ON THE ORIGIN AND EVOLUTION OF NEST BUILDING BY PASSERINE BIRDS[1]

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Abstract. The object of this review is to relate nest-building behavior to the origin and early evolution of passerine birds (Order Passeriformes). I present evidence for the hypothesis that the combination of small body size and the ability to place a constructed nest where the bird chooses, helped make possible a vast amount of adaptive radiation. A great diversity of potential habitats especially accessible to small birds was created in the late Tertiary by global climatic changes and by the continuing great evolutionary expansion of flowering plants and insects. Cavity or hole nests (in ground or tree), open-cup nests (outside of holes), and domed nests (with a constructed roof) were all present very early in evolution of the Passeriformes, as indicated by the presence of all three of these basic nest types among the most primitive families of living passerine birds. Secondary specializations of these basic nest types are illustrated in the largest and most successful families of suboscine birds. Nest site and nest form and structure often help characterize the genus, as is exemplified in the suboscines by the ovenbirds (Furnariidae), a large family that builds among the most diverse nests of any family of birds. The domed nest is much more common among passerines than in non-passerines, and it is especially frequent among the very smallest passerine birds the world over. Each basic type of nest built by passerines has advantages and disadvantages in specific ecological situations, and nest type depends on a balance of multiple factors that involve the nest site, the physical environment, the community, and the size and behavior of the birds.

Key words: evolution, nest, Passeriformes, body size, Furnariidae, Asthenes anthoides, Myiornis auricularis.

INTRODUCTION

This review attempts to determine how nest building relates to the origin and early evolution of a major taxonomic category—the passerine birds. The Order Passeriformes includes three-fifths of the living species of birds, and the origin and adaptive radiation of passerine birds is arguably the most important problem in ornithology, after the origin of birds themselves.

More explicitly, the goals of this review are to attempt to answer four inter-related questions: (1) what are the most general or basic nest types among present-day passerine birds? (2) what were the basic nest types among ancestral or early passerines? (3) what was the history and subsequent specializations of these basic nest types in the evolution of the larger, more successful phylogenetic lineages of suboscine birds? (4) what selection pressures and ecological conditions led to the evolutionary origins of the basic nests types among passerine birds? The four main sections of this review paper correspond to these four questions.

On the basis of various derived traits, Raikow (1982) presents evidence that the Order Passeriformes is a monophyletic group. The perching foot of passerines, unlike that of other birds, has a large hind toe whose tendon is not joined to the tendons of other toes, thus permitting maximum flexibility of the large and opposable hind toe. It is a reasonable assumption that this arrangement should help many passerines in escaping from enemies by moving speedily and

skillfully inside bushes and other dense vegetation where they often nest. This does not exclude other possible functions of the hind toe.

Passeriformes share other very important ancestral traits that are not unique to this order. Two of these traits that may well be keys to their success in evolution are small body size (Fitzpatrick 1988, Kochmer and Wagner 1988) and the building of elaborate nests (Collias and Collias 1984). Since passerine birds are in general smaller than birds of most other orders, and include more species than all other orders combined, it is clear that passerine birds have generally done better than larger birds in invading the diverse terrestrial habitats of the earth.

Small body size may not be the only trait responsible for success of passerine birds. Fitzpatrick (1988:75) states: "some aspects of being small-bodied, large-brained, arboreal, diurnal, largely insectivorous, with high metabolic rate, short generation time, and vocally sophisticated appear to have endowed members of the passerine clade with the opportunity or propensity to radiate at a rate faster than that characterizing birds of any other clade." To this list, I would add and emphasize passerine nest-building behavior.

In general, small body size combined with powers of flight has important implications for nest-building behavior. Small birds often build relatively small nests that can be placed and hidden in a great variety of nest sites by different species. Small birds can build with lighter materials and may thus reduce the energetic costs of building.

Most modern orders of birds seem to have arisen in the early Tertiary, but fossil passerine birds do not appear in large numbers until the late Cenozoic (Olson 1989, Fedducia 1995). The Passeriformes were not important components of the avian fauna until the Miocene. The previously dominant arboreal perching birds were the Coraciiformes (Olson 1989, Fedducia 1995), all modern representatives of which are hole-nesters (Collias and Collias 1984).

The most evident environmental change world wide during the late Cenozoic has been the diminishing of forests and the concomitant expansion of open woodlands, grasslands, and deserts (Behrensmeyer et al. 1992). Increased global diversification and seasonality of environments was accompanied by a continuing great increase in diversity of flowering plants (Beh-

rensmeyer et al. 1992) and insects (Labadeira and Sepkoski 1993), and a great diversity and abundance of passerine birds. Nectar from flowers and small seeds are especially available to small birds, while insects were probably the major food of early passerines judging from primitive passerines today.

A theoretical basis for the evolution of the Order Passeriformes as a major taxonomic category stems from the book by Simpson (1944) *Tempo and Mode in Evolution,* and his later book (1953) on *The Major Features of Evolution* where he states (p. 346): "As a generalization, the development of a higher category seems always to involve the rise of some distinctive sort of adaptation related to spread into a major adaptive zone." Simpson deduced certain broad principles of evolution from the best known fossil histories of vertebrates, especially mammals. He recognizes three modes or phases in the evolution of a major taxonomic category. I apply these three phases to the evolution of the Passeriformes in an attempt to interpret the early evolution of nest building by passerine birds. These three phases are about as follows:

NEW ECOLOGICAL OPPORTUNITIES

A vast number of new ecological niches in the Late Tertiary must have opened up with the greatly increased environmental and biotic diversification over the world (Behrensmeyer et al. 1992). Early passerine birds were uniquely preadapted to invade many such new habitats by their small body size, powers of flight, and flexible nesting behavior. The ability of passerine birds to construct their nests where they wish must have greatly increased the number and variety of nest sites available to them, enabling them to compete effectively with the hole-nesting and often larger coraciiform and piciform birds (Collias 1964). Numerous nest sites, more available to small than to large birds, must have included nesting on green land plants or on emergent green plants over water, or on twigs and fine branches of bushes or trees, as well as nests pensile from drooping twigs or vines.

PRIMARY ADAPTIVE RADIATION

Radiation initially at the level of species and genera gives a trial and error mechanism for evolution. Early in evolution of primitive passerines, there were three basic nest types: hole nests (in ground or tree), nests open above, and

domed (constructed roof) nests. Evidence for this conclusion comes from the nests of the most primitive living passerines (see below).

SECONDARY ADAPTIVE RADIATION AND SPECIALIZATION

Secondary radiation and specialization involved persistence of the more successful lines in evolution. Different phylogenetic lines (genera, subfamilies and families) have elaborated different specializations of the basic nest types. Parallel and convergent evolution are common, especially among passerine birds (Mayr and Ashlock 1991) and their nests (Collias and Collias 1984). Secondary adaptive diversification of nests will be exemplified below with three large suboscine families, the Tyrannidae, Thamnophilidae, and especially the Furnariidae. Domed nests have evolved by two routes: roofs on ground nests, and on nests in trees hung from peripheral drooping branches, twigs and vines.

