (i.e., increased nest predation) with overlap in nest site use among coexisting species, whereas fitness costs of overlap in foraging sites are largely undocumented.

Constraints of evolved nest placement on local success

Predation may favor nest site specialization within species because use of new sites may either overlap sites already used by other coexisting species or because species may not be adapted to new sites in terms of, for example, cryptic coloration or physiological
generally only 35-70 m in length. The four ground-nesting bird species (identified
spruce woods (modified from MacArthur 1958). The diagram indicates six vertical
and three horizontal zones in trees that are most frequently used by each warbler
species. The zones of most concentrated activity are shaded such that at least 60%
of the observed foraging attempts are in the shaded zones (MacArthur only shaded
concentrated activity by at least three species. In fact, the cumulative percentage of
vertical layers (only the myrtle warbler uses lower zones) is usually used as a zone of
their use of any foraging zone even when only considering the zones that comprise
over 60% of the foraging activity. b. Schematic drawing of vegetation and bird distribution
along a moisture gradient in snow-melt drainages in Arizona (unpublished data). The lower parts of drainages are moist and characterized by plant species such as New Mexican locust (Robinia neomexicana). Small white firs (Abies concolor) were distributed throughout the entire gradient. These gradients (i.e., hillsides) are generally only 35-70 m in length. The four ground-nesting bird species (identified underneath the gradient) nest at the base of different plant species that occur at different points along the gradients. When the plant species that comprise 60% of the nest substrates for a species are examined, almost no overlap in nest substrate use occurs among species (see Figure 5). The three shrub-nesting bird species (identified above the gradient) all use small firs but use the firs in different parts of the gradient such that the microhabitat conditions surrounding the firs differ.

Figure 1. a. Foraging locations of five species of warblers coexisting in northeastern spruce woods (modified from MacArthur 1958). The diagram indicates six vertical and three horizontal zones in trees that are most frequently used by each warbler species. The zones of most concentrated activity are shaded such that at least 60% of the observed foraging attempts are in the shaded zones (MacArthur only shaded to 50% in his original article). Numbers are the percentage of observed foraging attempts in shaded zones. Note that any zone of concentrated activity in the top three vertical layers (only the myrtle warbler uses lower zones) is usually used as a zone of concentrated activity by at least three species. In fact, the cumulative percentage of time spent in any zone by all species combined is generally greater than for any individual species that concentrates activity in that zone. In short, species overlap markedly in their use of any foraging zone even when only considering the zones that comprise 60% of the foraging activity. b. Schematic drawing of vegetation and bird distribution along a moisture gradient in snow-melt drainages in Arizona (unpublished data). The lower parts of drainages are moist and characterized by plant species such as New Mexican locust (Robinia neomexicana). Small white firs (Abies concolor) were distributed throughout the entire gradient. These gradients (i.e., hillsides) are generally only 35-70 m in length. The four ground-nesting bird species (identified underneath the gradient) nest at the base of different plant species that occur at different points along the gradients. When the plant species that comprise 60% of the nest substrates for a species are examined, almost no overlap in nest substrate use occurs among species (see Figure 5). The three shrub-nesting bird species (identified above the gradient) all use small firs but use the firs in different parts of the gradient such that the microhabitat conditions surrounding the firs differ.

tolerance to the microclimatic conditions. Indeed, data from Arizona show
nest predation is greater in less frequently used nest sites, and most
species were substrate specialists (more than 60% of nests in one sub-
strate type; e.g., Figure 5). Moreover, a review of the literature also revealed
that most species are specialized in their nesting substrate. This speciali-
ization contrasts with foraging sites where species are much less special-
ized and overlap more (Figure 1a).

Specialization may also lead to stereotypy in nest placement. Nest heights
of 17 warbler species were compared over latitudes differing by as much as
14°, and only 4 species shifted heights significantly despite geographic
changes in vegetation structure and types of coexisting species (Martin 1988c).
Moreover, in many cases, all or most bird species within a genus use the same vegetation layer or general substrate type for nesting. Such results suggest that nest placement often is evolutionarily conservative.

Nest placement may be set for a species over a large geographic area
based on events during speciation or their evolutionary history. Stereotypy
in nest placement could result in poor reproductive success in some habitats
and even select against occupation of those habitats, potentially providing
a mechanism for favoring coexistence of species that differ in nest place-
ment. For example, hermit thrushes are subject to more intense predation
than any other species on my study sites in Arizona. This intensity of pre-
dation is closely related to the use of small firs for nesting.

Given that nesting is so unsuccessful in small firs, why choose such
sites? Hermit thrushes may be immigrating to my sites from other sites
where small firs are an appropriate choice for nesting. Firs may elicit a
settling response when encountered by dispersing birds, because firs are an
appropriate proximate cue over the larger range of the population. Indeed,
the race of hermit thrush that occurs on my sites usually uses small
conifers for nesting throughout its western range (Harrison 1979). Such
sites may be appropriate over most of the range, but inappropriate on my
study areas.

