

# PATTERNS OF NEST USURPATION: WHEN SHOULD SPECIES CONVERGE ON NEST NICHES?<sup>1</sup>

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**Abstract.** The acceptability of a nest to more than one species and the convergence of species on a nest niche is demonstrated through nest usurpation. I compiled examples of nest usurpation from the literature to examine patterns regarding the species and nest sites that tend to be usurped, those species likely to be usurpers, and the habitats in which usurpation occurs. Cavities and enclosed nests are more likely to be usurped than cup nests. Species that excavate or build these types of nests, like the Picidae and the Furnariidae, are likely to be the hosts of usurpers. Particular groups are prone to usurping nests, including introduced species like the House Sparrow (*Passer domesticus*) and European Starling (*Sturnus vulgaris*). Cavity usurpations were more likely to be observed in temperate than tropical/subtropical zones, and about equally likely to be observed in closed and open habitats, while enclosed nest usurpations were observed more frequently in open than closed habitats, and more often in tropical/subtropical than temperate zones. Usurpation of all nest types is more likely to occur in tropical/subtropical zones than expected, based on the number of studies in the literature conducted in these zones. Usurpation of all nest types is less likely to occur in open, and more likely to occur in moderately open habitats than expected, based on the number of studies in the literature conducted in these habitats. Instances of cavity usurpation, recorded primarily in temperate zones, across a variety of habitats, do not contribute to these general patterns. Nest-site convergence through nest usurpation may be more likely to occur in moderately open tropical habitats because of: 1) the availability of enclosed nests, 2) the limited structural heterogeneity of the vegetation, which limits the possibility of nest-niche partitioning, and 3) the high diversity of potential nest competitors and predators. In such environments, interspecific nesting associations may be a more effective generalized nest defense strategy than using a nest site that is difficult to find.

**Key words:** nest site; nest usurpation; nest-niche convergence; cavities; enclosed nests; nesting association.

## INTRODUCTION

Finding a suitable nest site is a key component of the breeding cycle in numerous taxa. Characteristics of the nest site often influence the probability of success of a particular breeding attempt (Plezczyńska 1978, Gore and Kinnison 1991, Seddon and van Heezik 1991, Albano 1992, Vinuela and Sunyer 1992, Norment 1993), and the success or failure of breeding attempts is directly related to an individual's lifetime reproductive success. Hence, investigation and explanation of patterns of nest-site use are central to understanding the population ecology and evolution of species, including how nest-site use affects a species' interactions with coexisting species. The purpose of this article is to examine

patterns linked with one nesting strategy, in which species take over active nests/nest holes of other species for breeding purposes. This interaction previously has been referred to as nest usurpation (Favaloro 1942) or nest piracy (Robinson 1985). In addition, I will discuss some of the implications of these data in light of recent theory regarding nest placement patterns in avian communities. Unlike brood parasites that lay their eggs in another bird's nest and leave, providing no parental care, nest usurpers incubate and feed their young in the nest of another. Henceforth, when I use the term "nest" I refer to both nests and nest holes because my main points emphasize the use of nests and nest holes as nest sites.

Species actively choosing nests occupied by other species appears to run counter to current theory that predicts divergent nest placement among coexisting species (Collias and Collias 1984, Martin 1988a, 1988b, 1988c, 1993). However, this behavior may be expected under particular environmental conditions. Collias and

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Collias (1984) stated that past interspecific competition has led to the differentiation of nest sites used by related species, resulting in niche partitioning (Hutchinson 1957). Martin (1988a, 1988b, 1988c, 1993) proposed that nest site partitioning among coexisting species results from density-dependent predation on eggs and nestlings, rather than competition. Both of these hypotheses predict that coexisting species' nest niches will diverge over evolutionary time, assuming particular conditions. For example, if the costs of competition outweigh the benefits of particular nest sites, species may develop non-overlapping nest niches. However, the benefits may be great when nest sites are costly to construct, and/or when individuals experience enhanced reproductive success by forming interspecific nesting associations in these nests. A corollary of Martin's hypothesis (1988a, 1988b, 1988c, 1993) is that, if nest predation is low in a particular nest niche, there will not be strong selection for species to diverge in their nest placement. Hence, one would predict an alternative pattern of nest placement, convergence on particular nest niches, when the benefits associated with such convergence outweigh the costs. The benefit/cost ratio will be determined by several factors including the number of potential nest-site competitors, the availability of valuable nest sites, and the frequency and type of nest predation.

