# Why Migrate? A Test of the Evolutionary Precursor Hypothesis

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ABSTRACT: The question of why birds migrate is still poorly understood despite decades of debate. Previous studies have suggested that use of edge habitats and a frugivorous diet are precursors to the evolution of migration in Neotropical birds. However, these studies did not explore other ecological correlates of migration and did not control for phylogeny at the species level. We tested the evolutionary precursor hypothesis by examining the extent to which habitat and diet are associated with migratory behavior, using a species-level comparative analysis of the Tyranni. We used both migratory distance and sedentary versus migratory behavior as response variables. We also examined the influences of foraging group size, membership in mixed-species flocks, elevational range, and body mass on migratory behavior. Raw species analyses corroborated some results from studies that put forth the evolutionary precursor hypothesis, but phylogenetically independent contrast analyses highlighted an important interaction between habitat and diet and their roles as precursors to migration. Foraging group size was consistently associated with migratory behavior in both raw species and independent contrast analyses. Our results lead to a resource variability hypothesis that refines the evolutionary precursor hypothesis and reconciles the results of several studies examining precursors to migration in birds.

*Keywords:* diet, evolution of migration, foraging flock, phylogenetically independent contrasts, resource variability, Tyranni.

Migration of birds has attracted much attention from biologists, especially those interested in the physiological and navigational challenges posed by long-distance movements (Gauthreaux 1996; Alerstam and Hedenstrom 1998). Despite this interest, many ecological and evolutionary aspects of migration remain unknown, and the ultimate causes of migration are still debated (Rappole et al. 2003; Greenberg and Marra 2005). Many alternative hypotheses have been proposed to explain why some sedentary birds became migratory (Cox 1985; Alerstam 1990; Berthold 2001), but few studies have tested these alternatives. One impediment to testing hypotheses related to the evolution of bird migration is the difficulty in conducting manipulative experiments. However, comparative analyses that identify ecological correlates associated with variation in migratory behavior across species can contribute to our understanding of why migration evolves, why it is maintained, and what factors are associated with further evolutionary changes in migratory behavior (Zink 2002).

Most hypotheses proposed to explain ultimate factors influencing the evolution of bird migration have invoked one or more of the following three ecological processes: food limitation, direct climatic effects on physiological function, and risk of nest predation (e.g., Fretwell 1980; Cox 1985; Alerstam 1990; Berthold 2001). Variation in food resources may favor annual migration by forcing individuals out of unproductive areas during lean seasons, by enabling exploitation of seasonal peaks in local food availability for breeding, or via both mechanisms. Climate could lead to migratory movements if seasonality in temperature or humidity results in conditions exceeding the range in which an individual can survive or reproduce. Latitudinal (or altitudinal) gradients in predation risk may favor migratory movements if geographic differences in nest predation enable migrants to reduce the probability of nest failure relative to that of nonmigrants. These processes are not mutually exclusive, but few studies have attempted to elucidate their relative importance to the evolution of migration in birds.

Hypotheses explaining migration based on food resource variability assume that with increasing seasonal variation in food abundance, there will be increasing likelihood that food availability will fall below threshold levels, which should increase the likelihood that a bird will migrate. The degree of climatic seasonality varies among habitats, and climatic seasonality probably influences the degree of seasonality of food resources. However, the link

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between climatic seasonality and differential seasonality of food resources (e.g., fruit, insects, or nectar) is not clear. Some authors have assumed that in the Neotropics, the magnitude of temporal fluctuation in fruit resources is greater than that in insect resources (Levey and Stiles 1992). However, Janzen (1973) provided some evidence for strong seasonality in abundance of Neotropical insects across seasons and among sites. Currently, no convincing evidence exists that shows fruit resources to be any more seasonally variable than insect resources within a single tropical site. Nevertheless, many short-distance tropical migratory species are frugivores or nectarivores, a fact that suggests that either fruit and nectar resources are indeed more seasonal than insect resources or some other factor associated with diet is important in promoting migration. If either of these associations is real, then diet should explain a significant proportion of the variation in migratory behavior independent of an association between habitat and migration.

Two previous articles that attempted to identify traits associated with the evolution of bird migration focused on the role of resource fluctuation in promoting the evolution of migration. Levey and Stiles (1992) noted that many short-distance Neotropical migrants are primarily frugivorous and inhabit what they termed "open habitats" (forest canopy, forest edge, or nonforested areas). They suggested that these open habitats are subject to large fluctuations in temperature and humidity relative to "buffered" forest interiors. They went on to note that many long-distance Neotropical migrants are drawn from the same families as these short-distance migrants. These observations led Levey and Stiles (1992) to propose the evolutionary precursor hypothesis to explain why some birds evolved migration whereas others did not. The evolutionary precursor hypothesis states that birds in lineages dependent on certain habitats ("unbuffered" areas) or resources (fruits) were preadapted to evolve long-distance migration.

Chesser and Levey (1998) tested the evolutionary precursor hypothesis by examining the association among habitat, diet, and migration in South American austral migratory birds, controlling for the effects of phylogeny at the family level. They concluded that habitat type (unbuffered open areas vs. buffered forest interior) was more closely associated with migration than was diet type (fruits vs. insects) among families and subfamilies of South American birds. The association between unbuffered open areas and migration could reflect direct physiological intolerance to climatic conditions in those habitats (i.e., fluctuations in temperature and humidity), response to climate-driven seasonality (or absolute scarcity) of food resources in those habitats, or predictable differences in predator densities between habitats. Hence, the association between habitat and migration could reflect a number of ecological processes through a variety of mechanisms.

