

Austral Migrants and the Evolution of Migration in New World Birds: Diet, Habitat, and Migration Revisited

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Temperate-tropical migrants are integral parts of tropical bird communities (e.g., Keast and Morton 1980) and their ecological attributes in the tropics may have influenced the evolution of their migratory behavior (Rappole 1995). An earlier article (Levey and Stiles 1992), for example, proposed that a continuum of seasonal movements exists among Neotropical birds in response to resource fluctuations and that the evolutionary end point of this continuum is Neotropical-Nearctic migration. Most Neotropical resident species that engage in small-scale movements are frugivores or nectarivores of edge, canopy, or open habitats—traits that entail reliance on variable resources (e.g., Croat 1975; Levey 1988; Blake and Loiselle 1991). Avian taxa that undertake seasonal migrations out of the Neotropics were hypothesized to have most likely been drawn from lineages with these dietary and habitat characteristics because of their predisposition for tracking highly variable resources across space and time (Levey and Stiles 1992). Thus, a nonrandom group of Neotropical lineages—those with at least partially frugivorous or nectarivorous species of edge, canopy, and open habitat—were hypothesized to be most likely to contain Neotrop-

ical-Nearctic migrants (species that breed north of the Tropic of Cancer and spend the nonbreeding season to its south).

In evaluating this hypothesis (hereafter referred to as the “evolutionary precursor hypothesis”), passerine families of presumed Neotropical origin were categorized by habitat, diet, and migration (Levey and Stiles 1992). The hypothesis was generally supported; Neotropical-Nearctic migration tended to develop in families with the hypothesized evolutionary precursors to migration. The four families characteristic of tropical forest interior were found to be wholly nonmigratory, whereas those found solely or additionally in canopy or secondary habitats were all migratory to some degree. In addition, families primarily consisting of exclusively insectivorous species were found, with one exception, to contain neither short- nor long-distance (i.e., Nearctic) migrants, whereas families with frugivorous species were found in six of eight cases to have evolved Neotropical-Nearctic migration.

Although these results were consistent with the evolutionary precursor hypothesis, the earlier analysis (Levey and Stiles 1992) had two shortcomings. First, it did not provide a true test of the hypothesis because the data were not independent of the Central American bird observations that initially generated the hypothesis. Second, the use of the comparative method did not incorporate phylogeny in a way that transitions between character states could be inferred and evaluated, and likely violated statistical independence (Felsenstein 1985; Harvey and Pagel 1991).

Here we explore further the relationship among diet, habitat, and migration, improving on the earlier approach (Levey and Stiles 1992) through examination of a separate migratory system—austral migration in South America—and by incorporating the avian phylogeny of Sibley and Ahlquist (1990) into our analyses. Austral migrants breed in southern South America during the austral summer and migrate north, toward or into the Neotropics, for the austral winter. They are drawn from the same taxonomic pool as Neotropical-Nearctic migrants but otherwise represent a largely independent migratory system. The two groups of migrants have presumably en-

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countered similar selection pressures and evolutionary constraints. Thus, any theory on the evolution of migration out of the Neotropics should hold for both the austral and Nearctic systems.

We characterize lineages of Neotropical origin by habitat, diet, and austral migration, optimize these characters on a phylogenetic tree, and test for associations between character states. To compare austral and Neotropical-Nearctic systems, we also reanalyze the earlier data (Levey and Stiles 1992) on Neotropical-Nearctic migrants. We show that habitat is a likely contributing factor in the evolution of migration out of the Neotropics, but that diet appears to be only weakly related to migration. These results are relatively consistent at the family/subfamily level in both migration systems.

Methods

We focus on passerine migrants, a relatively uniform group in terms of body size and general ecology. Species of austral migrants were taken from a previous study (Chesser 1994), which considered latitudinal migrants only, excluding taxa that undergo strictly local movements or solely intratropical or elevational migrants. In keeping with our objective of examining the evolution of migration out of the Neotropics, austral migrants moving strictly within the south temperate zone were excluded from our analyses.