Convergence of more than one species on a nest site is demonstrated most clearly by interspecific competition for nest sites (Trivelpiece and Volkman 1979, van Balen et al. 1982, Nilsson 1984, Ingold 1989, Kerpez and Smith 1990, Wallace et al. 1992), interspecific nest usurpation and nesting associations within a nest (Favaloro 1942, Roberts 1955, Skutch 1960, MacLean 1973, Konrad and Gilmer 1982, Robinson 1985, Ingold 1989, Lindell 1994), and species using the old nests of other species (Hudson 1920, Favaloro 1942, Lack 1945, Roberts 1955, Colahan 1982, Finch 1982, Wilson 1988). I concentrated my efforts on interspecific nest usurpation because of the lack of a recent comprehensive survey of this phenomenon, and to determine ecological conditions under which this behavior is likely to occur. Short (1979) considered nest usurpation as it relates to woodpeckers, while Favaloro (1942) and Roberts (1955) conducted surveys of nest usurpation and appropriation, respectively, although the bulk of their examples were of species using old nests of other species.

An extensive anecdotal literature on nest usurpation exists (Lindell 1994), but few studies have focused on the phenomenon (MacLean 1973, Trivelpiece and Volkman 1979, Robinson 1985, Ingold 1989). Like predation events, actual takeovers will be observed much less frequently than more lengthy interspecific interactions like brood parasitism. Reports of one species using another's nest or nest hole does not confirm that there was an aggressive takeover, although it does confirm that one nest niche is suitable for more than one species. Aggressive takeover implies the resource is of sufficient value to risk a physical contest, and that it may be limiting to the species involved. I gathered data concerning the types of nests usurped because studies indicate that cavities and enclosed nests are less susceptible to nest predation than cup nests (Lack 1948, Nice 1957, Ricklefs 1969, Oniki 1979). Hence, one might expect that cavities and enclosed nests are of greater value than cup nests and species may be more likely to compete aggressively for them. In addition, habitat type may influence the number and kinds of nests usurped since some habitats will have more or fewer potential nest sites. In habitats with relatively little heterogeneity, and fewer nest sites, greater convergence on nest sites is expected.

As a caveat, although the terms nest usurpation and nest piracy imply negative effects on the "hosts" of the usurped nests, I showed in an investigation of Plain-fronted Thornbirds (*Phacellodomus rufifrons*) and the birds that breed in their nests, that even in situations in which obvious aggression is directed toward the hosts by the usurpers, the net short-term effect of the interaction on the hosts may be positive, particularly when the hosts are able to continue nesting in the same nest or immediate area (Lindell 1994). Hence, although I used aggression as a criterion to classify interactions as nest usurpation, aggression need not imply a net detrimental effect on the hosts. In cases where effects on hosts are unknown, usurpers should be labelled more neutrally as nest associates.

## MATERIALS AND METHODS

To uncover examples of nest usurpation in natural nest sites, excluding nest boxes, I conducted keyword searches and checked sources in all papers discovered. In addition, I reviewed all volumes of *The Auk*, *The Condor*, *The Emu*, *El*

TABLE 1. Percentage of cavity and enclosed nest usurpation records across four habitat types.

Habitat	Cavity usurpation	Enclosed nest usurpation
	Percentage (n)	Percentage (n)
Open	7.4 (2)	15.9 (7)
Moderately open	40.7 (11)	63.6 (28)
Moderately closed	37.0 (10)	2.3 (1)
Closed	14.8 (4)	18.2 (8)

*Hornero*, *Ibis*, and *The Ostrich* issued from 1983 to 1993 inclusive. These journals were chosen to provide some coverage of various parts of the globe. I classified an interaction between two species as usurpation if authors provided evidence of: 1) physical aggression by the usurpers toward the hosts and/or persistence by the usurpers in returning to the nest site, 2) the nest/nest hole being sought for breeding purposes. In a few instances these types of evidence were lacking but the authors described the incident as nest-site usurpation. I have included these examples in the analyses. I have excluded examples in which authors made general statements about the occurrence of nest usurpation among various species but did not describe specific examples of the interaction (Wood 1924, Roberts 1955, Short 1979). All examples that met these criteria are available from the author by request or at Web site <http://amazon.sr.unh.edu/lindell>. I did not include examples of species destroying the nests of other species for reasons other than breeding (cf. Picman and Picman 1980, Robinson 1985, Simons and Simons 1990).