BASIC NEST TYPES AMONG PASSERINE BIRDS

Knowledge of the basic nest types sets the stage for further analysis. Basic nest types refer especially to nest form and general nest site, and among passerine birds include hole nests, open-cup nests (not in holes) and domed nests with a constructed roof. Hole nests may be in the ground, in rock crevices, or in trees. The reason these nest types are termed "basic nest types" is because each basic nest type has been elaborated in evolution into a wide variety of subsidiary and specialized kinds of nest (Collias and Collias 1984).

Table 1 shows the frequency of the basic nest types in the Passeriformes. This table is based on the number of families having each nest type (Collias and Collias 1984). It should be recognized that some bird families may have more than one basic nest type and may be entered into the table more than once. In general, the taxonomy followed is that in the references cited in the table.

Table 1 first compares passerine with non-passerine families. In both cases a nest open above is the most frequent type. For this table, chi-square (χ^2) tests were used for comparisons of two independent groups within columns. Although the table shows percentages of different nest type for each group, the actual nest frequencies were used for calculations of significance of differences; df = 1 for all these tests.

TABLE 1. Percentages of bird families with species having the basic nest type indicated.* Hole nests in ground or tree. Open nests (not in holes) may be a cup, bowl, or platform. Domed nests have a constructed roof.

	Number of families	Percentage of families**		
		Hole nest	Open nest	Domed nest
Non-passerine families	96	34	77	7
Passerine families	65	56	68	52
Comparing suborders:				
Suboscines	12	50	42	58
Oscines	53	55	74	51
Comparing nest sites:				
Ground nests	27	37	41	52
Nests above ground	62	44	63	48

* For references see Harrison 1978, Collias and Collias 1984, Stiles and Skutch 1989. Also see Table 2.
** Percentages do not equal 100 because some bird families have more than one basic nest type.

Passerines nest in holes more often than non-passerines ($\chi^2 = 7.0$, $P < 0.01$). The domed nest is several times more frequent in passerines than in non-passerines ($\chi^2 = 41.4$, $P < 0.001$). Open nests are more frequent in passerine nests above the ground than on the ground ($\chi^2 = 3.8$, $P = 0.053$), and open nests are much more frequent in the oscines than in the suboscines ($\chi^2 = 4.56$, $P = 0.03$).

Table 1 shows that within the suboscines, domed nests are the most frequent nest type; but the number of suboscine families (12) is probably inadequate for a statistical test. The McNemar test (χ^2_{mc}) is appropriate for the same set of families examined twice (Altman 1991); in this case we asked whether each family did or did not have an open and/or domed nest. Within the oscine suborder open nests (32/53 families; 60%) are more frequent than domed nests (20/53 families; 37.8%) ($\chi^2_{mc} = 4.23$, df = 1, $P = 0.04$). Furthermore, there are 23 families of oscines that have open but not domed nests, and only 11 families of oscines that have domed but not open nests. In passerine nests above ground, open nests (not in holes) are more frequent than nests in holes ($\chi^2_{mc} = 3.8$, $P = 0.05$), but do not differ from the frequency of domed nests ($\chi^2_{mc} = 1.80$, $P = 0.18$)

ORIGIN OF BASIC NEST TYPES IN PASSERINE EVOLUTION

Before considering nests of the possible ancestors of passerine birds, one may ask what was

the evolutionary sequence for the basic nest types: hole, open, or domed nest? Simpson (1944, 1961) and Mayr and Ashlock (1991) have discussed criteria for helping to decide whether a given trait is ancestral or derived within a given taxonomic group. None of these criteria (e.g., generality, simplicity, ontogeny, or outgroup comparison) is sufficient by itself.

A hole nest in the ground is very common among reptiles, the class ancestral to birds, suggesting that the hole nest is probably most primitive for birds that sit on their eggs. Nests built in pre-existing holes generally lack the site flexibility of nests constructed in a site of the bird's own choosing, because open nests and domed nests can be placed in a greater number of sites above ground as well as on the ground than can hole nests.

The open nest, by the criteria of commonality (general occurrence), relative simplicity, and ontogeny, appears closer to the ancestral type of bird nest than does the domed nest. We cannot use the criterion of outgroup comparison with much confidence to distinguish ancestral from derived nest types for the Order Passeriformes because the non-passerine order most closely related to the Passeriformes is controversial, and because parallelism and convergence are rampant among passerines (Mayr and Ashlock 1991), including their nests (Collias and Collias 1984).

Evidence from bird ectoparasites, i.e., feather lice (order Phthraptera; Turner 1971) and feather mites (Order Acarina; Cerny 1973), that have evolved with their hosts supports the traditional view (AOU 1983) based largely on morphology that the closest common ancestors with the passerine order are the coraciiform and piciform orders (Collias and Collias 1984), all species of which nest in holes. The ultrastructure of feathers (Chandler 1916, Brom 1990) supports close relationship of the Passeriformes to piciform birds and to hummingbirds. Evidence from DNA hybridization (Sibley and Ahlquist 1990) does not support close phylogenetic relationship of the passerine order to the coraciiform-piciform birds, but places the Passeriformes closest to various open-nesting orders. It is possible that the common ancestor of the passerine and related orders built an open nest, but the matter cannot be regarded as settled because of the prevalence of parallel and convergent evolution in nest building.

Based on syringeal structure, the Order Passeriformes is often divided into suboscine and oscine birds. Ames (1971) concluded that the suboscines, which together with the lyrebirds (Menuridae) and scrubbirds (Atrichornithidae) have a simpler syrinx, are more primitive than the rest of the oscine passerines. For further analysis of early nest evolution, I focus on the suboscines and the lyrebirds and scrubbirds.

There is agreement, based on both morphology (Raikow 1987) and DNA hybridization (Sibley and Ahlquist 1990) combined with numerical cladistic analysis (by these authors), that the most primitive families of the Order Passeriformes are the nine small families listed in Table 2. These include seven families of suboscine passerines plus the Australian lyrebirds and scrubbirds which often are considered to be the most primitive oscine passerines and are sometimes placed in a suborder of their own (Menurae). Except for the lyrebirds, 8 of the 9 primitive families are generally small birds and have one or more species only 15 cm or less in body length. Table 2 also shows the number of species for which nest-type data exist in each of these families that builds the nest type indicated. However, there is no general agreement as to which of these nine primitive families most closely resembles the passerine ancestors. Presumably they all share some traits of the common ancestor.