My study sites are drainages that are located within 8 km of the edge of
the Mogollon Rim, an abrupt cliff that represents the southern extension
of the Colorado Plateau. The edge of the rim has a narrow band of moist
vegetation (e.g., maple) associated with greater precipitation formed by
the upward deflection of air at the rim face. My study sites are in this narrow
band of moist vegetation. Red squirrel distribution and densities are asso-
ciated with maple on these sites (Uphoff 1990). Photos from automated

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MacGillivray's warbler poses a similar problem: Given that nesting success is so much greater in maple thickets (Figure 6), why use firs? MacGillivray's warbler usually places only approximately one third of nests in small firs (Table 1). This use of conifers again reflects a common pattern throughout their range. However, small firs may be used when short maple thickets are not available. Many of the territories where small firs are used have less short maple.

Cameras at artificial nests showed that red squirrels are the major predators on nests and account for more than 80% of nest predation events (Martin 1988b). Moreover, these maple habitats contain MacGillivray's warblers and green-tailed towhees, both of which use small firs as nest sites and thereby overlap hermit thrushes and increase the cumulative density of nests in firs.

If the low nesting success of hermit thrushes in maple drainages is due to the high density of red squirrels and high cumulative density of nests in small firs, then nesting success should be higher in the same nest sites (small firs) in other habitat conditions without coexisting species. Indeed, success of hermit thrush nests in small firs in nearby drainages that do not contain maple or the other two coexisting species was markedly higher than in maple drainages (Figure 7).

Moreover, annual differences in nest sites also suggest that availability is important. In the four years before 1988 and 1989, maples were used for approximately two thirds of the nests. In 1988 and 1989, late freezes and a drought, respectively, inhibited leaf development in maples, and MacGillivray's warblers placed two thirds of their nests in small firs (Table 1). The increased use of small firs by MacGillivray's warblers in 1988 and 1989 was associated with significantly greater nest predation in these two years compared with the four previous years. Moreover, predation rates were correlated with the proportion

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Figure 2. Daily mortality rate (rate at which nests are lost to predators per day) and its standard error for nests in patches with less (few) or more (many) than the median number of stems that represent potential nest sites or total vegetation (total stems). Z-values were calculated using the z-test of Hensler and Nichols (1981). For the MacGillivray's warbler, 62 nests were observed. For potential nest sites, \( z = 2.5 \) (\( p = 0.006 \)); for total stems, \( z = 0.9 \) (\( p = 0.19 \)). For the hermit thrush, 109 nests were observed. For potential nest sites, \( z = 2.5 \), \( p = 0.006 \); for total stems, \( z < 0 \), \( p > 0.5 \).

Figure 3. Schematic drawing of substrate and prey distribution for two experimental nest treatments. In both cases, four types of nest sites are represented by four open symbols. Four bird species are represented by four solid symbols. In the first treatment (case a), each species occupies a different nest site. In the second treatment (case b), density is the same as in case a, but all species occupy the same nest site. The result is that cumulative density in a nest site (e.g., circles) is four times greater when species use the same nest site (case b) than when each species uses a different nest site (case a). Note that almost all circles are occupied in case b, rewarding predators to continue searching the substrate type but to ignore other substrate types because they are empty. This situation increases predation rates on all species using the substrate type. In contrast, in case a, the predator must search all substrates to encounter the same number of prey, and the increased encounters with unoccupied sites may cause the predator to give up before finding a prey, thereby reducing the cost of coexistence.
Figure 4. Mean (and standard error) in daily mortality rates (rate at which nests are lost to predators per day) for artificial nests when nests were placed among four different types of sites (open bars, case a of Figure 3) and when nests were all placed in the same type of sites (striped bars, case b of Figure 3). Density of nests was held constant between the two treatments. A total of 480 nests were used among three replicate sites and over two temporal replicates. The situation of nests placed in the same type of sites was not tested for the 3-meter maple. Data from Martin (1988b).

Table 1. Annual variation in nest predation as a function of variation in use of nesting substrates by MacGillivray’s warblers. The increased use of firs in 1988 and 1989 was associated with significantly greater nest predation than in the previous four years ($X^2 = 6.95, p = 0.008, \text{multiple comparison test of Sauer and Williams 1989}$). Predation rates were correlated with proportion of nests built in firs ($r = 0.89, p < 0.05$).

![Figure 5](image_url) - Frequency that ground nests were placed below the indicated plant species by the four ground-nesting species. Orange-crowned warbler ($Vermivora celata; n = 90$; black bars), Virginia’s warbler ($Vermivora virginiae; n = 27$; open bars), red-faced warbler ($Cardellina rubrifrons; n = 30$; shaded bar), and dark-eyed junco ($Junco hyemalis; n = 55$; cross-hatched bar).
Figure 6. Daily mortality rates (and standard errors) for nests of MacGillivray’s warblers in small white firs and canyon maple. Daily mortality rates were much greater ($z = 2.85$, $p = 0.0022$) for nests in firs than for nests in maple. There were 30 nests in firs and 32 nests in maple.