The articles by Levey and Stiles (1992) and Chesser and Levey (1998) differ in important ways (table 1). Although Levey and Stiles (1992) contrasted sedentary species with short-distance intratropical migrants, Chesser and Levey (1998) compared lineages of entirely sedentary species with lineages in which one or more species has evolved long-distance migration between tropical and temperate regions. This difference is important because selective pressures imposed by longer migratory flights and decreasing similarity of resources and habitats available during breeding and nonbreeding seasons may change the strength or nature of the associations among habitat, diet, and migration. The evolutionary precursor hypothesis does not explicitly predict that traits associated with short-distance migration are the same as traits associated with long-distance migration, although lineages are presumed to pass through an intermediate stage of short-distance migration during this evolutionary pathway toward long-distance migration. A second major difference between these two articles is the taxonomic level of the data analyzed. Levey and Stiles (1992) conducted a species-level study without the use of phylogenetically independent contrasts, whereas Chesser and Levey (1998) conducted a family-level study. Because habitat, diet, and migration can vary greatly among species within a family (del Hoyo et al. 2004), and because relatively few (12) families and subfamilies were considered, Chesser and Levey's (1998) results were probably influenced by how habitat, diet, and migration categories were assigned to families. For example, based on Chesser and Levey's (1998) diet classification rules, an entire family could be categorized as frugivorous if it contained at least one frugivorous species that might not belong to a subfamilial lineage in which migration arose. Finally, neither study included both habitat and diet in the same analysis. A thorough understanding of how these traits affect migration requires an analytical approach that reveals whether habitat and diet explain similar portions of the variation in migratory behavior, act independently, or interact in their association with migration. Furthermore, the importance of habitat and diet should be evaluated relative to other ecologically relevant traits not considered by either previous study (especially those potentially correlated with habitat and diet).

Chesser and Levey (1998) recognized many of these limitations and made three recommendations for future tests of the evolutionary precursor hypothesis: (1) a species-level analysis using phylogenetically independent contrasts, (2) consideration of other potential ecological correlates of migration, and (3) a more detailed coding of migratory behavior that begins to capture the diversity of movement patterns called migration. In this article, we

**Table 1:** Differences in methodological approaches among three studies examining the evolutionary precursor hypothesis to explain why some birds evolved migration while others did not

| | Levey and Stiles 1992 | Chesser and Levey 1998 | This study |
|---|---|---|---|
| Geographic scope | Atlantic slope of Costa Rica | South America | North, Central, and South America |
| Taxonomic scope | Landbirds in wet forests | Passerines | Tyranni |
| *n* | 346 | 12 | 379 |
| Taxonomic level | Species | Family/subfamily | Species |
| Methods to control for phylogeny | None | Ridley (test of association), Maddison (concentrated changes) | Phylogenetically independent contrasts |
| Migratory behaviors considered | Sedentary, altitudinal, short-distance, intratropical migrants | Sedentary versus long-distance (austral) migrants | Sedentary versus migratory and migratory distance |
| Habitat categories | Four: forest interior, canopy, second growth, aquatic | Two: buffered (forest interior), unbuffered (canopy/edge) | Six: thickets/ground, understory, forest midstory, canopy, disturbed, open/arid |
| Diet categories | Many; three discussed: no fruit, some fruit, mostly fruit | Two: insects, fruits (including nectarivores) | Four: mostly insects, insects > fruit, fruit > insects, mostly fruit |
| Habitat and diet in same model? | No | No | Yes |
| Other correlates? | No | No | Yes |

test the evolutionary precursor hypothesis using an approach that incorporates all three recommendations. We use both raw species data and phylogenetically independent contrasts from the Tyranni to address the following questions. First, are habitat and diet independently associated with sedentary versus migratory behavior across species? Second, are traits other than habitat and diet more strongly associated with migratory behavior? Third, are the traits associated with increases in migratory distance the same as the traits associated with transitions from sedentary to migratory behavior?

## Methods

The Tyranni is a clade of New World suboscine birds made up of 556 species in 143 genera that are grouped by different authors into one to several families. The Tyranni includes all mionectine and tyrant flycatchers, manakins, cotingas, tityras, becards, and their allies. As such, the Tyranni is one of the largest radiations of New World birds and includes the largest family of birds in the world. It is an excellent group in which to test the evolutionary precursor hypothesis because species exhibit a range of migratory behaviors, habitat associations, and diets typical of other migratory passerine species. Additionally, this clade includes both austral and Nearctic migrants.

### *Raw Species Data*

We searched for published information on nonbreeding habitat, diet, foraging flock behavior, elevation, body mass, and migratory movements for all species in the Tyranni. We began with field guides and reference volumes on birds of the world and of North, Central, and South America (Snow 1982, 2004; Belton 1985; Hilty and Brown 1986; Stiles and Skutch 1989; Fjeldså and Krabbe 1990; Bond 1993; Dunning 1993; Sick 1993; Ridgely and Tudor 1994; Howell and Webb 1995; Stotz et al. 1996; National Geographic Society 1999; Poole and Gill 2000; Hilty 2003; Fitzpatrick et al. 2004; Snow et al. 2004). We then supplemented these sources with many journal articles, book sections, and theses (Morton 1971, 1977; Fitzpatrick 1980, 1985; Sherry 1984; Loiselle and Blake 1991; Chesser 1994, 1995, 1997, 1998, 2005; Poulin and Lefebvre 1996; Blake and Loiselle 2002; Greenberg and Salewski 2005). We eliminated species from our data set for which (1) we failed to locate information for one or more of our explanatory variables or (2) the appropriate classification for any explanatory variable was ambiguous. Our final data set consisted of the 379 mainland species of Tyranni for which we found at least one source of information for the six variables of interest. We then sent the data set to four ornithologists with extensive field experience with South American birds for review and made changes to the classifications of seven species based on comments received. The complete data table and a detailed explanation and rationale of how we compiled information from different sources and assigned species to categories are available in appendix A in the online edition of the *American Naturalist*. We followed the American Ornithologists' Union checklist of North American birds (American Ornithologists' Union 2005) and the preliminary checklist of the birds of South America (Remsen et al. 2006) for species names and taxonomic order.