It is unlikely that I found every example of nest usurpation in the literature, but it is unlikely that I missed examples in any systematic way with regard to species, nest types, and/or habitats. Because I conducted research on one community in which I discovered numerous species usurping the nests of Plain-fronted Thornbirds and these results are included in Table 1, I have calculated statistics testing the independence of nest type and habitat, and nest type and latitude, using each distinct species pair as a data point and using, for example, all instances of species usurping thornbird nests as one example of the usurpation of enclosed nests.

I used authors' descriptions of their study sites and Whittaker's 1975 classification of biome-

types to classify the habitats into four categories: (1) open, in which canopy cover was less than 10% such as marshes; (2) moderately open, in which canopy cover varied from 10–50%, or in which the habitat was a mosaic of open and closed canopy areas with open areas predominating such as suburban areas and some woodlands; (3) moderately closed, in which canopy cover varied from 50–90%, or in which the habitat was a mosaic of open and closed canopy areas with the latter predominating such as disturbed forests; (4) closed, in which canopy cover was greater than 90% such as tropical rain forests. The latitudes at which studies took place were recorded and, for analyses, were divided into three categories: (1) 0–29° N or S (tropic/subtropic zone); (2) 30–59° N or S (temperate zone); (3) 60–90° N or S (polar zone). I used these categories because my expectation regarding the conditions under which usurpation should occur relates to species diversity at different latitudes. Hence it was important to compare areas covering similar amounts of change in latitude, rather than using the climatically defined locations of the tropical/temperate and temperate/polar boundaries.

To compare the distributions of bird families, habitats, and latitudes in examples of usurpation to the distributions of families, habitats, and latitudes in the literature generally, I recorded the first study in each issue of each journal mentioned above from 1983–1993 that involved some field activity in which birds were observed. Excluded were studies in which field activity involved only the removal of nestlings, eggs, stomach contents, feathers, or other parts of birds. Also excluded were broad field surveys resulting in long species lists. I then adjusted the number of studies from each journal so the full sample represented the proportions of studies published in each journal over the 11-year time period. For each study, I recorded the families of the species studied, and the habitats and latitudes in which the study took place.

Sample sizes sometimes vary from one analysis to the next because authors did not always provide a detailed enough description of their study site to permit its classification by habitat. Also, I excluded from the latitude analyses those few studies that took place in two of the three latitude zones. All G-tests of Goodness of Fit and Independence were calculated using Williams' Correction.

RESULTS

TYPES OF NESTS USURPED

Of the 84 instances of nest usurpation in the database, 52.4% ( $n = 44$ ) involve an enclosed nest, 38.1% ( $n = 32$ ) a cavity, and 9.5% ( $n = 8$ ) a cup nest. Of the 51 species that had their nests usurped, 41.2% ( $n = 21$ ) use enclosed nests, 43.1% ( $n = 22$ ) use cavities, and 15.7% ( $n = 8$ ) cup nests.

SYSTEMATIC PATTERNS

Species of 18 families had their nests usurped and species of 17 families were usurpers. The distribution of families with species that had their nests usurped is significantly different from the distribution of families in the sample of journal articles (Kolmogorov-Smirnov two-sample test:  $D = 0.584$ ,  $n_1 = 84$ ,  $n_2 = 231$ ,  $P < 0.0001$ ). The three most common families in the usurped group were the Furnariidae, Picidae, and Hirundinidae, contributing 61.9%, 52 out of 84 instances, of serving as a host to usurpers (Fig. 1). These same three families made up only 3.9%, or 9 of 231, of the total sample of families from journal articles. Similarly, the distribution of families in the usurping group is significantly different from the distribution of families in the sample of journal articles (Kolmogorov-Smirnov two-sample test:  $D = 0.488$ ,  $n_1 = 84$ ,  $n_2 = 231$ ,  $P < 0.0001$ ). Members of the families Tyrannidae, Passeridae, Sturnidae, Picidae, and Falconidae were the most likely usurpers, making up 59.5%, or 50 of 84 examples, of species usurping other species' nests (Fig. 1). These same seven families made up only 12.6%, or 29 out of 231, of the total sample of families from journal articles.