Traditionally, the broadbills (Eurylaimidae) of Old World tropical forests have been considered to be the most primitive living family of passerine birds, and they often have been listed first in classifications of passerine families (Harrison 1978). Broadbills and philepittids build pensile nests with a side entrance and the nests may be high up in trees. Prum (1993) studied the phylogeny of the broadbills, and concluded that the rather specialized nests were all derived within the family. He also united the Eurylaimidae and Philepittidae into one family.

Sibley and Ahlquist (1990) concluded from DNA hybridization studies that "the acanthisittids are the survivors of an ancient passerine lineage with no close relatives" and that it is possible that they should be assigned to a third suborder as the sister group of the suboscines and oscines. The three living species of New Zealand wrens (acanthisittids) build enclosed nests, often nesting in tree holes or in rock crevices.

Feduccia and Olson (1982) suggested that the

TABLE 2. Basic nest types within the most primitive families of passerine birds. Number of species having each nest type are tabulated (some species have more than one nest type). Number of species examined per family in parenthesis.

Family (n species) and reference no.*	In burrow or crevice	Nest on ground		Nest above ground		
		Domed	Open	In tree hole	Domed	Open
Acanthisittidae (3) 1	3	2		2		
Atrichornithidae (2) 2					2	
Menuridae (2) 2		2		1	1	
Pittidae (12) 3,4		9		1	7	
Philepittidae (2) 5					2 pensile	
Eurylaimidae (10) 3					10 pensile	
Formicariidae (8) 6 (ground antbirds)				3		7
Conopophagidae (2) 7			1			2
Rhinocryptidae (14) 8	12	1		3	2	
Total (55 species)	15	14	1	10	24	9

* 1 (Oliver 1955, Falla et al. 1978), 2 (Frith 1979), 3 (Medway and Wells 1976, Smythies and Cranbrook 1981, Ali and Ripley 1983, Keith et al. 1992), 4 (Coates 1990), 5 (Langrand 1990), 6 (Wiedenfeld 1984, Hilty and Brown 1986, Quintela 1987, Stiles and Skutch 1989, Whitney 1992, Ridgely and Tudor 1994), 7 (Fraga and Narosky 1985, Hilty and Brown 1986), 8 (Johnson and Goodall 1967, Stiles 1979, Fraga and Narosky 1985, Hilty and Brown 1986, Rosenberg 1986).

Australian lyrebirds (Menuridae) and scrubbirds (Atrichornithidae) together with the New World tapaculos (Rhinocryptidae) "are among the most primitive of the Passeriformes and are representative of the ancestral stock that gave rise to the remainder of the passerines." But Rich et al. (1985) attributed some of the skeletal similarities between these groups to convergence resulting from weak powers of flight. Birds of these families build enclosed nests, the Australian species on or just above the ground, whereas the tapaculos build a variety of hole or domed nests and many of the species nest in burrows or rock crevices.

Ames (1971) and Fedducia and Olson (1982) described certain primitive characteristics of the ground antbirds (*Formicarius, Grallaria,* and their allies), Formicariidae in the narrow sense of Sibley and Ahlquist (1990), and the allied gnateaters (Conopophagidae). These traits agree with the DNA hybridization results of Sibley and Ahlquist (1990). Helmut Sick (1993:394) states that "Various indications lead me to believe that the oldest Passerines were terrestrial resembling formicariids such as the *Grallaria* antpittas." The ground antbirds and the gnateaters generally have open-cup or open-bowl nests, unlike the other primitive families of suboscines which have hole or domed nests (Table 2).

To recapitulate, the four or five families each considered by different authorities to be the most primitive passerine family or families, when taken together build all the basic nest types: hole (ground or tree-hole), open, and domed nests. Thus passerine birds probably built all the basic nest types very early in their evolution, even though the very first ancestor of the Order Passeriformes and its nest form remains uncertain.

If all nine primitive passerine families are considered together, Table 2 brings out this same point somewhat differently. Hole-nesters include 25 species in five families, birds with open nests include 10 species in two families, while birds with domed nests include 38 species in seven families. Compared with passerine birds in general (Table 1), there seems to be a smaller percentage of open nests in the primitive families. However, the main point is again, that all the basic nest types are present among primitive living passerines, suggesting a similar range of adaptability in nest-building behavior of early passerine birds.

Table 2 also shows that primitive passerine families taken together often build their nests above the ground (43 species in all nine primitive families), and also fairly often in or on the ground (30 species in five families). This suggests that early passerines had considerable flexibility in choice of nest sites.

Six of the nine primitive passerine families have more than one of the basic nest types and nest sites (Table 2), suggesting adaptive flexibility within as well as between these families. In fact, in three of these families, the same species may build on the ground or above the ground, in holes or outside holes, including the

Rifleman (*Acanthisitta chloris*; Gray 1969), the Superb Lyrebird (*Menura novaehollandiae*) and the Noisy Pitta (*Pitta versicolor*) (Frith 1979). The Rainbow Pitta (*P. iris*) helps bridge the gap between two basic nest types; it builds a domed nest varying to a shallower, partly open nest on the ground or up to 3 m above ground.

In conclusion, the nine most primitive passerine families, taken together, have all the basic nest types of passerine birds: hole nests (in ground or tree-holes), open-cup or open-bowl nests (outside of holes), and domed nests with a constructed roof. If these nine primitive families and their varied nests are representative of early passerine birds, one can conclude that such passerines were pre-adapted by their nest diversity for invasion and specialization into a great variety of nest sites. The primary adaptive radiation of species and their nests in the primitive passerine families fits into Simpson's (1944) general picture of the initial "explosive" adaptive radiation of a major taxonomic group, here the Order Passeriformes.

EVOLUTION OF INCREASED NEST DIVERSITY WITHIN LARGE SUBOSCINE FAMILIES

The object of this section is to illustrate secondary adaptive radiation and specialization of nests within the largest and most successful suboscine families, the New World flycatchers (Tyrannidae, 384 species, Stiles and Skutch 1989), typical antbirds (Thamnophilidae, 188 species, Sibley and Ahlquist 1990), and ovenbirds (Furnariidae, 214 species, Stiles and Skutch 1989). The Tyrannidae and the Furnariidae build among the most diverse nests of any family of birds.

The preceding section showed how primary adaptive radiation of nests, illustrated by primitive passerine families, helped to lay the basis for expansion of the passerine order. The present section illustrates how secondary adaptive radiation and diversification within large suboscine families leads to multiplication of genera with characteristic nests, especially exemplified by the ovenbirds. Nest form and structure often help to characterize genera in birds (Collias and Collias 1984). About half (48%) of 65 passerine families have more than one of the basic nest types (hole, open, or domed) compared with only about 16% of 96 non-passerine families (χ^2 = 19.5, $P < 0.001$), suggesting more active evolution of nest-building behavior at subfamily and

generic levels in the passerine order (Collias and Collias 1984).

