Point-of-View

Splendid isolation: historical ecology of the South American passerine fauna

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A few years ago, I had my first opportunity to visit the Amazonian Basin in eastern Ecuador. Several days of mist-netting and birding within an intact forest and in surrounding disturbed habitats turned out to be a pivotal experience, finally crystallizing in my mind a pattern that every Neotropical ornithologist knows but whose significance has largely escaped us. I am referring to the fact that most of the birds of the forest understory belong to the large South American endemic radiation of songbirds, the suboscines, called the infraorder Tyrannides (suborder Tyranni) by Sibley and Ahlquist (1990). This clade includes the ovenbirds, woodcreepers, antbirds, manakins, cotingas, and flycatchers, among others. Birds more familiar to North American's, the oscine passerines (suborder Passeri), including the New World orioles, tanagers, and emberizine finches, dominate the forest canopy and habitats outside the forest, along with a few species-rich clades of tyrannine flycatchers (family Tyrannidae, subfamily Tyranninae).

South America was an isolated island continent throughout most of the Tertiary, during which time passerine birds diversified throughout the world. As a result of its isolation, however, South America supported the evolutionary diversification of many unusual (compared to the rest of the world) lineages of plants and animals, retaining perhaps the highest level of endemism of any of the continents. The unique history of the mammalian fauna of South America is well known from the abundant fossils in deposits in the southern part of the continent. The paleontologist George Gaylord Simpson (1980) celebrated the "splendid isolation" of South America that led to so many endemic forms. Fossils also reveal the fates of many South American endemic mammals, including the litopterns and notoungulates, as well as much of the endemic marsupial fauna, as occasional migrants made their way from North America. Following the establishment of a land bridge connecting North and South America about 3 million years ago (Mya), the rate of dispersal between the continents accelerated. This "Great American Interchange" greatly favored North American forms in the end (Webb 1976, 1991). Many of these more recently invading lineages diversified and displaced endemic South American clades.

Birds, especially small ones, leave few traces. Taxonomic relationships clearly show that South America has provided fertile ground for numerous northern invaders, notably among the oscine passerines. Without a time line, however, we cannot fully appreciate the revolution that took place in the avifauna during the late Tertiary. Furthermore, we need to connect phylogenetic relationship to ecology to see how the endemic South American avifauna might have been displaced as a result. Much of the ecological space of South America is dominated by relatively recent arrivals from the north, which presumably replaced endemic forms that occupied this space before the northern invasion began. At least, it is difficult for an ecologist to imagine that the large resource base that now supports many species with North American roots was previously unexploited. Two questions come to mind. First, what were the now missing South American endemics? Did they comprise members of groups that we are familiar with today, or, like the notoungulates and many of the marsupials, were they highly unusual local products of South America's splendid isolation? Second, what might have allowed the more recent invaders to replace the native forms? Endemic lineages presumably are better adapted to their homes than new arrivals, but the evidence from faunal exchange and studies of island faunas often show otherwise (Ricklefs and Cox 1972, Ricklefs and Bermingham 1999). Thus, some lineages might have intrinsically superior traits whose value is independent

of the local environment, at least under some conditions. Such traits may differ from "key innovations," which can promote diversification by allowing organisms to exploit new niches or habitats (Heard and Hauser 1995, Barraclough et al. 1998, Owens et al. 1999).

Where ornithologists lack fossils, they now have molecular phylogenies to provide inference about history. The most complete appraisal of avian diversification remains Sibley and Ahlquist's (1990) study of relationships based on DNA hybridization. Genetic distance is expressed as a difference in the temperature of the melting points of homoduplexed and heteroduplexed (hybridized) DNA. The larger the temperature difference ($\Delta T_H 50$), the greater the genetic distance and the more remote the relationship. Furthermore, if genetic distance were to scale linearly with time, $\Delta T_H 50$ would provide a relative time scale.