We collected information for each species based on its behavior during the nonbreeding season for three reasons. First, most migrants spend more time on their nonbreeding grounds than on their breeding grounds (Keast and Morton 1980). Second, migratory species in the Tyranni are believed to be derived from Neotropical ancestors (Traylor 1977; Rappole and Jones 2002), so habitat associations and behaviors in the nonbreeding range may be more likely to represent ancestral states than breeding-range traits. Third, comparisons of habitat and diet are meaningful only between sedentary tropical species and wintering migrants because many long-distance migrants utilize habitats and resources during the breeding season that are unavailable to sedentary tropical species.

*Migration.* We used a more detailed classification of migratory behavior than simply sedentary versus migratory categories. Increasing evidence suggests that both temperate-breeding and tropical-breeding birds migrate annually over distances from only a few kilometers to voyages of ≥7,000 km (Berthold 2001). By including migration distance (in addition to sedentary vs. migratory) as a response variable in analyses, we assessed the implicit assumption of the evolutionary precursor hypothesis that similar selective pressures favor the evolution of all types of migratory behavior.

We considered a species to be migratory when at least some populations of the species migrate annually. To estimate migratory distance, we compiled an equal-area projection map of North, Central, and South America from the *Macmillan World Atlas* (Macmillan 1996). We classified the 140 migratory species into one of seven migratory distance categories (sedentary, <100 km, 100–300 km, 300–700 km, 700–1,500 km, 1,500–3,000 km, and >3,000 km), using range maps and range descriptions in the sources listed above. We constructed distance categories to be linear on a $\log_2$ scale. We assigned a species to the shortest migratory distance category (<100 km) when at least some populations of that species migrate locally. The number of species in this category undoubtedly underestimates the true number of species undertaking such movements because our understanding of the annual movements of many Neotropical species is still growing

(e.g., Ramos-Olmos 1983; Winker et al. 1995). For all other migratory species, we measured the shortest distance between the reported northern edge of the nonbreeding range and the northern edge of the breeding range (for Nearctic migrants) or the shortest distance between the reported southern edge of the nonbreeding range and the southern edge of the breeding range (for austral migrants). These distances correspond to the minimum distance that at least some individuals of that species must migrate. We classified partially migratory species as migratory, and when migratory distance varied among populations within a species, we used the population with the longest estimated migratory distance to represent the species as a whole.

*Habitat and diet.* We assigned species to one of six general habitats: thickets or ground, forest understory, forest midstory, forest canopy, disturbed habitats and woodland, and open/arid habitats with few trees. These habitats are similar to (but more detailed than) those used by Levey and Stiles (1992) and Chesser and Levey (1998) and may represent a gradient of buffering from daily (and possibly seasonal) fluctuations in temperature and humidity (Fetcher et al. 1985; Didham and Lawton 1999). Where classifications from different sources conflicted, we chose the habitat designation that was best supported among the various sources, referring to descriptions found in del Hoyo et al. (2004) to resolve conflicts because that source is the most taxonomically complete and thus probably the most consistent among species. We used dummy variables for habitat in all analyses (Zar 1999).

Quantitative information on degree of insectivory or frugivory was unavailable for the majority of species, so we classified diet descriptions from each data source on a discrete scale. Diet categories ranged from 1 (insectivorous, rarely or never eating fruit) to 4 (frugivorous, rarely eating insects). We classified species of *Phytotoma* as frugivores, although these species consume much vegetative material (Snow et al. 2004). We examined information on diet from all available sources and eliminated three species whose diet classifications varied by more than two categories among sources. We took the average score among sources for all other species.

*Foraging group size and mixed-species flocking.* We included these two measures of foraging behavior because flocking may be an important correlate of resource dispersion and predictability in tropical environments (Beauchamp 2002). For example, birds feeding on locally abundant but spatially unpredictable resources such as mast-fruiting trees may forage in flocks more than do other birds (Beauchamp 2002). Such structuring of resources led previous authors to first hypothesize the role of diet in the evolution of migration (Morton 1971; Fretwell 1980). Alternatively, flocking could be negatively associated with migration if annual migratory movements limit the ability of birds to form foraging flocks. The foraging group size variable refers to the number of conspecifics an individual typically forages with during the nonbreeding season. We assigned species to one of three group size categories based on whether individuals were reported to forage alone, in pairs, or in larger groups (three or more individuals).

We also included information on whether a species was known to join mixed-species foraging flocks during the nonbreeding season. Mixed-species flocking may be associated with migratory behavior in many of the same ways as foraging group size. However, because mixed-species flocking may form as a result of different patterns of resource availability or require that a bird possess different behavioral adaptations than are required to form single-species flocks, we chose to treat membership in mixed-species flocks separately in our analyses.

*Elevation.* We included elevational distribution because many factors relating to migration routes, climatic seasonality, and availability of food types are believed to be constrained by the biogeography of New World mountain ranges (O'Neill and Parker 1978; Bates and Zink 1994; Roy et al. 1999; Chesser 2000). We classified species into three categories based on where they spend their nonbreeding season: (1) those found primarily in lowland areas (<700 m), (2) those found over very broad elevational ranges, and (3) those found primarily in montane regions (>700 m).