The Tyrannidae is one of the largest bird families in the world (Stiles and Skutch 1989). Traylor and Fitzpatrick (1982) tabulated the nests of the many genera. Nest form is generally consistent for different species in the same genus. There are about twice as many genera with an open-cup nest (60%) as with a domed (not in a hole) nest (31%), whereas nests in holes (10%) are much less frequent.

Traylor and Fitzpatrick (1982) place the genus *Elaenia* (cup nest) as most primitive in the family. Based on phylogenetic studies of many tyrannid groups, cup nests have apparently evolved independently and repeatedly into globular (domed) nests in New World flycatchers (Prum and Lanyon 1989). In Helmut Sick's general account of the Tyrannidae, he states "Many species with closed nests ... have colored eggs, demonstrating their descent from ancestors with open nests" (1993:458). Fitzpatrick has seen the Great Kiskadee (*Pitangus sulphuratus*) "building a perfectly normal open cup, which it then gradually covered over during the first two weeks of incubation" (Traylor and Fitzpatrick 1982:16). All this evidence suggests that the immediate ancestors of the Tyrannidae built open-cup nests.

Based on results with DNA hybridization, Sibley and Ahlquist (1985) recognized a lineage of tyrannids which separated from the other tyrannids before the radiation of the typical tyrants, becards, cotingas, and manakins began. They designated this group the subfamily Pipromorphinae and considered it to be the sister group of the other subfamilies of Tyrannidae. They suggest that the Pipromorphinae may include at least eight genera. Of these eight genera, information on the nest is available for six: *Mionectes* (including *Pipromorpha*), *Leptopogon*, *Pseudotriccus*, *Corythopis*, *Hemitriccus*, and *Todirostrum*. Insofar as it is known, all of these six genera build domed (roofed) nests. Considering the frequency of parallel and convergent evolution of nests in the Tyrannidae, it still is possible that the common ancestor of this family built an open-cup nest and that the pipromorphs independently evolved domed nests.

Within the Tyrannidae, many specialized subtypes of cup and domed nests have evolved; these are described by Skutch (1960), and by Hilty and Brown (1986). For example, the open-

cup nest in different species and genera may vary greatly in depth, mode of attachment to the substrate, thickness of walls, compactness or looseness, and in nature of the nest materials used. In this family, open-cup nests may often be saddled on a branch or suspended by the rim, whereas domed nests in trees or bushes generally are pensile.

Besides the tyrant flycatchers and the ovenbirds, the largest family of New World suboscines is the typical antbirds (Thamnophilidae). Like the tyrant flycatchers, their center of abundance is the lowland rainforest. The antbird family has specialized on variations on the open-cup nest. The typical antbirds parallel many tyrant flycatchers in similar specializations of the open-cup nest which, as in nests of the tyrant flycatchers, varies with different species in depth, attachment, thickness, compactness or looseness, and in nature of nest materials, as described by Skutch (1969a, 1996), Hilty and Brown (1986), and Stiles and Skutch (1989). These particular convergences in the two different families suggest specific selection pressures that remain to be investigated. For example, many of the typical antbirds, like some flycatchers, have open-cup nests suspended by the rim in a twig fork, but the adaptive significance of this mode of attachment is unknown. Rarely, thamnophilid antbirds place the nest in a hollow stump (Bicolored Antbird *Gymnopithys bicolor*) or build a domed nest in a bush as by the tiny Brown-bellied Antwren *Myrmotherula gutturalis* or by the White-backed Fire-eye *Pyriglena leuconota* which places its domed nest on or near the ground in herbaceous vegetation (Oniki 1979, Sick 1993).

The ovenbirds (Furnariidae) will be used here to exemplify secondary adaptive radiation among enclosed nests. Virtually all furnariids, as far as we know, have enclosed nests, either in a burrow, rock crevice, tree hole, or other protected place, or else construct their own roof, so furnariid ancestors must have built enclosed nests. Only two furnariids have been described as having an open nest. The Band-tailed Hornero (*Furnarius figulus*) does not build the adobe oven nest typical of its genus, but makes a simple, open nest of grass in a well-protected place, e.g., beneath roof tiles, hidden among epiphytic bromeliads, or among bases of large, erect palm leaves (Studer and Veilliard 1990, Sick 1993). It is evident that such nest sites in effect provide

a roof. The Bay-capped Wren-Spinetail (*Spartonoica maluroides*) builds a more or less open nest on or very close to the ground amidst dense clumps of rushes (*Scirpus*) and grasses (*Zizaniopsis*) that effectively roof over the nest (Narosky 1973).

Cladistic analysis of ovenbird genera by Fitzpatrick (1982) based on Vaurie's 1980 monograph indicates certain genera as the outgroups to the rest of the Furnariidae. Omitting the highly specialized adobe nests of horneros (*Furnarius*), this analysis suggests that ground-hole nesters, such as the miners (*Geositta*) which excavate and nest in tunnels, are closest to the ancestral type. But DNA hybridization studies of the ovenbirds indicated the leaftossers (*Sclerurus*) as the sister group to the rest of the ovenbirds (Sibley and Ahlquist 1990). Leaftossers, like miners, also excavate a tunnel in soil for their nests, which also suggests that nesting in holes in the ground was the primitive nest type in Furnariidae. There is an interesting parallel with an oscine family, the swallows (Hirundinidae), which also has diverse nests and in which a phylogenetic analysis suggested that digging a burrow was the primitive nest type (Winkler and Sheldon 1993).

Nests of Furnariidae, insofar as then known, were described by Vaurie (1980). Other important general descriptions of furnariid nests are by Hudson (1920), Johnson and Goodall (1967), Skutch (1969a, 1996), Hilty and Brown (1986), Stiles and Skutch (1989), Sick (1993), and Ridgely and Tudor (1994). A very useful book by Narosky et al. (1983) describes nests of the Furnariidae of Argentina, where 76 species of ovenbirds have been recorded (Narosky and Yzurieta (1987). In Argentina during the southern spring of 1989, I saw examples of most of the main types of furnariid nests.

Table 3 lists the main types of nests built within different genera of the ovenbirds. This table is based on 116 species and 31 genera with adequate information on the nest, out of 214 species and 34 genera of Furnariidae listed by Vaurie (1980) in his monograph of the family. Information on the nest of more species of ovenbirds probably would not radically change the general picture because general nest form and structure is usually characteristic of the genus in passerine birds (Collias and Collias 1984). Vaurie combined many old monotypic genera into fewer genera, resulting in considerable taxonom-

TABLE 3. Nests of ovenbirds, Furnariidae; summary table for genera. Number of species per genus with adequate information on nest in parenthesis. Some species build in more than one type of nest site.