We base our analyses on the phylogenetic hypothesis of Sibley and Ahlquist (1990) and concentrate on the family/subfamily level because their taxonomic sampling is complete and their tree is well resolved to this level. Although an ideal comparative test of the relationship among habitat, diet, and migration would involve a complete phylogeny of Neotropical birds down to species level, such a phylogeny is not available. We note, however, that tests of the evolutionary precursor hypothesis at the level of family/subfamily are consistent with the original formulation of the hypothesis (Levey and Stiles 1992)—that is, that migration out of the Neotropics was more likely to have evolved within lineages characterized by frugivorous diet and nonbuffered habitat.

Because the evolutionary precursor hypothesis concerns migration that originated in the Neotropics, we have included in our analysis only groups believed to have originated in the Neotropics or those believed to have undergone major radiations in the Neotropics (table 1). We have deleted two families included in the original study (Levey and Stiles 1992), Vireonidae and Troglodytidae, which are believed to have originated in what is now the north temperate zone (Cracraft 1973). However, we include the subfamily Emberizinae (family Emberizi-

dae in Levey and Stiles 1992), which may also have originated in what is now the north temperate zone, because of the major Neotropical diversifications characteristic of large clades of this subfamily (e.g., tanagers, tribe Thraupini).

Our diet and habitat classification scheme is slightly modified from the original (Levey and Stiles 1992). Families were placed into one of two categories for both diet and habitat: those containing a hypothesized evolutionary precursor of migration (frugivorous diet, nonbuffered habitat) and those lacking the same hypothesized precursor. A family was categorized as “frugivorous” (we subsume nectarivory here because of its rarity at the family/subfamily level) if it contains heavily frugivorous species or if most of its species take fruit regularly or occasionally (“++” and “+” in Levey and Stiles 1992) and as “insectivorous” if most of its species rarely or never take fruit (“0” in Levey and Stiles 1992). Habitat classification was “forest interior” (or “buffered”) if most species are primarily found in mature forest understory and “non-buffered” (“edge,” “canopy,” and “second growth” in Levey and Stiles 1992) if many species occur additionally or exclusively in the canopy, along forest edges, or in other habitats with a distinct upper layer in the vegetation (e.g., old second growth), or if they are typical of habitats with few or no trees (e.g., pasture, scrub). We stress that these categories are necessarily broad and that ecological boundaries are rarely as distinct as our classification schemes imply because of variability within lineages. Data on diet and habitat were taken from Haverschmidt (1968), Meyer de Schauensee (1970), Hilty and Brown (1986), Isler and Isler (1987), Ridgely and Tudor (1989, 1994), Karr et al. (1990), Terborgh et al. (1990), and Poulin et al. (1994). Because the evolutionary precursor hypothesis distinguishes primarily between lineages that have developed migration and those that have not, families were considered migratory if they contain austral or Neotropical-Nearctic migrant species and non-migratory if they lack such species.

Diet, habitat, and migration were optimized on the tree derived from Sibley and Ahlquist (1990), using the computer program MacClade, version 3.04 (Maddison and Maddison 1992). Optimizations containing equivocal branches were treated two ways, once using accelerated character transformation, once using delayed transformation; lack of migration was considered ancestral for the clade analyzed. Accelerated transformation resolves ambiguities in character reconstruction by accelerating character changes toward the root of a tree, thereby favoring reversals over parallel gains, whereas delayed transformation resolves ambiguities by postponing character changes on a tree, thereby favoring parallel gains over re-

Table 1: Dietary, habitat, and migratory characteristics of 12 Neotropical families or subfamilies, based on the taxonomy of Sibley and Ahlquist (1990)

<i>Family or subfamily</i>	<i>Diet</i>	<i>Habitat</i>	<i>Migration</i>
Tyranninae	Frugivorous	Nonbuffered	Both systems
Tityrinae	Frugivorous	Nonbuffered	Both systems
Cotinginae	Frugivorous	Nonbuffered	Austral only
Piprinae	Frugivorous	Forest interior	Neither system
Pipromorphinae	Frugivorous	Forest interior	Neither system
Furnariinae	Insectivorous	Nonbuffered	Austral only
Dendrocolaptinae	Insectivorous	Forest interior	Neither system
Formicariidae	Insectivorous	Forest interior	Neither system
Rhinocryptidae	Insectivorous	Forest interior	Neither system
Conopophagidae	Insectivorous	Forest interior	Neither system
Thamnophilidae	Insectivorous	Nonbuffered	Neither system
Emberizinae	Frugivorous	Nonbuffered	Both systems