The data are consistent with the limited-breeding-opportunities hypothesis. Nest sites are much more limited for cavity-nesting birds than for open nesters (13% of nests are lost) than nonexcavators (36% loss; Martin and Li 1992). Yet, excavators have smaller clutches (Martin and Li 1992) and greater adult survival (Figure 9) than nonexcavators, counter to the nest-predation hypothesis, which predicts that excavators with reduced nest predation should have larger clutch size and lower or similar adult survival compared with nonexcavators. Moreover, analysis of life-history traits for 110 species of North American birds shows that clutch sizes of nonexcavators are outliers for their nest predation rates (Martin in press a). Such results indicate that the large clutch sizes of nonexcavating cavity nesters cannot be explained by the nest predation hypothesis. Plus, the patterns are not explained by phylogenetic effects (Martin in press b, Martin and Li 1992).

The similar adult survival of residents and migrants when nest type is controlled (i.e., within open nesters and nonexcavators) falsifies the winter-mortality hypothesis, which predicts that residents suffer greater adult mortality than migrants. Moreover, not all resident cavity nesters suffer greater adult mortality than nonmigrants; resident cavity-nesting species that excavate their own nest holes (excavators) have adult survival rates that are greater (0.65 ± 0.028 [standard error], $n = 5$) than for either resident nonexcavators (species that do not excavate but instead use existing holes) or resident open nesters (Figure 9) with body mass controlled (ANOVA, $F = 12.73$, $p < 0.001$).

The evidence also favors rejection of the nest-predation hypothesis. Nest mortality predictably averages much less for excavators (13% of nests are lost) than nonexcavators (36% loss; Martin and Li 1992). Yet, excavators have smaller clutches (Martin and Li 1992) and greater adult survival (Figure 9) than nonexcavators, counter to the nest-predation hypothesis, which predicts that excavators with reduced nest predation should have larger clutch size and lower or similar adult survival compared with nonexcavators. Moreover, analysis of life-history traits for 110 species of North American birds shows that clutch sizes of nonexcavators are outliers for their nest predation rates (Martin in press a). Such results indicate that the large clutch sizes of nonexcavating cavity nesters cannot be explained by the nest predation hypothesis. Plus, the patterns are not explained by phylogenetic effects (Martin in press b, Martin and Li 1992).

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logical differences, and species with weaker excavating morphology depend on existing holes more; such species potentially are more limited in their nesting opportunities, and clutch sizes increase with this dependence on existing holes as expected under the limited-breeding-opportunities hypothesis (Martin in press b). Moreover, excavators that use old holes apparently suffer greater nest predation (Nilsson et al. 1989), and, hence, the larger clutch sizes of these species is further evidence against the traditional nest predation hypothesis. Predation may contribute to clutch size differences indirectly by influencing nest site preferences, nest size, or number of broods (Lima 1987, Martin 1988d, in press a, Martin and Li 1992, Moller 1987, 1989, Slagsvold 1982). However, nest site attributes apparently are more important to differences in clutch size and adult survival among cavity-nesting bird species than are differences in nest predation or food limitation (Martin and Li 1992, Martin in press b).

These results emphasize the importance of examining new hypotheses rather than blindly accepting longstanding dogmas. Indeed, although nest predation appears to be less important to life histories of cavity-nesting birds, nest predation apparently influences life-history traits among many groups of birds for which food limitation traditionally has been considered to be more important (Kulesza 1990, Martin 1993, in press a).

Conservation implications

The pervasive nature of nest predation and the influence of nest sites on predation risk indicates that nest sites are important habitat components and that the nesting season can be a critical period for maintenance of bird populations. Conservation of species depends on knowing their breeding biology and identifying and preserving the habitat features that affect breeding productivity and survival (Martin 1992a). Yet, insufficient information is available for most species with regard to their habitat needs, reproduction, and survival.

Nest predation has gained considerable attention in conservation studies because nest predation can increase with fragmentation (e.g., Wilcove 1985) and potentially cause loss of species (local extinction) from fragments. Such effects have been considered primarily in terms of the increase in predators along edges of habitat fragments (Wilcove 1985 and many others). Yet, nest predation cannot fully explain losses of species from fragments (see Martin 1992a), and some assumptions regarding vulnerability of species to nest predation are incorrect (Martin 1993).

Other ecological requirements of species are undoubtedly important to their loss. For example, the arguments and evidence presented here suggest that species commonly differ in their nest site preferences, and these preferences may be fixed. Habitat fragmentation can cause direct loss of habitat features needed by some species and thereby cause loss of those species (Martin 1992a).

Even in large forest tracts without edge problems, alteration of conditions by grazing, lumber production, or other anthropogenic activities can potentially cause loss of necessary habitat conditions for some species. Moreover, habitat degradation may reduce the diversity of nesting sites available and cause increased predation on species that still use such habitats because they are forced to use similar (overlapping) nest sites and increase cumulative nest density, or because species are forced to use poor-quality nest sites.

Such effects added to increased predation along edges (Wilcove 1985) may cause many populations to reproduce well below levels necessary for maintaining populations. Indeed, a number of bird species are showing alarming population declines (Robbins et al. 1989). Correction of such population problems will depend on determining the habitat features that allow successful reproduction by a variety of species on their breeding grounds, as well as habitats needed for survival on the wintering grounds. Given the importance of nest predation and nest sites to nest success, much greater attention is needed for these issues.

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