Genus (n species)	In burrow or crevice	Nest on ground		Nest above ground		
		Domed	Open	In tree hole	Domed	Open
Geositta (7) and Cinclodes (9)	16					
Upucerthia (7)	7			1		
Chilia (1)	1			1		
Furnarius (4)		1 (rare)			3 adobe	1*
Eremobius (1)					1	
Aphrastura (1)				1		
Spartonoica (1)		1				1*
Limnornis (2)					2 woven	
Phleocryptes (1)					1 woven	
Sylviorthorhynchus (1)					1	
Leptasthenura (5)	2	1		2	4	
Schizoeaca (2)					2 mossy	
Schoeniophylax (1)					1	
Certhiaxis (2) and Cranioleuca (8)					10	
Synallaxis (12)		2			11	
Asthenes (13)	1	5		1	5**	
Coryphistura (1)					1**	
Anumbias (1)					1**	
Phacellodomus (7)					7	
Pseudoseisura (3)					3	
Margarornis (1)				1 mossy		
Pseudocolaptes (2)				2		
Philydor (7)	2			6		
Automolus (5), Sclerurus (3) and Thripadectes (3)	11 (saucer lining)					
Lochmias (1)	1 (globular lining)					
Pygarrhichas (1) and Xenops (3)				4		
Total: 116 species (31 genera)	41 (11)	10 (5)	0	19 (10)	53 (16)	2 (2)

* F. figulus (Sick 1993), S. maluroides (Narosky 1973).
** Asthenes baeri, Coryphistura, and Anumbias with narrow superior entrance tunnel to chamber in thick, oval nests.

ic simplification, although further study may be needed in some cases (Fitzpatrick 1982).

Table 3 shows that, in general, the type of furnariid nest helps characterize and is usually consistent with the genus. Genera are defined by several characters (Mayr and Ashlock 1991), of which the nest is only one, but a very helpful one. Of 19 genera in Table 3 with more than one species listed, 16 or 84% build only one basic type of nest, either a hole-nest or a domed nest. Only 3 genera (Furnarius, Leptasthenura, and Asthenes) have more than one basic nest type (binomial test, $P = 0.002$, comparing 3 genera versus 0 if one assumes all genera have the same basic nest type). The tit-spinetails (Leptasthenura) have four types of nests and nest sites, but these birds often occupy old nests of various other species of birds. They characteristically line their nests heavily with feathers.

Table 4 describes well-established examples of nests of different species representing various

types of nests built in the Furnariidae. The impressive diversity of enclosed nests built in this family is evident. Figures 1–3 illustrate three of the most distinctive nest types.

Some species and a few genera of ovenbirds vary greatly in their nest building, which might suggest how one kind of nest may have evolved into another. Some ground-nesting species (in Geositta, Cinclodes, and Automolus) may dig their own nest tunnel or use other holes such as rodent burrows. Treehunters (Xenops) may dig their own nest hole in a tree, or use one dug by a piculet (Picumnus). Some furnariid species may nest in holes in the ground and also in holes in trees, e.g., Philydor rufus, the Buff-fronted Foliage-Gleaner. Domed nests of Synallaxis (spinetails) are generally built of twigs, but S. albescens, the Pale-breasted Spinetail often uses straws or grasses instead of twigs. Domed nests of species of Asthenes may be placed on the ground or in bushes, whereas the nest entrance

TABLE 4. Examples of species representing special types of ovenbird (Furnariidae) nests.

A. Hole nests
   1. In tunnel dug in soil, *Geositta cunicularia* (Common Miner); *Automolus leucopthalmus* (White-eyed Foliage-Gleaner) with cup-nest of plant stems in chamber at end of tunnel; *Lochmias nematura* (Sharp-tailed Streamcreeper) builds globular nest of plant material with side entrance in tunnel.
   2. Natural cavities in ground or tree. *Cinclodes patagonicus* (Dark-bellied Cinclodes) nest usually in ground; *Aphrastura spinicaudus* (Thorn-tailed Rayadito) nest usually in cavities of trees or behind piece of bark.
   3. An excavated tree-hole. *Pygarrhichas albogularis* (White-throated Treerunner) digs its nest hole in decaying wood.
B. Domed (with constructed roof) nests with one compartment.
   1. Adobe nest. *Furnarius rufus* (Rufous Hornero).
   2. Grass nest on ground. *Asthenes hudsoni* (Hudson's Canastero).
   3. Twig nest with side entrance, on bushes or trees. *Pseudoseisura gutturalis* (White-throated Cacholote, Fig. 1); *Schoeniophylax phryganophila* (Chotoy Spinetail); *Synallaxis spixi* (Chicli Spinetail).
   4. Mossy nest. *Margarornis squamiger* (Pearled Treerunner) nest with side entrance; *Cranioleucus erythrops* (Red-faced Spinetail) nest with bottom entrance.
   5. Nest woven of flexible plant materials in aquatic vegetation. *Limnornis curvirostris* (Curve-billed Reedhaunter); *Phleocryptes melanops* (Wren-like Rushbird) nest exterior with pellets of mud or clay.
C. Thick-walled twig nests with narrow top entrance tunnel. *Anumbias annumbi* (Firewood-gatherer); *Coryphistera alaudina* (Lark-like Brushrunner).
D. Compound nest of twigs. Roofed pensile nest with more than one compartment. *Phacellodomus rufifrons inornatus* (Plain-fronted Thornbird, Fig. 2).
E. Uses and lines tree cavities or domed nests of another species of furnariid. *Leptasthenura platensis* (Tufted Tit-Spinetail).

varies in this genus from one side to a narrow entrance tunnel opening at the top of the nest.

Compound nests of *Phacellodomus rufifrons inornatus,* the Plain-fronted Thornbird (Fig. 2), vary considerably in length and number of nest compartments, up to eight or nine that are built one above the other, each with its own side entrance (Skutch 1969b, 1996, Thomas 1983). A nest is occupied by only one pair of thornbirds and their young, and the eggs are laid only in the bottom compartment. The Greater Thornbird (*P. ruber*) has only one or two compartments in its large twig nest (Narosky et al. 1983).

The different nest types of canasteros (*Asthenes*) suggest that a change from nesting in the ground to nesting above ground in shrubs might

FIGURE 1.   Nest of White-throated Cacholote.

FIGURE 2.   Nest of Plain-fronted Thornbird.

have evolved in this genus. Five of seven plain-backed species of *Asthenes* build domed nests on branches of shrubs, whereas the other two species nest either in a hole in the ground (*A. modesta*) or in a cactus (*A. cactorum*) (Vaurie 1980, Narosky et al. 1983). Four other species of *Asthenes* have black-streaked upperparts and build domed nests on the ground (Vaurie 1980, Narosky et al. 1983, Ridgely and Tudor 1994). To this list we add a fifth species, *A. anthoides* with black-streaked upperparts.