According to Sibley and Ahlquist (1990), the distance between the South American suboscines and their closest sister lineage, the Old World pittas and broadbills (Infraorder Eurylaimides), is $\Delta T_H 50 = 15.8°C$. The deepest split between endemic lineages in South America, joining the Parvorder Tyrannida (538 species) to all other suboscines (560 species), occurred at $\Delta T_H 50 = 13.8°C$. The deepest node among oscine passerines globally is $\Delta T_H 50 = 12.8°C$. Thus, the South American suboscines are an old radiation, which has produced 1098 species of birds (Sibley and Munroe 1990), most of them occurring in South America (966 species; Ridgley and Tudor 1994) and tropical Central America. A few tyrannine flycatchers (27 species in 6 genera) breed in North America. I have estimated elsewhere (Ricklefs in press) that, in contrast, the South American oscines represent 14 clades with an average relative age of $\Delta T_H 50 = 5.3° (\pm 2.5° SD, range 2.0°–9.7°)$ C, comprising 702 species. The most important South American lineages of oscines, in terms of contemporary species richness, are the wrens (Certhiidae: Troglodytinae: 9.0°C, 106 species) and three emberizid tribes of the family Fringillidae: the emberizine finches (Fingillidae: Emberizini: 6.0°, 155), the New World orioles (Icterini: 4.0°, 57), and the tanagers (Thraupini: 5.5°, 217) (Ridgley and Tudor 1989, Sibley and Ahlquist 1990). In each of these individual oscine clades, the basal branches are represented among extant forms by South American species. The average genetic divergence encompassed by the basal nodes represents a little more than one-third of the time spanned by the diversification of the endemic suboscines. Thus, almost two-thirds of the passerine history of the South American avifauna proceeded without the presently dominant lineages of canopy and open-habitat birds.

Sibley and Ahlquist (1990) suggested that each degree C of $\Delta T_H 50$ is equivalent to 2.3 million years of time (My) in small birds with short generation times. This would place the deepest South American node of the suboscines at $13.8 \times 2.3 = 31.7$ My, and the average age of oscine clades in South America at $5.3 \times 2.3 = 12.2$ My, that is, during the middle to late Miocene. Alternatively, we may estimate age from the node connecting the South American suboscines and their sister group, the pittas and broadbills (Infraorder Eurylaimides) of southern Asia, which is at a depth of $\Delta T_H 50 = 15.8°C$. Setting this point at the severing of the land connection between South America and Australia, approximately 49 Mya, would place the deepest node in the Tyrannides at 42.8 Mya (middle Eocene) and the average of oscine clades in South America at 16.4 Mya, during the mid-Miocene.

The ecological displacement between suboscines and the younger, newcomer oscines is apparent in both habitat distribution and occurrence within habitats. Ricklefs and Schluter (1993) noted that 31 of 41 species of passerine recorded by Karr (1971) in a Panama forest census site were suboscines, compared to 24 of 47 species in scrub habitat. Most of the difference resulted from fewer suboscines (31 versus 24) and markedly more fringillid oscines (3 versus 17) in scrub. Several lineages of tyrannine flycatchers are common in open habitats, and these are the only lineages of suboscines that have been successful in North America.

Central America has many elements of the endemic South American avifauna, but as one enters the Amazonian Basin proper the proportion of suboscines in forested habitats increases (Fig. 1). Further south, in Mediterranean and temperate environments of South America, the mix of major groups remains about the same as it is in the Amazon Basin, although the clades within each group differ. For example, Cody (1970) listed 9 tyrannines, 11 other suboscines, and 14 oscines in study plots in central Chile, while Ralph (1985) listed 9, 10, and 13 species, respectively, in study plots in Patagonia, Argentina.

Habitat and diet also differ among the major groups of South American passerine birds. Distribution with respect to vertical strata in four Neotropical forests show that non-tyrannine suboscines are most numerous in the forest interior and avoid the forest canopy, reinforcing the general impression expressed at the outset (Fig. 1). Pearson (1971) reported a similar pattern from a dry forest site in Amazonian Peru (Table 1). Like the oscine passerines, however, the Tyranninae are also prominent in the canopy and in open environments. Each of the major groups of birds includes small insects as a major component of the diet. However, non-tyrannine suboscines uniquely exploit large insects, often using sit-and-search tactics, while the oscines make greater use of fruit resources, consistent with their dominance in the canopies of forests.