Note: Families were considered “frugivorous” if they contain heavily frugivorous species or if most species in that family are at least partially frugivorous, and “insectivorous” if their species are almost exclusively insectivorous. Species in families whose habitat is considered “forest interior” occur mainly or exclusively in forest interior; “nonbuffered” indicates preference for edge, canopy, or secondary habitats by many species. Families considered migratory in “both systems” contain species of Neotropical-Nearctic as well as austral migrants.

versals (Swofford and Maddison 1987; Maddison and Maddison 1992). Because of debate concerning the relative merit of discrete comparative methods (e.g., Ridley and Grafen 1996), we used two tests designed for investigation of evolutionary hypotheses involving pairs of binary characters: Ridley’s (1983) test of association and Maddison’s (1990) concentrated changes test. Ridley’s test examines branches on a cladogram on which changes in either character occur and notes the state of both characters at the end of each of these branches. These data are then tested with a χ^2 or Fisher Exact test. Maddison’s test examines the distribution of one character (the hypothesized independent variable) on a cladogram and tests whether particular states of another character (the hypothesized dependent variable) occur more often than expected in areas of the cladogram showing a particular state of the original, independent character. A significant result in either test indicates that the two characters under consideration are significantly associated with each other.

We investigated all combinations of characters using both Ridley’s and Maddison’s tests. First, we tested the relationship between South American austral migration and diet and then the relationship between austral migration and habitat. Then we did the same thing for Neotropical-Nearctic migrants. Finally, to determine whether the results of the migration/diet and migration/habitat

tests were independent, we conducted identical tests on diet and habitat.

Results

Migratory species occur in five of 12 passerine families and subfamilies (hereafter referred to as “families”) of presumed Neotropical origin (table 1); austral migrants are found in each of these five families (Tyranninae, Tityrinae, Cotinginae, Furnariinae, and Emberizinae) and Neotropical-Nearctic migrants in three (Tyranninae, Tityrinae, Emberizinae). Six families, four of which contain migratory species, are characterized by at least partial frugivory, a proposed evolutionary precursor to migration; only one almost exclusively insectivorous family (Furnariinae) contains migratory species, and this family is migratory only in the austral system. Five of the six families characterized by nonbuffered habitat (a proposed evolutionary precursor) contain migratory species; none of the six families characterized by forest interior habitat contains migratory species.

The phylogenetic hypothesis of relationships of passerine families of presumed Neotropical origin (from Sibley and Ahlquist 1990; fig. 1) indicates the monophyly of the suboscine passerines (infraorder Tyrannides, including the Tyranninae, Tityrinae, Cotinginae, Piprinae, Pipromorphinae, Furnariinae, Dendrocolaptinae, Formicariidae,