HABITAT TYPES

The results reported here include only those examples of usurpation for which habitat data were available. "Open habitats" refers to open + moderately open habitats as defined in the Methods (habitat types #1 and #2) and "closed habitats" refers to closed + moderately closed habitats as defined in the Methods (habitat types #3 and #4). Of the 27 instances of cavity usurpation, 48.1% ( $n = 13$ ) were recorded in open habitats, and 51.9% ( $n = 14$ ) in closed habitats. Of examples of enclosed nest usurpation, 79.5% ( $n = 35$ ) were recorded in open habitats and 20.5% ( $n = 9$ ) were recorded in closed habitats (Table 1).

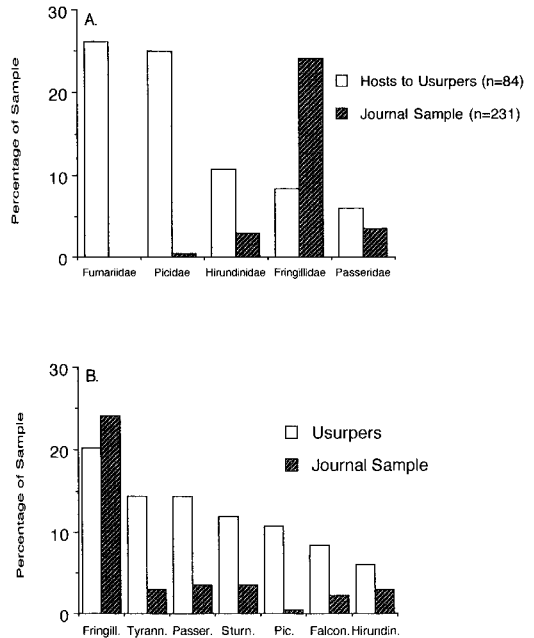


FIGURE 1. (A) Families with more than two examples of having nests usurped compared to the distribution of these families in the sample of journal articles; (B) Families with more than two examples of usurping nests compared to the distribution of these families in the sample of journal articles. The full distributions are significantly different in both cases (Kolmogorov-Smirnov Tests,  $P < 0.0001$ ).

Eighty percent ( $n = 4$ ) of the examples of open cup usurpation occurred in open habitats and 20% ( $n = 1$ ) in closed habitats. Of the 17 cavity nesting species that had cavities usurped, 47.1% ( $n = 8$ ) occupied open habitats, while 52.9% ( $n = 9$ ) were found in closed habitats. For the 21 species using enclosed nests, 57.1% ( $n = 12$ ) inhabited open habitats, and 42.9% ( $n = 9$ ) were found in closed habitats. Of the five species of open cup nesters, 80% ( $n = 4$ ) were found in open canopy habitats and 20% ( $n = 1$ ) occupied closed habitats. Nest type (cavity, enclosed, or cup) was not independent of the habitat type (G-test of independence:  $G = 17.42$ ,  $df = 6$ ,  $n = 76$ ,  $P < 0.01$ ), when including all instances of usurpation. When including each species that served as a host only once (for example counting *Colaptes auratus* as one case of a cavity nester being usurped in moderately open habitat although there are three examples of its cavities being usurped by different species), the result of non-

independence is marginally significant (G-test of independence:  $G = 12.10$ ,  $df = 6$ ,  $n = 44$ ,  $P < .06$ ), with cavity usurpation occurring about equally in open and closed habitats, and enclosed nest and cup usurpation occurring more frequently in open habitats.

Using the distribution of habitats found in the sample of journal articles to determine expected frequencies of habitat distribution in the instances of usurpation, I found that the distribution of habitat types where usurpation occurred did not match expectation (G-test for goodness of fit:  $G = 63.37$ ,  $df = 3$ ,  $n = 76$ ,  $P < .0001$ ). Usurpation occurred much less frequently than expected in the most open habitats (#1 type habitats) and much more frequently than expected in the moderately open habitats (#2 type habitats).