The striking stratum and diet differences among the three groups of birds suggest that they might separate morphologically as well. A discriminate analysis based on eight log-transformed external measurements (see
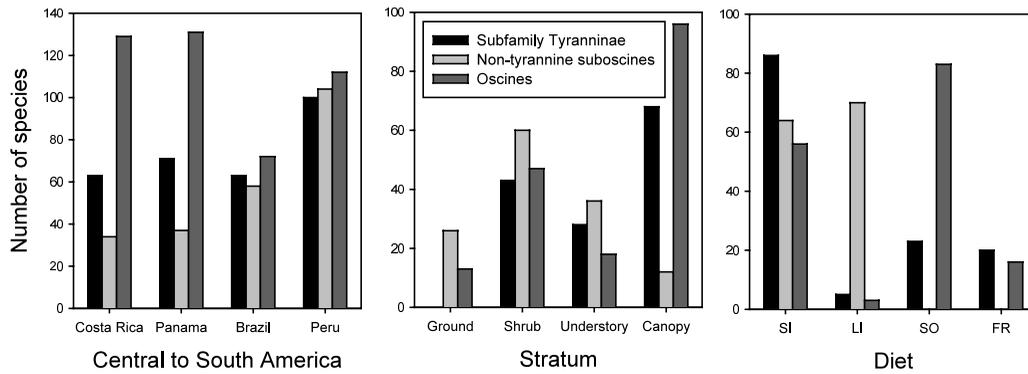
Fig. 1. Relative representation of tyrannines, non-tyrannine suboscines (primarily Funariinae, Dendrocolaptinae, Thamnophili-dae, and Formicariidae), and oscines geographically from Central America to the Amazon Basin, vertically in the forest vegetation profile, and with respect to broad diet categories (SI = small insects; LI = large insects; SO = mixed small insects and fruit; FR = fruit) (From data in Karr et al. 1990, Appendix 14.1).

Table 1. Species and distribution of foraging observations among vertical strata for non-tyrannid suboscines (S), tyrannines (T), and oscines (O) in a tropical dry forest at Yarinacocha, Peru (1523 mm annual precipitation, data from Pearson 1971).

	Total recorded species	Common species with observations	Proportion of foraging observations			
			Ground	Low shrubs	Subcanopy	Canopy
Non-tyrannine suboscines	20	6	0.072	0.621	0.307	0.000
Tyrannine suboscines	28	8	0.000	0.245	0.113	0.642
Oscine newcomers	20	8	0.125	0.019	0.105	0.751

Ricklefs and Travis 1980) confirms this (Fig. 2). The first canonical variate represents a general size axis but especially with relatively longer legs and toes towards higher values and shallower broader bills towards more negative values. This axis separates the tyrannines from the non-tyrannine suboscines and oscines. The second canonical variate places birds with longer wings and tails, and with shorter and heavier bills, at the higher end of the scale, and separates the oscines from the non-tyrannine suboscines. Among the oscines, only the wrens (Certhiidae) and the thrashers (Sturnidae: Mimini) have similar morphology to the non-tyrannine suboscines, and the wrens are one of the few prominent oscine groups in the understory of South American forests. The tyrannines are more distinctive from the oscines and non-tyrannine suboscines (generalized squared distances, 6.8 and 7.5; 90% correct posterior classification) than the latter groups are from each other (distance, 2.4; 72 and 78% classification).

The oscine passerines differ from the non-tyrannine suboscines with respect to habitat and diet and from the tyrannines with respect to diet and associated differences in morphology. Thus, with the exception of the wrens, which were among the earliest to arrive in South America, the oscines occupy a portion of the combined ecological/morphological space in South America that is not filled by suboscine clades. This implies either that the ecological opportunities represented by this space

were not available for 20–25 My of passerine evolution in South America, that they were available but not utilized, or that various suboscine clades previously filled these ecological roles. Possibly, small fruit in the
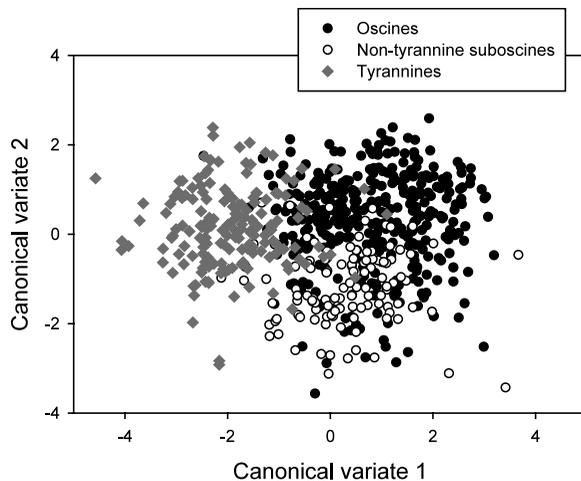