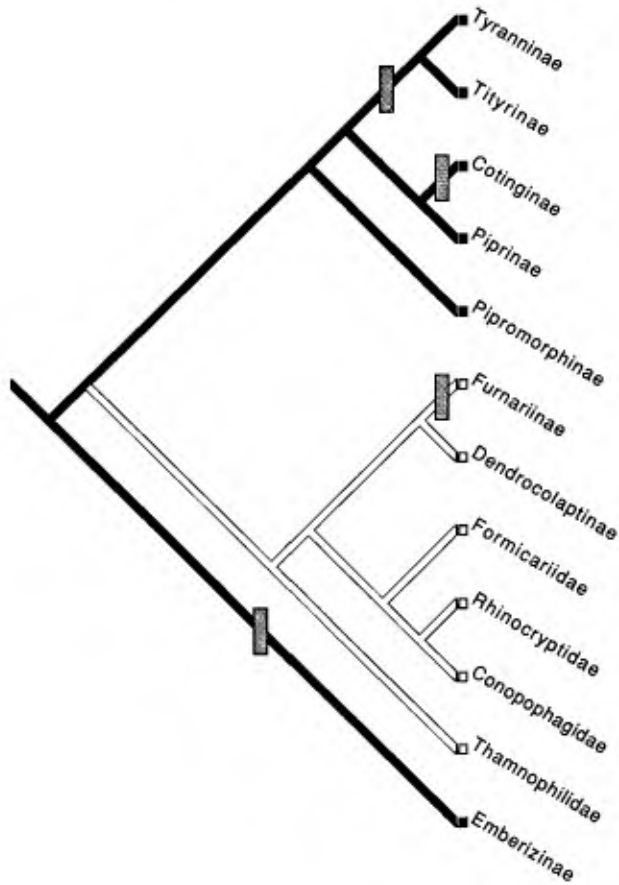


Figure 1: Phylogeny of Neotropical passerine families and subfamilies showing optimizations of the characters “diet” and “austral migration.” Shading of terminal branches indicates the character state of diet for each family; shading of other branches indicates reconstruction of dietary character states (*black branches* = frugivorous; *white branches* = insectivorous). Gray rectangles are reconstructions of the origin of migratory tendency within families and subfamilies in the South American austral migration system, using delayed transformation. The phylogeny is based on Sibley and Ahlquist (1990). See text for further details.

dae, Rhinocryptidae, Conopophagidae, and Thamnophilidae), with oscine passerines (represented by the Emberizinae) as sister to the suboscines. Two large clades constitute the suboscines: parvorder Tyrannida (Tyranninae, Tityrinae, Cotinginae, Piprinae, and Pipromorphinae) and parvorders Furnariida and Thamnophilida (Furnariinae, Dendrocolaptinae, Formicariidae, Rhinocryptidae, Conopophagidae, and Thamnophilidae).

Optimization of diet on this phylogenetic hypothesis for austral migrants (fig. 1) and for Neotropical-Nearctic migrants (fig. 2) indicated an at least partially frugivorous ancestor and a single evolution of more or less exclusive insectivory encompassing the parvorder Furnari-

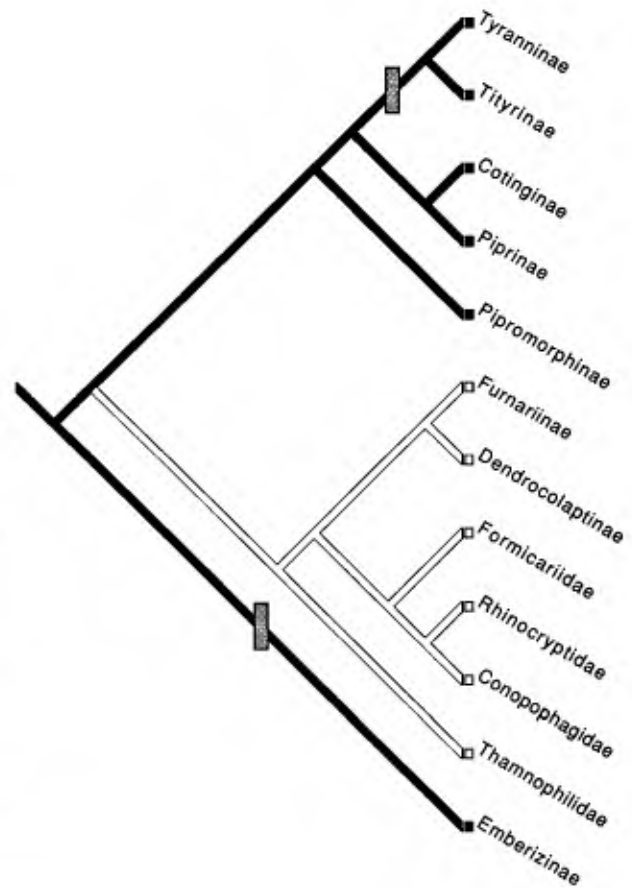


Figure 2: Phylogeny of Neotropical passerine families and subfamilies showing optimizations of the characters “diet” and “Neotropical-Nearctic migration.” Gray rectangles are reconstructions of the origin of migratory tendency within families and subfamilies in the Neotropical-Nearctic migration system. See figure 1 for further explanation of key.