*Body mass.* We included body mass to account for physiologically caused variation in migratory behavior unassociated with the ecological factors we considered. Because many species-level attributes are associated with body mass (Brown 1995), we sought to explore the ecological correlates of migration after accounting for any physiological constraints on migration associated with body mass. When we found multiple estimates of body mass, we used the average of all estimates, sexes combined. We ln transformed body mass before analysis.

### *Phylogeny*

We searched the primary literature for published phylogenies at the subfamily, genus, and species level for the Tyranni. This search produced a large number of sources of phylogenetic information: Fitzpatrick (1973); W. E. Lanyon (1984*b*, 1984*a*, 1985, 1986, 1988*a*, 1988*b*, 1988*c*); Zink and Johnson (1984); S. M. Lanyon (1985); Lanyon and Lanyon (1989); Prum and Lanyon (1989); Prum (1990, 1992, 1994*a*, 1994*b*, 1997); Sibley and Ahlquist (1990); Bates and Zink (1994); Mobley and Prum (1995); García-Moreno et al. (1998); Roy et al. (1999); Bostwick (2000); Chesser (2000, 2004); Prum et al. (2000); Brumfield and Braun (2001); Irestedt et al. (2001); Birdsley (2002); Cicero

and Johnson (2002); Johansson et al. (2002); Johnson and Cicero (2002); Fjeldså et al. (2003); Höglund and Shorey (2004); Joseph et al. (2004); Cheviron et al. (2005). We gleaned additional sources of phylogenetic information from the preliminary checklist of the birds of South America (Remsen et al. 2006), incorporating sister taxa relationships among species wherever mentioned in that source.

Because we lacked a species-level phylogeny for the entire Tyranni, we constructed composite phylogenies, or supertrees, based on all the phylogenetic sources listed above. The supertree method is an algorithm for combining the topologies of many phylogenies of overlapping sets of taxa (Sanderson et al. 1998). Several variations on supertree construction have been proposed (Bininda-Emonds 2004). We compiled phylogenetic information by entering all source phylogenies into the program Mesquite (Maddison and Maddison 2005) and constructing an MRP (matrix representation with parsimony) matrix with which to run supertree analyses.

We performed two heuristic tree searches in PAUP* 4.0 beta (Swofford 2002) to generate supertrees of the Tyranni. During both searches, we constrained all genera to be monophyletic except for those (*Inezia*, *Mecocerculus*, *Myiophobus*, *Muscisaxicola*, and *Pipra*) suspected of paraphyly or polyphyly by authors of our phylogenetic sources. The assumption of genus-level monophyly allowed us to incorporate taxa not represented by any of the source phylogenies for which we had complete ecological data by adding those taxa to completed supertrees as basal polytomies within their respective genera. The assumption of genus-level monophyly also overcame the problem of misleading phylogenetic information resulting from taxa being represented in source phylogenies only as outgroups to distantly related genera. We used *Sapayoa aenigma* as the outgroup taxon in the construction of our trees (Fjeldså et al. 2003).

In the first search, we used an additional "backbone" constraint in the following seven subclades: Pipridae, Cotingidae, Elaeniinae, Platyrinchinae, Fluvicolinae, Tyranninae, and a group of eight *incertae sedis* genera (*Iodopleura*, *Laniisoma*, *Laniocera*, *Pachyramphus*, *Phibalura*, *Schiffornis*, *Tityra*, and *Xenopsaris*) believed to be closely related to each other (Johansson et al. 2002; Chesser 2004). We followed the American Ornithologists' Union (1998, 2005; Remsen et al. 2006) for assignment of genera to subclades. The placement of *Onchorhynchus*, *Lipaugus*, *Piprites*, and *Calyptura* was too uncertain to constrain to any subclade, and they were thus free to be grouped within constrained subclades. In this first search, we performed 1,000 heuristic search replicates, of which two replicates recovered equally parsimonious trees (tree length = 980); we sampled 100,000 trees from each of these two replicates to generate two majority-rule consensus trees. Although the consensus trees from these replicates resulted in similar phylogenetic hypotheses, one of the trees recovered some questionable relationships among constrained and unconstrained taxa (e.g., placement of *Calyptura* within the Elaeniinae) and was discarded. We used the remaining consensus tree (hereafter referred to as tree 1; see fig. B1 in the online edition of the *American Naturalist*) to calculate phylogenetically independent contrasts.

For the second search, we again performed 1,000 heuristic search replicates, removing the backbone constraints on the seven subclades but still constraining genera to be monophyletic. During this search, nine replicates recovered equally parsimonious trees (tree length = 965); we sampled 1,000 trees from each of these nine replicates. The 9,000 resulting trees were then used to generate a single majority-rule consensus tree (hereafter referred to as tree 2; see fig. B2 in the online edition of the *American Naturalist*).

Before calculating phylogenetic independent contrasts, we pruned both trees to include only the 379 taxa for which we had complete ecological data. For analyses in which migratory distance was our response variable, we further pruned trees to include only the 142 migratory taxa.

### *Analysis*

We examined the ecological correlates of migration using two analytical approaches, treating migration as either a dichotomous trait (sedentary vs. migratory) or a continuous trait (migratory distance). To identify factors associated with sedentary versus migratory behavior, we used all data. To examine whether the same factors were associated with increases in migratory distance, we limited our data set to migratory species only, using migratory distance as our response variable. To enable a comparison between our results and results of past studies, we first examined the relationships proposed by Levey and Stiles (1992) and Chesser and Levey (1998) among habitat, diet, and migration, except that we also included the habitat × diet interaction term. The habitat, diet, and habitat × diet models are referred to hereafter as restricted models. We then constructed complete models that also included foraging group size, mixed-species flocking, elevation, and body mass. Finally, we conducted each of these analyses once with raw species data and again with phylogenetically independent contrasts.