Fig. 2. Discriminant analysis of South American passerines based on eight external measurements of 659 Neotropical and North American species of passerines (SAS CANDISC procedure). Species to the right have longer legs, toes, and bills, while those to the left have shorter and flatter bills. Species to the top have longer wings and tails, but shorter and heavier bills.
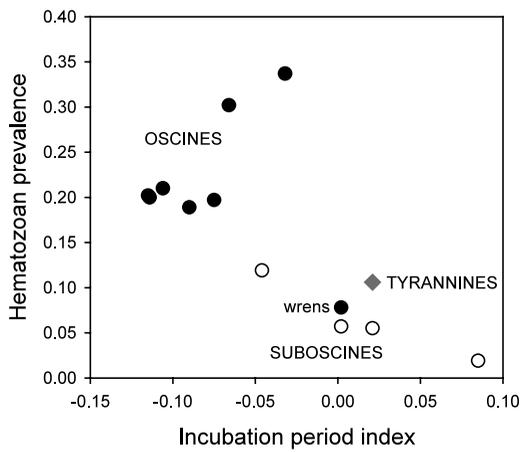
Fig. 3. Relationship between the prevalence of hematozoan blood parasites (especially *Plasmodium* and *Haemoproteus*) and the length of the incubation period relative to egg size (Ricklefs 1992, 1993). All samples for parasite prevalence > 200 individuals. Non-tyrannine suboscines (open symbols) are represented by Dendrocolaptinae (woodcreepers), Funariinae (ovenbirds), and Formicariidae (antbirds).

canopies of tropical forests and in open habitats became abundant only after the invasion of South America by oscine lineages that could disperse them efficiently. This idea is amenable to observation and experiment. However, assuming that these resources, along with insects, were plentiful before this time, replacement would be a more likely scenario. Ecologically, the tyrannine flycatchers match the oscines more closely than do the non-tyrannine suboscines. The only conspicuous difference is the relatively lesser importance of fruit eating among the tyrannines. Nonetheless, several tyrannid clades are almost exclusively frugivorous (e.g., manakins, Piprinae; cotingas, Cotinginae), and the canopy and open-habitat fruit-eating niche may have been filled by various tyrannines not substantially different from some present-day taxa.

If this were the case, we may ask why oscine newcomers were able to replace the native suboscines in this ecological role. The longer legs and toes of the oscines (axis 1 in Fig. 2) suggest more active movement through vegetation, which is consistent with the higher proportion of species with mixed small insect and fruit diets. Possibly, more generalized behavior and diets of oscines, including greater intratropical migratory tendencies (Levey and Stiles 1992), may have provided an advantage during the deteriorating climates of the late Tertiary. The oscines and suboscines also differ in basic aspects of their life histories, including the duration of the incubation period and the prevalence of blood parasites (Ricklefs 1992), possibly an index to the responsiveness of their immune systems (Fig. 3). Suboscines tend to have long incubation periods for a given egg size, and this is associated with lower prevalence of blood parasites. Oscine passerines may favor

the higher reproductive success associated with rapid development over a well-developed immune system, and thus their populations may respond more rapidly to resource fluctuations. Among the oscines, the wrens atypically resemble suboscines and this is the one group of oscines that has been successful in forest interior habitats in South America. Among the suboscines, a few lineages of tyrannine flycatchers, which have life-history characteristics that more closely resemble the oscines, have colonized North America. It is probably no accident, however, that most of the South American invaders of North America have been migratory oscine passerines from clades originated by earlier colonizers of South America.

The relationship between oscines and suboscines in South America provides a plausible example of the replacement on a continental scale of one or more major clades of birds by new arrivals. This phenomenon is not unique to birds. It has been characterized for mammals, as we have seen, and also for South American and Central American clades of Xenodontine snakes (Cadle and Greene 1993). Because the ecology, behavior, and life histories of birds are relatively accessible, the South American and, more generally, the Neotropical passerine avifauna should allow us to study the roles of phylogenetic conservatism and key innovations in the development of a regional fauna.

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