ida. Optimization of habitat on the phylogenetic hypothesis for austral migrants (fig. 3) and for Neotropical-Nearctic migrants (fig. 4) indicated an ancestor of edge, canopy, and secondary habitat, and several independent evolutions of forest interior habitat (e.g., on the branches leading to the Piprinae and Pipromorphinae in parvorder Tyrannida). Near-exclusive preference for forest interior habitat also evolved once or twice within parvorder Furnariida, depending on treatment of equivocal branches, and was subsequently lost in the Furnariinae.

In the austral system, optimization of migratory tendency on the diet tree indicated that it evolved three times on branches characterized by heavy or partial frugivory and once on a branch characterized by near-exclusive insectivory (using delayed transformation; fig. 1), or that it evolved twice on branches characterized by heavy or partial frugivory, and once on a branch characterized

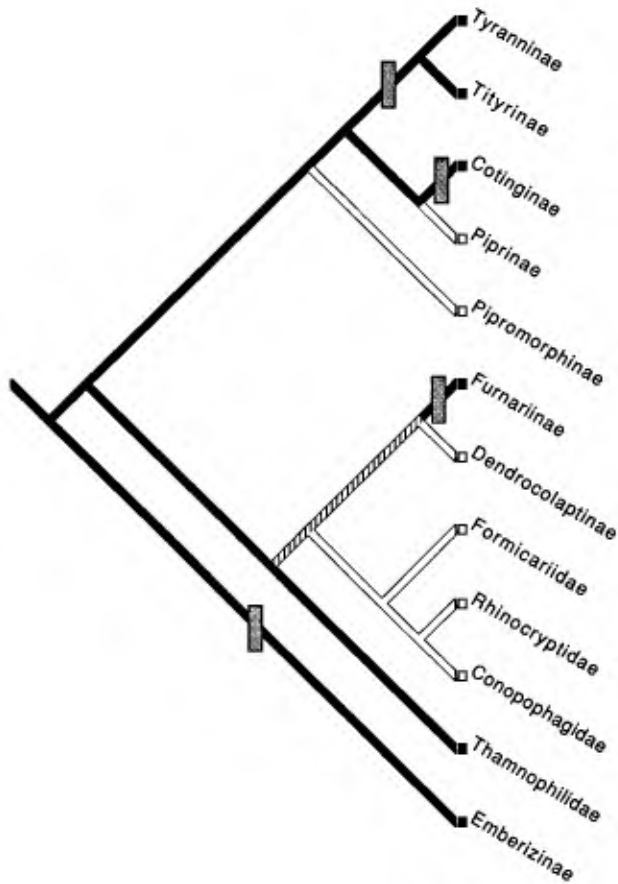


Figure 3: Phylogeny of Neotropical passerine families and subfamilies showing optimizations of the characters “habitat” and “austral migration.” Shading of terminal branches indicates the character state of habitat for each family; shading of other branches indicates reconstruction of dietary character states (*black branches* = edge, canopy, or secondary; *white branches* = forest interior; *striped branches* = equivocal). Gray rectangles are reconstructions of the origin of migratory tendency within families and subfamilies in the South American austral migration system, using delayed transformation. The phylogeny is based on Sibley and Ahlquist (1990). See text for further details.

by near-exclusive insectivory, and was lost once on a branch characterized by heavy or partial frugivory (using accelerated transformation). The relationship between frugivory and austral migration was nonsignificant using both Ridley’s test ($P = .400$ and $P = .600$, for delayed and accelerated transformations, respectively) and Maddison’s test ($P = .241$ and $P = .231$, respectively; table 2). Optimization of migratory tendency on the habitat tree indicated that it evolved four times in the austral system on branches characterized by nonbuffered habitat and never on branches characterized by the ecologically buffered forest interior habitat (using delayed transformation; fig. 3), or that it evolved three times on branches