*Phylogenetically independent contrasts.* We used the Mesquite-module (Maddison and Maddison 2005) version of the program PDAP (Midford et al. 2005) to calculate independent contrasts in order to examine the association between traits in the absence of phylogenetic effects (Harvey and Pagel 1991). We performed all phylogenetically

independent contrast analyses twice using contrasts calculated from each of our supertrees. Because branch lengths were not available for our supertrees, we set all branch lengths equal to 1. Arbitrary branch lengths can influence contrast estimates (Garland et al. 1992; Díaz-Uriarte and Garland 1998). Thus, we checked diagnostic plots for evidence of violation of the assumptions of independent contrast analyses. We found no indication of systematic bias associated with branch length, so we performed all contrast analyses using untransformed branch lengths. All regression analyses on contrast data were forced through the origin (Pagel 1993).

*Statistical analyses.* We used multiple linear regression and logistic regression to model migratory behavior with both raw species data and contrast data. For the analyses of sedentary versus migratory species based on raw species data, we used a logistic regression framework treating migration as a binary response. For all contrast analyses and for the analyses of migratory distance, we used multiple linear regression, treating migration as a continuous response. When choosing among candidate models, we used Akaike's Information Criterion (AIC; Burnham and Anderson 2002). When more than one model was supported by the data (i.e., $\Delta\text{AIC} < 0.5$), we chose the model with the most explanatory variables. To examine the association between migration and both habitat and the habitat × diet interaction, we conducted extra sum-of-squares *F*-tests.

For raw species data, we treated foraging group size and elevation as continuous explanatory variables because they vary continuously in nature. However, to ensure that our results were not influenced by treating these ordinally coded variables in a continuous manner, we repeated our analyses using dummy variables for foraging group size and elevation. Because our results were qualitatively identical, we present only the results obtained by treating these variables as continuous.

## Results

Results of phylogenetically independent contrast analyses from the two supertrees were qualitatively identical. We report here only the results based on tree 1 (fig. B1). Associations among habitat, diet, and migration differed between models using raw species data and those using phylogenetically independent contrasts (table 2). Moreover, factors associated with sedentary versus migratory behavior were not the same as those associated with migratory distance (table 2).

### *Sedentary versus Migratory Species: Restricted Model*

In the restricted model based on raw species data, the association between habitat and migration was strong (table 2), and the nature of this association was consistent with that predicted by earlier studies: forest understory and midstory birds were least likely to migrate, followed by thicket and canopy birds, with birds of open, arid, and disturbed areas most likely to migrate. Overall, increasing frugivory was associated with a slight increase in likelihood of migration. However, the nature of the relationship between diet and migration appears to depend on where a bird lives ($P = .071$ for the habitat × diet interaction; table 2). To explore this interaction, we plotted the regression lines for the relationship between diet and percentage of migratory species for each of the six habitat types (fig. 1). Increasing frugivory is associated with an increasing incidence of migratory behavior among birds living in thickets, forest understory, and forest canopy. Conversely, increasing frugivory is associated with a decreasing incidence of migratory behavior among birds living in disturbed and arid areas.

PDAP calculated contrasts for 378 nodes in the phylogeny. The restricted model based on independent contrasts revealed a strong positive association between increasing frugivory and the likelihood of migration. However, as in the model based on raw species data, the association between diet and migration depended on habitat ($P < .0001$ for the habitat × diet interaction term; table 2; fig. 1). To facilitate comparison of these restricted model results with those of Levey and Stiles (1992) and Chesser and Levey (1998), we grouped birds in our six habitats and our range of diet values into four general categories: those living in forested habitat versus those living in nonforested habitats and those consuming mainly fruit versus those consuming mainly insects. Although only 19% of insectivores living in forested habitats migrate (compared to 61% of insectivores in nonforested habitats), roughly equal proportions of frugivores living in forested and nonforested habitats are migratory (fig. 2). Hence, habitat is correlated with migratory behavior in insectivores but not in frugivores.

### *Sedentary versus Migratory Species: Complete Model*

In the complete model based on raw species data, habitat was again strongly associated with the likelihood of being migratory, and we found suggestive evidence that the relationship between diet and migration depended on habitat ($P = .080$ for habitat × diet interaction; table 2). As with the restricted model based on raw species data, birds living in the forest interior were less likely to migrate than birds living away from forests. Foraging group size was negatively associated with the likelihood of migrating, although it appears that this relationship is not linear (fig. 3); birds that typically forage alone were the most likely to be migratory, whereas birds that typically forage in pairs

**Table 2:** Factors associated with migration in 379 species in the Tyranni based on eight analytical models that varied in response variable (sedentary vs. migratory or migratory distance), number of potential explanatory variables (three vs. seven), and whether we controlled for phylogeny (raw species means vs. phylogenetically independent contrasts)

| | Sedentary versus migratory species | | | | | | | | Migratory distance | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Restricted model | | | | Complete model | | | | Restricted model | | | | Complete model | | | |
| | Raw species | | Contrasts | | Raw species | | Contrasts | | Raw species | | Contrasts | | Raw species | | Contrasts | |
| | $\chi^2$ | $P$ | $F$ | $P$ | $\chi^2$ | $P$ | $F$ | $P$ | $F$ | $P$ | $F$ | $P$ | $F$ | $P$ | $F$ | $P$ |
| Whole model | 72.0 | <.0001 | 3.8 | <.0001 | 85.4 | <.0001 | 4.0 | <.0001 | 4.9 | <.0001 | .7 | .697 | 7.6 | <.0001 | 3.4 | .038 |
| Habitat | 50.6 | <.0001 | 1.3 | .284 | 63.6 | <.0001 | 1.4 | .223 | 2.5 | .032 | .4 | .837 | 3.1 | .013 | … | … |
| Diet | 4.4 | .036 | 11.3 | .001 | 1.6 | .209 | 10.2 | .002 | .6 | .457 | .1 | .721 | 15.7 | .0001 | … | … |
| Habitat × diet | 10.2 | .071 | 5.1 | <.0001 | 9.8 | .080 | 5.2 | <.0001 | 1.3 | .262 | 1.2 | .309 | … | … | … | … |
| Group size | | | | | 9.3 | .002 | 4.2 | .041 | | | | | 8.6 | .004 | 2.8 | .095 |
| Mixed-species flocking | | | | | … | … | … | … | | | | | … | … | … | … |
| Elevation | | | | | … | … | … | … | | | | | 2.2 | .143 | 3.6 | .058 |
| Body mass | | | | | 4.7 | .031 | 5.3 | .022 | | | | | … | … | … | … |