#### LATITUDE

The results reported here include only those examples of usurpation for which latitude data were available. Excluded are the few instances in which studies were conducted in more than one of the latitude zones I considered. Of 30 instances of cavity usurpation, three (10.0%) occurred in the tropics/subtropics (latitude zone #1) and 27 (90.0%) occurred in temperate regions (latitude zone #2). Of the 20 cavity nesting species that had cavities usurped, two (10.0%) inhabited the tropics/subtropics and 18 (90.0%) inhabited temperate regions. Of 39 instances of enclosed nest usurpation, 32 (82.1%) occurred in the tropics/subtropics and seven (17.9%) occurred in temperate areas. Of the 18 species using enclosed nests that had their nests usurped, 15 (83.3%) inhabited the tropics/subtropics and three (16.7%) inhabited temperate regions. For cup nest usurpation, three of seven instances (42.9%) occurred in the tropics/subtropics, two of seven (28.6%) occurred in temperate areas, and two of seven (28.6%) occurred at or above 60° N or S latitude. Three of seven host species (42.9%) inhabited the tropics/subtropics, two species (28.6%) inhabited temperate regions, and two species (28.6%) lived at or above 60° N or S latitude. Nest type was not independent of latitude (tropical/subtropical, temperate, or polar zones) when including all examples of usurpation (G-test of independence:  $G = 37.67$ ,  $df = 4$ ,  $n = 76$ ,  $P < .0001$ ), or when including each host species only once (G-test of independence:  $G = 25.39$ ,  $df = 4$ ,  $n = 45$ ,  $P < .0001$ ). Observations of cavity

usurpation occurred most often in temperate zones, enclosed nest usurpation occurred most often in tropical/subtropical zones, and cup usurpation occurred with about equal frequency in all zones.

Using the distribution of latitudes found in the sample of journal articles to determine expected frequencies of latitude distribution in the instances of usurpation, I found that the distribution of latitudes where usurpation occurred did not match expectation (G-test for goodness of fit:  $G = 6.05$ ,  $df = 2$ ,  $n = 76$ ,  $P < .05$ ). Usurpation occurred more frequently than expected in the tropics/subtropics and less frequently than expected in the temperate and polar zones.

#### INTRODUCED SPECIES

Introduced European Starlings (*Sturnus vulgaris*), and House Sparrows (*Passer domesticus*), were the usurpers in 17.9% ( $n = 15$ ) of all incidents compiled, although these two species represented only 1% ( $n = 2$ ) of all species recorded in the journal sample.

#### DISCUSSION

Particular nest sites are more valuable than others. The great majority of the nests usurped were cavities or enclosed nests, 90.5% ( $n = 76$ ), far out of proportion to the percentage of bird species that use cavities or enclosed nests (Collias and Collias 1984). Several studies indicate that cavities and enclosed nests are safer nest sites than open cups (Lack 1948, Nice 1957, Ricklefs 1969, Oniki 1979). Moller (1989) found significantly higher predation rates on open nests compared to partially covered nests in an experimental study of nest predation. Nilsson (1986), in contrast, reported similar numbers of fledglings produced by cavity-nesting and open-nesting species. Interestingly, he cited interference competition as a primary reason for decreased cavity nester success. If cavities and enclosed nests enhance reproductive success, they may become the target of interspecific usurpers. This expectation is supported in the results of this study. Furthermore, if particular lineages tend to excavate cavities or build enclosed nests, these groups are more likely to experience usurpation. Hence, woodpeckers, ovenbirds, and swallows are the most prone to having their nest sites usurped.

The species that usurped nest sites were more evenly distributed among a number of families

than were those whose nests were usurped, although particular groups such as the flycatchers and falcons were more likely than others to usurp nests. Although some of the examples recorded may be sightings of rare events, some species appear to engage in habitual nest usurpation: Troupials (*Icterus icterus*) and Spot-winged Falconets (*Spizaipteryx circumcinctus*) in South America (Skutch 1969a, Thomas 1983, Voous 1983, Martella and Bucher 1984, Robinson 1985, Lindell 1994), Piratic Flycatchers (*Legatus leucophaius*) in Central and South America (Skutch 1960, Robinson 1985), Cut-throats (*Amadina fasciata*) and Chestnut Sparrows (*Passer emini-bey*) in Africa (Cunningham-van Someren 1971, Payne 1969), Large-billed Scrub-wrens (*Sericornis magnirostris*) and Blue-faced Honeyeaters (*Entomyzon cyanotis*) in Australia (Marshall 1930, Roberts 1955), Pygmy Falcons (*Polihierax semitorquatus*) in Africa (MacLean 1973), House Sparrows (*Passer domesticus*) on several continents (Buss 1942, Favalaro 1942, Burger 1976, Fraga 1980, Earle 1985), and European Starlings (*Sturnus vulgaris*) in native (Tracy 1933) and introduced (Troetschler 1976) habitats. The habit of usurping nests may be a good predictor of an introduced species' ability to maintain itself in a new habitat, given that nearly 20% of the examples were of introduced House Sparrows and European Starlings usurping the nest sites of native species.