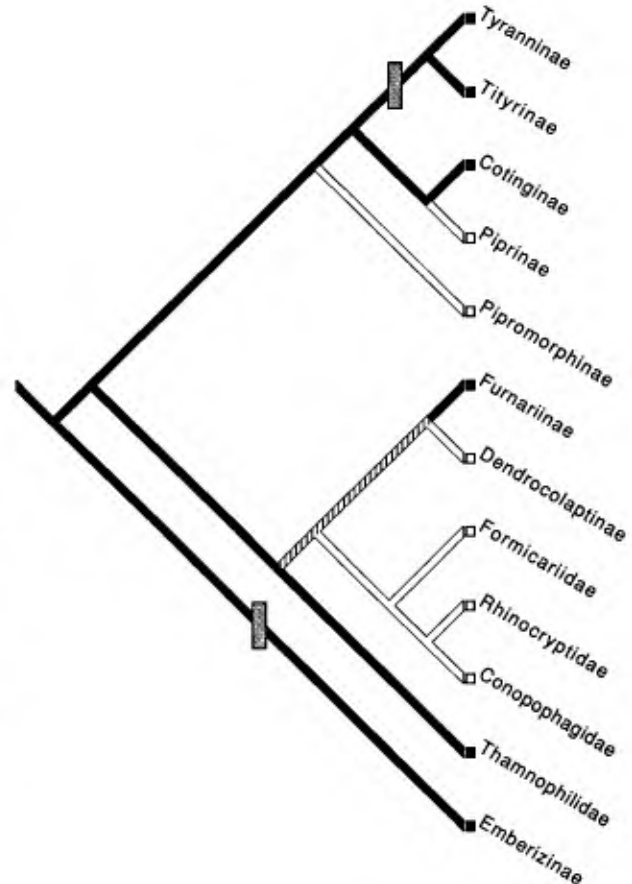


Figure 4: Phylogeny of Neotropical passerine families and subfamilies showing optimizations of the characters “habitat” and “Neotropical-Nearctic migration.” Gray rectangles are reconstructions of the origin of migratory tendency within families and subfamilies in the Neotropical-Nearctic migration system. See figure 3 for further explanation of key.

characterized by nonbuffered habitat and was lost once on a branch characterized by buffered habitat (using accelerated transformation; fig. 3). The relationship between nonbuffered habitat and austral migration was significant or near significant in all cases ($P = .029$ and $P = .050$, Ridley’s test, using accelerated transformation for habitat and delayed and accelerated transformation for migration, respectively; $P = .014$ and $P = .029$, Ridley’s test, using delayed transformation for habitat; $P = .027$ and $P = .046$, Maddison’s test, using accelerated transformation for habitat; and $P = .056$ and $P = .084$, Maddison’s test, using delayed transformation for habitat; table 2).

In the Neotropical-Nearctic system, optimization of migratory tendency on the diet tree indicated that it evolved twice on branches characterized by heavy or partial frugivory and never on a branch characterized by

Table 2: Summary of results (*P* values) of statistical tests for relationships among diet, habitat, and migration in Neotropical bird families

<i>Relationship tested and character transformation used</i>	<i>Statistical test</i>	
	<i>Ridley (1983)</i>	<i>Maddison (1990)</i>
Diet/austral migration:		
Accelerated transformation, migration	.600	.231
Delayed transformation, migration	.400	.241
Diet/Nearctic migration	.333	.168
Habitat/austral migration:		
Accelerated transformation, habitat:		
Accelerated transformation, migration	.050	.046
Delayed transformation, migration	.029	.027
Delayed transformation, habitat:		
Accelerated transformation, migration	.029	.084
Delayed transformation, migration	.014	.056
Habitat/Nearctic migration:		
Accelerated transformation, migration	.050	.240
Delayed transformation, migration	.067	.347

Note: Results using both accelerated and delayed transformation of character states are given for all ambiguous character state reconstructions. See text for further details.

near-exclusive insectivory (fig. 2); there were no equivocal branches. As was the case with austral migration, the relationship between frugivory and Neotropical-Nearctic migration was nonsignificant using both Ridley's and Maddison's tests ($P = .333$ and $P = .168$, respectively; table 2). Optimization of migratory tendency on the habitat tree indicated that it evolved twice in the Neotropical-Nearctic system on branches characterized by nonbuffered habitat and never on branches characterized by occupancy of buffered habitat (fig. 4). The relationship between nonbuffered habitat and Neotropical-Nearctic migration was nonsignificant using Maddison's test ($P = .240$, using accelerated transformation for habitat; $P = .347$, using delayed transformation) but significant or near significant using Ridley's test ($P = .050$, using accelerated transformation for habitat; $P = .067$, using delayed transformation; table 2).