Note: The $\chi^2$ and $P$ values for variables in logistic regression models are based on likelihood ratio tests, and the $F$ and $P$ values for linear regression models are based on partial sum-of-squares $F$-tests. We report the complete models with variables chosen based on Akaike's Information Criterion (AIC) values. Ellipses indicate data considered for inclusion in complete model but for which variable was not included in models with the lowest AIC scores.

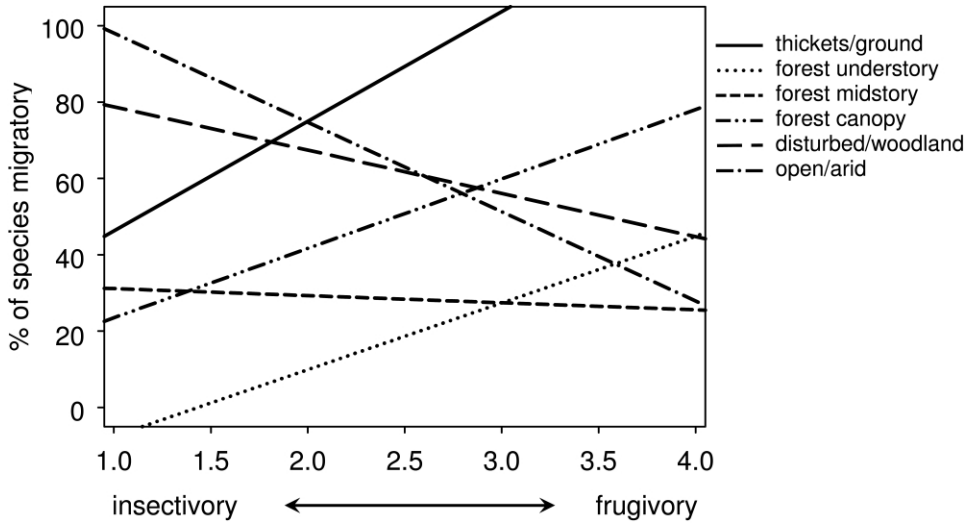


**Figure 1:** Percentage of species in the Tyranni that migrate varies with diet (highly insectivorous to highly frugivorous) and habitat use. The six lines illustrate how diet and habitat interact; birds of thickets, forest understory, and canopy are more likely to be migratory if they are frugivorous. In contrast, increasing frugivory is associated with a decreasing likelihood of being migratory for birds of disturbed and arid habitats. We plotted linear regression lines for each habitat category based on the proportion of species that migrate for each level of diet along a scale from highly insectivorous (1.0) to highly frugivorous (4.0).

were the least likely to be migratory. After the effects of other variables were accounted for, each increase in group size was associated with a 39% decrease in the odds of migrating. Body mass was positively associated with migration; the odds of migrating increased by 154% with each increase of 1 ln mass.

The complete model based on independent contrasts included habitat, diet, habitat × diet, foraging group size, and body mass (table 2). The strong effect of the habitat × diet interaction in this model indicated that, as in the restricted models, the associations between habitat, diet, and migration were interrelated. As in results based on raw species data, foraging group size was negatively associated with the likelihood of migrating, and body mass was positively associated with the likelihood of migrating.

### *Migratory Distance: Restricted Model*

The restricted model of migratory distance based on raw species data was similar to the equivalent model contrasting sedentary and migratory species in that migratory distance was more strongly related to habitat than to diet (table 2). Mean migratory distance was associated with habitats in the same way that the likelihood of migrating was associated with habitats. On average, forest understory birds migrate the shortest distances, with mean migratory distance increasing in the following way: forest understory < forest midstory < forest canopy < thickets < disturbed areas < open/arid areas. In contrast to the analyses of sedentary versus migratory behavior, we found no evidence for an effect of diet or for a habitat × diet interaction in the restricted model.

PDAP calculated contrasts for the 141 nodes in the phylogeny based on the 142 migratory species. The restricted model based on independent contrasts suggested little association between migratory distance and habitat or diet (table 2).

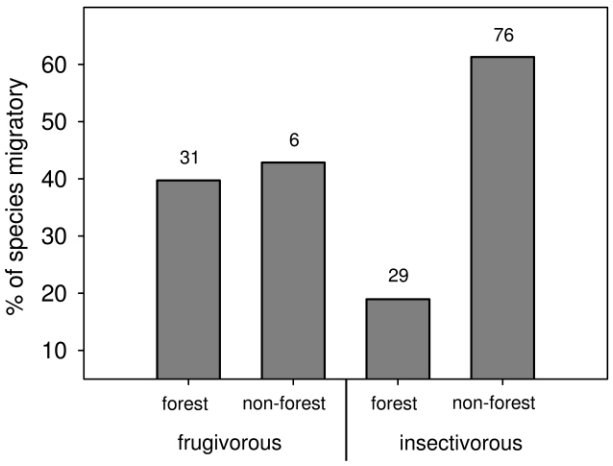


**Figure 2:** Percentage of species in the Tyranni that migrate in each of four categories based on habitat (forest vs. nonforest) and diet (mainly frugivorous vs. mainly insectivorous). The number of migratory species in each category appears above the bar.