In Patagonia we found a ground nest of *A. anthoides,* the Austral Canastero, the nest site of which has not been described before. This nest is of interest because it may represent an inter-mediate stage between nesting in the ground, or above ground. The nest (Fig. 3) was found in Santa Cruz province in shrublands near the Rio Chico, southwest of the city of Rio Gallegos (approx. 52°S, 69°W). The nest was hidden on the ground just beneath the center of a low, densely branched juniper-like shrub. The parents brought insects to the nest bush, and on parting the dense foliage I saw the nest which was half-way in the ground. It was in a depression in the soil about 5 cm deep that had presumably been scraped out by the birds and which was lined with white feathers. This depression was cov-ered by a domed roof of twigs laid sparsely over some dark soft plant material, whereas sides of the entrance were of dry grass stems. The side entrance was about 5 cm in diameter. There were

FIGURE 3.   Nest of Austral Canastero.

two nestlings well down in the nest, so we did not disturb the nest further. The species was confirmed at the time as *Asthenes anthoides* by Steven L. Hilty and Maurice Rumboll. This species is the only canastero with a heavily streaked back (which we saw clearly) in that part of Argentina (Narosky and Yzurieta 1987).

Johnson and Goodall (1967) mention that Passler found *Asthenes anthoides* nesting "among shrubs" in central Chile, that the entrance hole was close to the top of the rounded nest and protected by a ring of twigs, and that the nest was lined with plant down, dry lichens, and flowers. Unfortunately, one cannot tell from this description whether the nest was on the ground, or up in a shrub.

Further progress in the analysis of the early evolution of passerine nest-building comes from comparing the ecological conditions that favor the evolution of each nest type.

ECOLOGICAL CONDITIONS THAT FAVOR EVOLUTION OF THE BASIC PASSERINE NESTS

The nests of birds, like foraging behavior patterns, give clues to significant problems of ecology (Collias and Collias 1984, Collias 1986, 1991). In forest birds of Arizona, Martin (1988) found that numbers of species were more correlated with density of nesting substrates than with foraging heights and places.

In this section I briefly consider some of the adaptive advantages and disadvantages of hole (cavity) nests, open-cup nests (not in holes), and domed (constructed roof) nests. A more comprehensive treatment is in our book on *Nest Building and Bird Behavior* (Collias and Collias 1984).

Hole nests in general are safer and fledge more young than do nests not in holes (reviewed by Collias and Collias 1984, Skutch 1985). Cavity nesting gives shelter from the weather, helps ameliorate temperature fluctuations, and conserves energy (Kendeigh 1961).

Hole nests in the ground protect from wind chill. In Patagonia, ground-tyrants (*Muscisaxicola,* Tyrannidae) escape strong cold winds by nesting in tunnels in the ground, a clear case of convergent evolution with the miners, *Geositta* (Johnson and Goodall 1967) and earthcreepers, *Upucerthia* (Narosky et al. 1987). These tunnels often are placed in slopes or banks giving some protection from rain or floods.

Nests in the ground may be less vulnerable to predators than nests on the surface of the ground, as shown by controlled field experiments with artificial nests (Martin 1987). Quail eggs in a wicker basket lined with leaves and placed on the surface of the ground in an Arizona forest had a significantly higher predation rate than similar artificial nests buried with the rim even with the ground and partially covered with dead leaves, or eggs simply placed in a hole in the ground.

Tree-hole nests probably provide enhanced protection from weather and from enemies, compared with ground-hole nests. Evidence also indicates tree-hole nests are safer from enemies than open nests not in holes. In central Arizona, nest success was shown for various species to be higher in tree-hole nests than in open nests, and best in tree holes that had been excavated by the birds (woodpeckers and smaller species of nuthatches) themselves (Martin and Li 1992).

The population density of hole-nesting birds often is limited by the availability of tree cavities suitable for nesting, and populations of such birds often have been increased by putting up nest boxes (Hogstad 1975, Bock et al. 1992). Nest cavities excavated by woodpeckers also may make it possible for hole-nesting swallows to nest in some areas (Daily et al. 1993). There are no woodpeckers in Australia and New Guinea and also relatively few passerine birds that nest in tree holes. Only 4 of 33 families (12%) in Australia (Frith 1979) and only 3 of 33 families (9%) in New Guinea (Coates 1990) include passerine species nesting in tree holes, much fewer than is general among passerines over the world (Table 1).

The disadvantages of nesting in tree cavities include intense competition for tree holes with other birds, as well as excessive exposure to arthropod nest parasites (Collias and Collias 1984). In a nine-year study in south Sweden, Nilsson (1984) found that rate of nest failure and rate of predation were greater in nest holes or nest boxes situated low in trees than higher up. High nest holes were preferred and four different species of passerine birds occupied decreasing nest heights according to their dominance status.

To a considerable extent, passerine birds probably were able to escape competition for nest holes by constructing their own nests in sites of their own choosing other than holes (Collias

1964). Birds with open nests tend to avoid areas with a high density of birds that nest in tree holes (Hogstad 1975, Bock et al. 1992)

Flexibility in nest site selection with a constructed nest makes it possible for some species of birds to shift from nesting on the ground to nesting in trees, and vice versa. Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in California usually build their open-cup nests in vegetation on the ground where they are better protected from storms and wind-chill, but in years of late snowfall during the breeding season, many nests are placed up in willows and scrub pines (Morton et al. 1972).

Open-cup nests have an advantage over domed nests in that they are often made of fewer materials and, other things being equal, should therefore generally take less time and energy to build. This difference reaches its climax in the nests of some cotingas (Cotingidae) in tropical South America (Hilty and Brown 1986), certain bulbuls (*Nicator chloris*; Pycnonotidae) in tropical Africa (Chapin, 1953), and certain cuckoo-shrikes (*Lalage leucomela*; Campephagidae) of Australia (Frith 1979), where the nest is so small that it may be completely hidden by the incubating bird. At the same time, very small nest size helps hide the nest from eyes of predators (Snow 1976).

The open-cup nest presumably favors a quicker escape from the attack of a predator, freeing the bird to breed again if its nest is predated. In contrast, a bird incubating in an enclosed nest is more likely to be trapped in the nest by a predator at the entrance. Antbirds generally, and manakins (Pipridae), have open-cup nests usually located in the lower levels of the tropical forest (Traylor and Fitzpatrick 1982), where the nests often are sheltered from the sun, rain and wind by surrounding vegetation, but where predators abound.