Using similar methods, dietary and habitat characteristics were found to be independent of each other. Optimization of habitat on the diet tree and of diet on the habitat tree both indicated the independence of diet and habitat (P values from .3 to 1.0, depending on test used and treatment of the equivocal branches).

Discussion

Our central conclusion is that, although temperate-tropical migration in New World passerines tends to be associated with lineages of at least partially frugivorous diet and, especially, nonbuffered habitat, these relationships,

when tested in a phylogenetic context, are significant or near significant only for habitat. Thus, the evolutionary precursor hypothesis—that migration in New World passerines evolved in a nonrandom set of tropical lineages, specifically those characterized by at least partially frugivorous diets and use of edge, canopy, or open habitat—is only partially supported.

The evolutionary precursor hypothesis centers on variability of resources driving local migratory movements and the continuity of local movements with long-distance migration. Our results bring both these points into focus, prompting us to reexamine how habitat and diet relate to resource variability and to each other and how these relationships may translate from local to regional to continental scales.

Edge, open, and canopy habitats are more temporally and spatially variable in their resource supply than forest understory (Croat 1975; Stiles 1978; Smythe 1982; Feinsinger et al. 1988; Levey 1988; Blake and Loiselle 1991), probably because the understory experiences less variation in wind, rain, and sunlight (Fetcher et al. 1985, 1994). Reliance on variable dietary resources may thus primarily be a consequence of habitat selection, regardless of whether a diet consists of fruit, insects, or a combination of the two. Indeed, even exclusively insectivorous species of canopy, edge, and second growth tend to have more heterogeneous diets than related species of forest understory (Sherry 1984; Cohn-Haft 1995). Therefore, although spatial and temporal variability of fruit is a predominant feature of the Neotropics, fruit is not the

only variable tropical resource nor is it a resource generally available for use during spring and early summer in the temperate zone. It seems unlikely that heavily frugivorous lineages would develop migration to breed in the temperate zone, due to the relative lack of fruit biomass there (Karr 1971; Willson 1986). Indeed, long-distance migrants are poorly represented among heavily frugivorous lineages of Neotropical birds (e.g., Piprinae, Cotinginae).

In cases where the association between migration and its proposed dietary and habitat precursors was nonsignificant, the lack of fit was primarily due to the absence of migration in lineages characterized by at least partial frugivory and nonbuffered habitats (table 1, figs. 1–4), rather than the presence of migration in lineages lacking one or both hypothesized ecological precursors to migration. For example, in the Neotropical-Nearctic system, three families with highly frugivorous species (Cotinginae, Piprinae, Pipromorphinae) and three families with large numbers of species in nonbuffered habitats (Cotinginae, Furnariinae, Thamnophilidae) lack migratory species, whereas no families lacking the hypothesized migratory precursors developed migration. Likewise, in the austral system, two families with frugivorous species (Piprinae, Pipromorphinae) and one family with large numbers of species in nonbuffered habitats (Thamnophilidae) lack migratory species; whereas in only a single family (the predominantly insectivorous Furnariinae) did migration evolve in the absence of one or both hypothesized precursors. Thus, although occupancy of forest interior habitat (and, to a much lesser extent, near-exclusive insectivory) appears to have constrained the evolution of migration, release from this constraint (e.g., occupancy of edge, canopy, or secondary habitats) has not necessarily led to the evolution of migration.