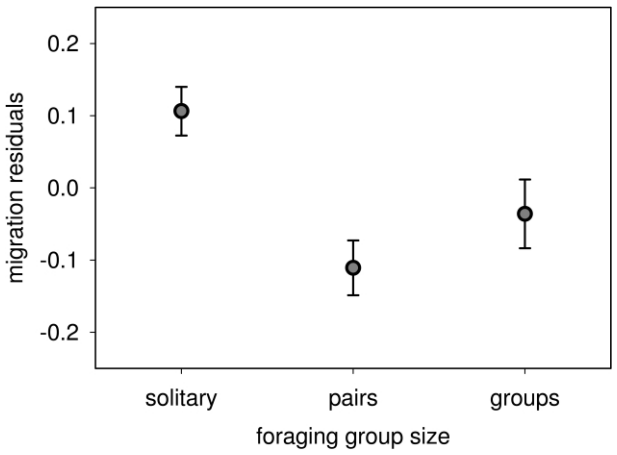


**Figure 3:** Relationship between foraging group size and migratory behavior. Values represent the residuals ( ± 1 SE) for likelihood of migration at each level of foraging group size after the effects of habitat, diet, and body mass were accounted for.

### *Migratory Distance: Complete Model*

The complete model based on raw species data included habitat, diet, foraging group size, and elevation (table 2). In contrast to the restricted model, diet was more strongly associated with migratory distance than was habitat. Furthermore, the nature of the relationship between diet and migratory distance was opposite to that of the relationship between diet and the likelihood of migrating. Insectivorous birds migrate longer distances on average than frugivorous birds. After the effects of habitat and diet were accounted for, foraging group size was again negatively associated with migratory distance, and lowland birds migrated farther than highland birds.

The complete model based on independent contrasts included only foraging group size and elevation as correlates of migratory distance (table 2). As in the equivalent model based on raw species data, both group size and elevation were negatively associated with migratory distance.

## Discussion

Migration is often considered an adaptation for exploiting seasonal peaks in food abundance or avoiding climatic extremes by dividing time among numerous locations. If variation in food or climate favors migration in some species, however, why has migration not evolved in all species? One possibility is that certain traits make some species more likely to migrate. The evolutionary precursor hypothesis (Levey and Stiles 1992) suggests that both a frugivorous diet and use of unbuffered habitats are precursors to the evolution of migration in birds. Our results show that habitat and diet are indeed related to migration but in more complex ways than previously proposed. Our comparative analysis of 379 species in the Tyranni provided ambiguous support for the evolutionary precursor hypothesis, with results depending on which migratory response variable we used and whether we analyzed raw species or independent contrast data.

The results of our raw species analyses suggest that sedentary species differ on average from migratory species in the habitats they occupy and in the broad types of foods they consume. However, our results also suggest that the relationship between diet and migration depends on where birds live, with most forest and thicket birds being more likely to migrate if they are frugivorous (consistent with the evolutionary precursor hypothesis) but birds of nonforested habitats being less likely to migrate if they are frugivorous (fig. 1). Analyses of independent contrast data strengthened the evidence that the association between evolutionary changes in migration and habitat depend on the type of foods consumed (support for the habitat × diet interaction term increased after controlling for phylogeny). The proportion of primarily frugivorous species that migrate was very similar regardless of the broad habitat in which birds lived (fig. 2). In contrast, the proportion of primarily insectivorous species that migrate was lower for birds living in the forest interior than for those living in canopy and open habitats. This suggests that differences in migratory behavior among birds occupying different habitats are attributable to the habitat-specific behavior of insectivores but not frugivores.

Our results differ from those of Levey and Stiles (1992), who concluded (for all birds and specifically for flycatchers) that living in open habitats and eating fruit were separately associated with being migratory. Differences in the results between studies could perhaps be explained by differences in taxonomic scope. Alternatively, habitat and diet may be confounded, but when habitat and diet were analyzed separately, both factors appeared to be associated with migration. However, the most likely explanation lies in the different types of migratory behavior considered among studies. On average, the diets of migrants as a whole may not differ from those of their sedentary neighbors, but those of short-distance migrants may differ from those of both long-distance migrants and sedentary species. Indeed, evidence from our analyses of migratory distance supports this explanation: short-distance migrants are more frugivorous than long-distance migrants (although this difference disappears when phylogeny is considered).

The most pervasive correlate of migration was foraging group size. In analyses of both sedentary versus migratory behavior and migratory distance, using both raw species data and independent contrast data, group size was con-

sistently and negatively associated with migration. Furthermore, in some of our models, foraging group size was more strongly associated with migration than was either habitat or diet. Our data suggest that birds foraging solitarily are more likely to migrate and migrate farther than birds foraging either in pairs or in groups (fig. 3), suggesting that migration could impede the maintenance of pair and family group foraging bonds. This hypothesis is supported by increasing evidence suggesting that individuals of different age and sex classes often migrate on different timetables and occupy different nonbreeding ranges or habitats (Conway et al. 1995; Marra et al. 1998; Lank et al. 2003). A more intriguing possibility is that migration and group foraging represent alternative evolutionary strategies. If migration evolves primarily in response to temporal variation in food resources, and if foraging with conspecifics overcomes some of the same problems of resource scarcity through improved foraging efficiency, then these two types of behavior could represent different evolutionary solutions to the same environmental constraint (i.e., food limitation).