Friedmann (1929) hypothesized that nest usurpation may be a behavior leading to brood parasitism over evolutionary time. Satisfying as such an evolutionary sequence may be, usurpation and brood parasitism are very different reproductive strategies, involving different behaviors and morphologies. Brood parasitism generally results from a cryptic female surreptitiously laying an egg in the nest of a host species (Friedmann and Kiff 1985) while usurpation often involves one or two aggressive, sometimes colorful individuals openly driving the nest builders away (Friedmann 1929, Skutch 1969a). The presence of both usurper and brood-parasitic species in a group such as the Icterini is likely a result of a flexible nest placement program in the group's common ancestor, and both usurpation and parasitism may be viewed as viable reproductive strategies, rather than one being the precursor to the other.

Nest type was not independent of latitude, with cavity usurpation more frequently observed in

temperate than tropical/subtropical zones, and enclosed nest usurpation observed more frequently in tropical/subtropical than temperate zones. Cup usurpation was observed with similar frequencies in all zones, although the sample size for this nest type is small. In addition, usurpation occurred more frequently in tropical/subtropical regions than expected, based on the number of studies conducted at low latitudes in the journal sample. A past bias toward conducting research in temperate zones may partially account for the skewed pattern regarding temperate vs. tropical observations of cavity usurpation, because woodpeckers are well-represented in tropical areas and have their cavities usurped in the tropics as well as in temperate habitats (Short 1979, 1982). However, one would expect such a skew to apply to observations of enclosed nests as well, assuming enclosed nesters have been studied proportionately as often as cavity nesters at various latitudes. Ricklefs (1969), in an analysis of oscine nest types, found that 6% of the species in New York, and 25% of the species in the Panama Canal Zone built enclosed nests, while 20% of the New York species and 12% of the Panama species used enclosed spaces, "niches," or natural cavities. Collias and Collias (1984) compiled data similarly illustrating that a higher percentage of species in tropical and subtropical areas built enclosed nests (range = 22–46% for six studies) than in temperate areas (range = 6–11% for three studies).

Why might enclosed nesters be more common in tropical/subtropical regions than in temperate regions? Numerous studies demonstrate that nest predation rates are higher in tropical than temperate regions (Snow and Snow 1963, 1973, 1979, Skutch 1966, Ricklefs 1969, Willis 1974, but see Oniki 1979, Gibbs 1991). Ricklefs (1969) suggested that higher predation rates in the tropics may have led to a more even distribution of nest types, with the result that a greater proportion of nests are enclosed.

Other factors may encourage the construction of enclosed nests in tropical and subtropical regions. Many species that breed in temperate zones migrate from wintering grounds, and it may not be worthwhile to construct an elaborate nest for the short breeding season. However, in tropical regions, where many species reside in one area all year long, it may be advantageous to invest in nests that can be used for breeding and roosting year-round. Plain-fronted Thorn-

bird nests, for example, are used as roosting sites outside the breeding season (Lindell 1994). In addition, temperate species that reside in one place all year may be less inclined to build substantial nests because the likelihood of nests surviving the harsh weather of a temperate winter is relatively low, compared to the probability in the more moderate climates of many tropical and subtropical environments. Ferguson and Siegfried (1989) demonstrated that 54% of the White-browed Sparrow-weavers' (*Plocepasser mahali*) enclosed nests oriented on the lee side of trees survived two years. These nests are used for breeding and roosting year-round. Finally, several groups that build enclosed nests inhabit tropical and subtropical regions, such as the Furnariidae in the New World and the Ploceinae in the Old World. These groups are speciose, indicating there may be a phylogenetic component to the pattern of more enclosed nests in such areas, perhaps a result of high predation rates over evolutionary time.

Hence, enclosed nesters are more common in tropical/subtropical zones than temperate zones and cavity nesters are relatively less common, which may partially explain the greater frequency with which enclosed nests are usurped in tropical/subtropical zones and cavity nests are usurped in temperate zones. However, the fact that usurpation occurred more frequently at low latitudes than expected, based on where studies have been conducted, indicates this is not the whole explanation.