North temperate regions have a much higher proportion of passerine species with open-cup nests versus enclosed nests, compared to tropical regions (Collias and Collias 1964, 1984, Ricklefs 1969). Walsberg (1981) used photos taken with a fish-eye lens and found that the cup nests of Warbling Vireos (*Vireo gilvus*) in the western United States were so placed in a tree as to get the sun's warmth in early morning, and yet be shaded in the afternoon when there is a danger that the eggs might die from overheating if long exposed to the hot sun. Hence, cup nests selectively placed often may be advantageous to birds breeding in the cool northern spring.

Parallel adaptations analogous to the above occur on mountains in tropical latitudes. In trees on the slopes of the Mauna Kea volcano in Hawaii, the open-cup nests of a honey creeper, the Common Amakihi (*Hemignathus v. virens*), were placed in sites more exposed to the sun during the cool early breeding period, but were placed deeper in the canopy later in the breeding season when the weather was warmer (van Riper et al. 1993).

Construction and evolution of a roof on ground nests may be favored because predators are generally more numerous on the ground, where open nests may be more subject to predation. In controlled experiments in lowland rainforest in Panama, artificial wicker nests, lined with green leaves and containing quail eggs, had significantly more predation when placed on the ground than when placed 1 m and 2 m up in trees. Predation rates also were greater on such artificial open-cup nests than on artificial enclosed nests placed in similar situations (Loiselle and Hoppes 1983). Haskell (1995) and Major and Kendal (1996) in an extensive review of artificial nest experiments have cautioned against various pitfalls in such experiments, but agree on their potential value.

In India and neighboring countries, 68% of 19 species of babblers (Timaliidae) that build their nests on the ground, build domed nests, whereas 92% of 63 species that build their nests above the ground, build open-cup or open-bowl nests (Ali and Ripley 1971, 1972).

Nests placed at the periphery of trees, especially when over open spaces, may be less subject to predation than nests placed more in the interior of the tree canopy. During a 5-year period in northeastern Gabon in equatorial Africa, Brosset (1974) found 550 nests of 110 species of rainforest birds and followed the fate of 337 of these nests. Location of the nest was more effective against predators than was concealment: 70% of nests located in small trees of the undergrowth were destroyed as compared to 50% of those nests built at the tip of projecting twigs, and only 35% of those nests overhanging water.

Domed nests placed well up in trees often are suspended from drooping twigs near the periphery of the tree, presumably providing less accessibility to arboreal predators. But such a site

also will expose the nest more to temperature changes, wind, sun, and rain, than sites toward the interior of the tree which are more sheltered from the weather. The more peripheral exposed sites should therefore favor evolution of a roof to the nest. A roof also would help prevent the eggs from rolling out when the nest is tossed about by the wind (Collias and Collias 1984).

Exposure to strong sun and to rain may be more frequent in tropical latitudes. Among Old World warblers (Sylviidae), only about one-fourth of 41 species in Europe have domed rather than open nests, compared with about half of 70 species in West Africa (Collias and Collias, 1984).

In conclusion, each basic nest type has ecological advantages and disadvantages, depending on the nest site in relation to predators, weather, and competitors, all favoring evolution of nest diversity among species.

The problems of predation (Lack 1954), environmental stress (Walsberg 1985), and energy balance (Walsberg 1980) are greatest for small birds such as passerines. According to Walsberg's calculations, based on averaging multiple estimates for species, the smaller species of birds definitely have higher ratios of daily energy expenditure to basal metabolic rate.

In order to exaggerate effects of small body size for further insights, I compiled a list of the smallest passerine birds of the world together with the general, basic type of nest built by each species when this information was available. Table 5 lists 24 species of tiny birds (< 9 g) from six continents and three major islands. These species represent 23 different genera and 16 different families. Fifteen (63%) of these 24 species build domed nests (not in holes), seven (29%) build open cup nests, and two (8%) species nest in holes in trees or in the ground.

Overhead vegetation may substitute for a constructed roof. The Goldcrest (*Regulus regulus*), the tiniest bird of Europe, always places its deep cup nest under a dense leafy branch (Thaler-Kottek 1988). The White-flanked Antwren (*Myrmetherula axillaris*) of tropical America always has a large overhanging leaf or leaves over its nest which is a deep cup fastened by its rim to a twig fork 0.2–4 m up (Hilty and Brown 1986). Very small birds often seem to have a need for some sort of roof over their nests.

Domed nests are more common (found in about two-thirds of 16 different families) in very

small passerines (Table 5) than among passerines in general, where only about half of 68 families have species building domed nests (Collias and Collias 1984). Since the great majority of passerine birds are larger than the 24 smallest passerines (Table 5), this comparison supports the conclusion that domed nests are more characteristic of very small passerine birds than of larger passerines.

Six large families in which the species generally build open nests, but in which a few species of relatively small birds (body length ≤ 15 cm) build domed nests, are the Thamnophilidae (*Myrmetherula gutturalis*; Oniki 1979), Turdidae (*Pogonocichla stellata*; Maclean 1985), Muscicapidae (*Erythrocercus livingstonei;* Maclean 1985), Meliphagidae *(Ramsayornis;* Frith 1979), Thraupidae (*Euphonia*; Hilty and Brown 1986), and Emberizidae (*Sporophila minuta*; Hilty and Brown 1986).

Two large families in which many species build open nests and many others domed nests are the Timaliidae and Tyrannidae. In the Timaliidae, 64 species of babblers building open nests had an average body length of 21 cm, whereas 25 species building domed nests averaged only 15 cm long ($t_{87} = 4.81$, $P < 0.005$) (Ali and Ripley 1971, 1972). But in the Tyrannidae, differences in body length between open nesters and domed nesters often are slight (Hilty and Brown 1986). Many tiny New World flycatchers and antbirds, as well as some very small birds from other families, build open nests (Table 5), indicating that other factors besides body size help determine type of nest built. However, in general, very small body size is most often associated with building a roof over the nest.

The Eared Pygmy-Tyrant (*Myiornis auricularis*: Tyrannidae) is one of the smallest (7 cm, 5.3 g) passerine birds of the world. Steven L. Hilty found a nest of this species in northeast Argentina (Misiones Province), and I photographed it *in situ* to illustrate the domed nest with side entrance (Fig. 4) of a tiny bird. This pensile nest was built of plant fibers, grass stems and dry bamboo leaves, and was about 2 m up in a small tree having many long spines.

The question arises that if a domed nest is so valuable to very small birds, why is it that, with very rare exceptions like the sylphs *Aglaiocereus* (Hilty and Brown 1986), the tiny hummingbirds (Trochilidae) build a cup nest? At least part

TABLE 5. Basic nest types built by the smallest birds (with adequate information on nest) on the different continents and on three major islands. Nest type: H = hole nest; D = domed nest; O = open-cup nest.