One reason for migration not evolving in lineages where expected is simply that temperate-tropical migration is an uncommon behavior relative to the frequency of partially frugivorous diets or occupancy of edge, canopy, or open habitat. Because temperate areas support far fewer breeding species than tropical areas, and temperate-tropical migrants by definition breed in the temperate zone, only a small fraction of New World birds (fewer than 20%) are temperate-tropical migrants. Thus, it is doubtful that every Neotropical lineage characterized by frugivory or nonbuffered habitat would develop migration. Such characteristics may make it more likely that migration will develop in the lineages possessing them but cannot ensure that migration will evolve.

Although we have characterized lineages in the manner most consistent with the hypothesis developed in the earlier article (Levey and Stiles 1992), we recognize that variability in ecological characters exists within lineages. Although lack of complete phylogenies for Neotropical

bird lineages makes impossible the incorporation of lower phylogenetic levels in the evaluation of character state transitions and thus precludes an ideal comparative test of the relationships among habitat, diet, and migration, it is prudent to consider whether, qualitatively, the patterns detected in our analyses appear likely to hold when lower phylogenetic levels are included. An examination of character states among genera and species of migrants suggests that the results would likely be similar, revealing a trend toward support for habitat as a contributing factor in the evolution of migration out of the Neotropics but showing weaker support for diet as an important factor. For example, species of austral migrants are almost exclusively characterized by nonbuffered habitat but are variable in their dietary preferences. Within Tyranninae, the dominant family of austral migrants (Chesser 1994), most migratory species are partially frugivorous, but migrants range from highly frugivorous (e.g., *Legatus leucophaeus*) to essentially nonfrugivorous (e.g., *Serpophaga* spp.). Likewise, no species of austral migrant is an exclusively forest interior insectivore, suggesting that the apparent constraints evident among lineages lacking the hypothesized ecological precursors to migration are in fact consistent at lower taxonomic levels. At the same time, investigation at the species and genus level would likely reveal limits in resolving power similar to those found among lineages, due to lack of development of migration in species or genera characterized by the proposed evolutionary precursors. For instance, many species of tyrannids (e.g., *Myiozetetes* spp., *Conopias* spp.), although characterized by both nonbuffered habitats and partially frugivorous diets, nevertheless are not long-distance migrants.

Understanding the evolutionary precursors of migration is important because it can influence our interpretation of migrant behavior and community patterns. For example, both Neotropical-Nearctic and austral migrants often use secondary habitats in the Neotropics (e.g., Karr 1976; Martin 1985; Robinson et al. 1988; Blake and Loiselle 1992; Greenberg 1992; Rappole 1995; Chesser 1997). The classic interpretation of this pattern was that migrants were outcompeted by residents and were thus forced to rely on the ephemeral food resources typical of secondary or edge habitats (Willis 1966; Keast 1980). Our view suggests a more parsimonious explanation: nonbreeding season habitat use by these species suggests they evolved from taxa with these traits and that their behavioral ecology is more a cause than a consequence of their migratory behavior (Levey and Stiles 1992).

Likewise, understanding the origins of migration can yield insights into the conservation and management of migrant birds. For example, since the behavioral ecology of long-distance migrants on their nonbreeding grounds

is similar to the behavioral ecology of their tropical relatives, the response of one group to habitat alteration may be used as a predictor for the response of the other (Levey 1994).

Avenues for Future Research

Clearly, a more rigorous test of the relationships among diet, habitat, and migration must await resolved phylogenetic hypotheses of Neotropical birds at lower taxonomic levels. We also see the need for further investigation of the relationship between ecological characteristics and movement patterns. In Central America, most elevational and intratropical migrants are taxonomically and ecologically inseparable from nonbreeding Neotropical-Nearctic migrants (Stiles 1980; Levey and Stiles 1992). In other words, a continuum of migratory movements across different scales is typical within many families that contain long-distance migrants. We predict that similar continua exist within families containing austral migrants. Preliminary data on austral migrant flycatchers in Bolivia indicate that many of these same taxa undergo seasonal elevational as well as latitudinal movements, consistent with this prediction (Chesser 1997). More detailed information on local movement patterns of the large number of species resident or wintering in tropical South America would provide further tests of the link between seasonal movements in the Neotropics, diet, habitat use, and the evolution of migration in New World birds.

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