Enclosed nest and cup usurpation occurred more frequently in open than closed habitats. Enclosed nests may be built in open areas (MacLean 1973, Burger 1976, Collias and Collias 1984, Ferguson and Siegfried 1989, Lindell 1994) and may be a better strategy than cavity nesting in areas where trees suitable for excavation are limited. Enclosed nest usurpation may occur more frequently in open areas, particularly tropical and subtropical savannas and grasslands, than in closed habitats in temperate regions because of the higher number of potential nest site competitors in open, tropical areas. Studies in temperate forests, where one expects a low ratio of the number of species to the number of potential nest niches support predictions of nest-niche divergence among species (Martin 1988a, 1988b, 1988c, 1993). In open tropical habitats, however, there may be a high ratio of the number of species to the number of potential nest niches, because

of the diversity of avifauna and the limited structural heterogeneity of the vegetation. Hence, in temperate forests, where the number of nest niches likely exceeds the number of species, nest-niche partitioning is possible; in open, tropical habitats like savannas, where the number of species likely exceeds the number of nest niches, it may be more difficult.

Observations of cavity usurpation occurred about equally frequently in closed and open habitats and, as mentioned, almost all occurred in the temperate zone. Hence, instances of cavity usurpation did not contribute to the overall patterns of usurpation being more common than expected at low latitudes and in moderately open habitats. I expect that cavity usurpation occurs commonly in tropical/subtropical zones but that very few studies have been conducted on cavity nesters in such areas. Picids occurred only once in the over 200 species represented in the journal sample. Also, given their dependence on trees for nest sites, it is not surprising cavity usurpation is not predominantly an open habitat phenomenon. Finally, given the high value of cavities (Lack 1948, Nice 1957, Ricklefs 1969), and the lack of enclosed nests in the temperate zone, cavity usurpation is expected there.

Usurpation took place more often than expected in moderately open habitats and less often than expected in fully open habitats, based on comparison with the sample of journal articles. I believe this pattern results from the large number of studies conducted on birds inhabiting aquatic environments, and for which very few cases of usurpation have been reported. Fifty of 103 instances of studies in fully open habitats (48.5%) in the journal sample involved species of the families Laridae, Procellariidae, Charadriidae, Scolopacidae, and Anatidae. It is unclear why so few instances of usurpation have been reported for these groups.

Nest usurpation is one process by which species are able to develop nesting associations. Associations can occur through nest usurpation when, as is the case with Plain-fronted Thornbirds, Sociable Weavers (*Philetarius socius*) and Monk Parakeets (*Myiopsitta monachus*) different sections of the nest are used simultaneously by the usurper species and host species (MacLean 1973, De Lucca 1992, Lindell 1994). Such associations may result in more individuals guarding the nest, and enhanced mobbing responses against predators (cf. MacLean 1973, Lindell

1994). Some studies provide strong evidence of greater reproductive success for individuals nesting in interspecific associations, compared to those nesting outside such associations (Clark and Robertson 1979, Wiklund 1979, 1982, Bijlsma 1984, Burger 1984).

Nesting associations may be particularly important in areas with diverse predator assemblages. Nest-niche divergence may be expected in situations in which a few predator species become more effective with increasing density of prey nests because of enhanced search images (Martin 1988b). However, nest-niche divergence may be less effective as an anti-predation strategy where many different species prey on nests. In temperate areas with low nest-predator diversity, making one's nest difficult to find may effectively protect against a few types of potential predators. In studies in Arizona, for example, the primary nest predators were squirrels and chipmunks (Martin 1988b). However, tropical areas have diverse assemblages of avian, mammalian, and reptilian nest predators with an associated diversity of sensory perception (Skutch 1954, 1960, 1967, Lindell, pers. obs.). It may be more difficult to hide one's nest from many different predators than just a few. In such environments nesting associations achieved through convergence of two or more species on a particular nest niche may be a more effective, generalized nest defense strategy than nest-niche divergence.

Hence it appears that strategies that may have evolved in particular lineages primarily to increase reproductive success, such as cavity nesting and the construction of enclosed nests, have provided alternative nest sites to a range of other species that are able to take advantage of such sites. Species furnishing the nest sites experience trade-offs between the advantages of a nest that is relatively safe from predators, and the disadvantages of constructing a nest that is covered by competing species. In some cases, the joint nesting that results may enhance the reproductive success of the hosts (Lindell 1994). Nest usurpation and nest-niche convergence are predicted to be most prevalent in areas with valuable nests such as cavities and enclosed nests, in areas of low structural heterogeneity of the vegetation and diverse assemblages of potential competitors/associates and predators. When one or several of these conditions prevail, species may converge, rather than diverge in resource use, leading to interspecific interactions that will

further influence the behavior and ecology of the interacting species.

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