Location and species	Length cm, (weight g)	Nest type	References*
New Zealand			
Rifleman *Acanthisitta chloris*	8 (6–7.5)	H	1, 17
Grey Warbler *Gerygone igata*	11 (6.4)	D	1, 11
Australia			
Weebill *Smicrornis brevirostris*	8–9 (5.1)	D	2, 3
Rufous-crowned Emu-Wren *Stipiturus ruficeps*	14, tail 8 (5.1)	D	2, 17
New Guinea			
Elfin Honeyeater *Myzomela adolphinae*	9 (7.4)	D	4, 17
Green-backed Warbler *Gerygone chloronota*	8 (6.3)	D	4, 17
India, Nepal, Southeast Asia			
Small Sunbird *Nectarinia minima*	8 (4–6)	D	5
Tickell's Flowerpecker *Dicaeum erythrorhynchus*	8 (6.3)	D	5
Pallas Leaf Warbler *Phylloscopus proregulus*	9 (4.5–6.2)	D	6
Pygmy Blue Flycatcher *Muscicapella hodgsoni*	8	O	18
Africa			
Grey Penduline Tit *Anthoscopus caroli*	8–9 (6.2)	D	7
Swee Waxbill *Estrilda melanotus*	9–10 (7.9)	D	7
Yellow-bellied Eremomela *Eremomela icteropygialis*	10–11 (8)	O	7
Madagascar			
Sunbird-Asity *Neodrepanis coruscans*	10–11	D	8
Common Jery *Neomixus tenella*	10 (6.4)	D	8, 17
Europe			
Goldcrest *Regulus regulus*	9 (5.4–5.8)	O	9, 10
Long-tailed Tit *Aegithalos caudatus*	14, tail 9 (8)	D	10
North America			
Black-tailed Gnatcatcher *Polioptila melanura*	11 (5)	O	11, 12
Bushtit *Psaltriparus minimus*	10 (5.5)	D	11, 13
Lucy's Warbler *Vermivora luciae*	10 (6.6)	H	11, 17
South America			
Short-tailed Pygmy-Tyrant *Myiornis ecaudatus*	6.5 (4.9)	D	14, 15
Torrent Tyrannulet *Serpophaga cinerea*	10 (8)	O	16
White-flanked Antwren *Myrmotherula axillaris*	9 (8.5)	O	14, 16
Ruddy-breasted Seedeater *Sporophila minuta*	9 (8)	O	14, 16

* 1 (Gray 1969, Falla et al. 1978), 2 (Frith 1979, Pizzey 1980), 3 (Recher and Major 1994), 4 (Coates 1990), 5 (Ali and Ripley 1974), 6 (Ali and Ripley 1973), 7 (Maclean 1985), 8 (Langrand 1990), 9 (Thaler-Kotteck 1988), 10 (Cramp 1993), 11 (Harrison 1979, Peterson 1990), 12 (Walsberg 1990), 13 (Chaplin 1982), 14 (Hilty and Brown 1986), 15 (Sick 1993), 16 (Stiles and Skutch 1989), 17 (Dunning 1993), 18 (Ali and Ripley 1972).

of the answer seems to be that hummingbirds frequently have a sheltering leaf or branch over the nest, and in addition, hummingbirds may conserve energy by nocturnal torpor (Calder 1974), whereas similar-sized sunbirds, like other passerine birds which have been studied, do not undergo nocturnal torpor (Prinzinger et al. 1992). In this respect, nocturnal torpor substitutes for the energy-conserving function of a roof. Correlated with their small body size, the Trochilidae also have many (330) species.

One important consequence of small body size in passerine birds is the ability to bind the nest with spider silk, enabling the bird to fasten its nest more effectively to diverse sites, to use finer and more varied nest materials, and to give a firmer shape to the nest (Collias and Collias 1984). Spider silk not only is widely available in nature, but also has great strength and elasticity, with a breaking point that can be 100 times greater than that of high tensile steel (Gosline et al. 1986). A great many tiny passerine birds use silk in their nests, including the great majority of the species in Table 5. In contrast, larger birds often make their nests of twigs (Collias and Collias 1984), materials not so easily

FIGURE 4.   Nest of Eared Pygmy-Tyrant.

bound with silk as are the finer materials used by small birds.

Very small passerine birds (Table 5) nest on every continent and in most habitats on land, from cool southern beech forests in New Zealand (Rifleman) to northern spruce forests in Scandinavia (Goldcrest), and from dry desert washes in Arizona (Lucy's Warbler) to lowland rainforest in the Amazon basin (Short-tailed Pygmy-Tyrant). This strengthens the general conclusion that small body size is a primary adaptation that has enabled passerine birds to invade and to nest in virtually every terrestrial habitat in the world, except the Antarctic.

CONCLUSIONS

The great diversity of nests built by birds of the order Passeriformes helps explain their success as indicated by their enormous number of species and individuals, and their occupation of most terrestrial habitats over the world. We may now answer the four questions which were posed in the introduction to this review of the

relationship of nest-building behavior and diversity to the success of passerine birds.

(1) What are the basic nest types among passerines? Hole, open (not in holes) and domed (constructed roof) nests are the basic nest types among passerine birds (Table 1). Open nests are the most frequent type among families of non-passerines and passerines alike, but hole nests and especially domed nests occur more frequently among passerines, particularly in very small passerines, than among non-passerines.

(2) When did the basic nest types originate in evolution? The basic nest types arose very early in passerine evolution. Hole, open, and domed nests occur among the nine passerine families considered to be most primitive and nearest the ancestral type (Table 2). This was the primary adaptive radiation.

(3) What were the subsequent adaptive specializations of basic nest types in the evolution of the largest, most successful families of suboscine birds? This was the secondary adaptive radiation. This was illustrated by indicating the diversity of nests based on hole, open, and domed nests in the Tyrannidae, of open-cup nests in Thamnophilidae, and especially by the great diversity of enclosed nests in the Furnariidae. Nest form and structure often help characterize the genus in birds.

(4) What conditions led to the origin in evolution of the basic nest types—hole, open, and domed nests—among passerine birds? Hole nests provide a relatively stable and protected environment, but expose small birds to intense competition for nest holes. This problem was partly solved by construction of open or domed nests in sites of the birds' own choosing. Open nests are generally the most adaptable, but evolve into domed (roofed) nests, especially in small passerines, by two main routes: either on the ground where a roof gives added protection from predators, or at the periphery of trees, where a pensile nest is less accessible to predators but with greater exposure to sun, wind and weather. The precise type of nest actually evolved in a given taxonomic group depends on a balance of factors involving the history of the group, the environment, the nest site, body size, behavior, and complex habitat and community relations.

The most general conclusion of this review is that adaptable and varied nest-building behavior, combined with small body size and powers of

flight, probably played an important role in the great adaptive radiation and expansion of passerine birds during the late Cenozoic period, coincident with an increase in terrestrial environmental diversification over the globe and a greatly enhanced food supply.

ACKNOWLEDGMENTS

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