### *Why Migrate Farther?*

Previous reviews of the evolution of bird migration have assumed that short-distance migratory movements are a necessary precursor to the evolution of long-distance migration. Our results do not support this assumption in that factors associated with changes in migratory distance differed from those associated with sedentary versus migratory behavior. Most important, the effects of diet and the interaction between habitat and diet helped differentiate sedentary and migratory species but were not correlated with migratory distance after controlling for phylogeny. Increasing frugivory was associated with increasing likelihood of migrating (at least in some habitats), but insectivory, not frugivory, was associated with increases in migratory distance (in models that included foraging group size). Consideration of habitat was critical in interpreting the association between diet and migration in models of sedentary versus migratory behavior, whereas foraging group behavior was critical in understanding the association between diet and migration in models of migratory distance.

A primarily frugivorous diet could constrain birds to short migratory distances regardless of whether frugivory predisposes lineages to evolving migration in the first place. Indeed, breeding seasons of long-distance migrants coincide with abundant insect resources and relatively scant fruit resources at northerly latitudes. Although many migrants consume fruit during migratory and nonbreeding seasons, the morphological, physiological, cognitive, and behavioral adaptations required to efficiently forage for and digest fruit conflict to some degree with adaptations for an insectivorous diet (Lepczyk et al. 2000; Levey and Martínez del Rio 2001; but see Parrish 1997). Because fruit is scarce at high latitudes during the breeding season, year-round insectivory may thus be a consequence, not a cause, of long-distance migration. Another possible explanation for the differences in importance of diet in Levey and Stiles (1992), Chesser and Levey (1998), and our study is that short- and long-distance migration may evolve in response to different sets of selective pressures. If true, this would further erode support for the evolutionary precursor hypothesis because an implicit assumption of this hypothesis is that short- and long-distance migration are endpoints of a single behavioral continuum.

The additional variables included in complete models also differed between analyses of sedentary versus migratory behavior and changes in migratory distance. Whereas increasing body mass was associated with increasing likelihood of migrating, body mass was not associated with changes in migratory distance. If birds migrate in response to resource scarcity and if increases in foraging efficiency do not scale 1 : 1 with increasing energetic requirements of larger body sizes, then as food levels decrease, heavier birds will experience food shortages sooner than lighter birds. In contrast to body mass, the nonbreeding elevational range occupied by a species was associated with changes in migratory distance but not with changes in likelihood of migrating. The longest-distance migrants we studied spend the nonbreeding season in lowland Amazonia, migrating to northern boreal regions to breed, whereas many of the shortest-distance migrants in our data set were montane species that migrate altitudinally. This suggests that highland birds are able to migrate much shorter distances than lowland birds to reach regions that differ in temporal patterns of food resource availability.

### *Raw Species Data versus Phylogenetically Independent Contrasts*

Use of phylogenetically independent contrasts helped clarify the ecological correlates of bird migration. In the analyses of sedentary versus migratory behavior, the effect of controlling for phylogeny was to strengthen the habitat × diet interaction, reinforcing the argument that the relationships between each of these factors and migration ought not to be evaluated separately. In the analyses of migratory distance, raw species analyses suggested effects of habitat and diet, but phylogenetically independent contrasts showed no correlation between habitat or diet and migration. Contrast models might fail to identify the same associations as raw species migratory distance models if the evolution of correlated traits occurred deep in the phylogeny and was subsequently conserved. To some

extent, this may be true in the Tyranni. For instance, most species in the genus *Empidonax* are characterized by long-distance migration and high levels of insectivory. Phylogenetic conservatism of trait associations may well imply that combinations of certain traits are adaptive and have persisted because they are adaptive (Price 1997), but such associations provide poor evidence for correlated trait evolution.

The discrepancies in results between raw species and independent contrast analyses are unlikely to be artifacts of the details of our methodology. Numerous modifications have elaborated on the simple calculation of independent contrasts by incorporating specific models of character evolution, maximum likelihood methods, and Bayesian inference. Because many of these methodological advances influence the estimation of branch lengths, understanding the consequences of branch length error is potentially important (Díaz-Uriarte and Garland 1998). Our results are unlikely to be affected by assigning arbitrary branch lengths for two reasons. First, large phylogenies are fairly robust to branch length errors (Freckleton et al. 2002), and second, branch length errors result in inflated Type I error rates (Díaz-Uriarte and Garland 1998). In our case, model type influenced results by both strengthening and weakening individual variable associations; we found no systematic pattern of increasing *P* values in independent contrast models as compared to raw species models (table 2).

### *Habitat and the Evolutionary Precursor Hypothesis*

What implications do the associations between habitat and migration have for hypotheses regarding the evolution of migration? Although our results are uninformative in evaluating the role of predation risk, we can speculate on the role of climatic effects and food limitation. It is unlikely that climate promotes the evolution of migration through direct effects limiting physiological efficiency. If so, we would have expected a stronger and more consistent association between elevation and migration; elevational gradients provide the strongest climatic gradients within the nonbreeding ranges of Tyranni species. However, we cannot rule out indirect climatic effects and their role in influencing resource variation. The observed relationship between habitat and migration may simply reflect lower temporal variation in microclimate in forests than in nonforested habitats. If this is the case, it is not clear how or why insectivores and their insect prey should be more strongly influenced by that variability than frugivores and their fruit resources. The inconsistency in associations among migration and habitat, diet, and foraging group size suggest that some unmeasured parameter related to variation in resource abundance has influenced the evolution of migration. Although resource seasonality and/or patchiness are likely to be major factors influencing the evolution of migration, our surrogates for resource seasonality do a poor job of capturing that variation. The logical next steps are to measure the magnitude of seasonality in fruit and insect resources within different habitats in tropical environments and to assess how solitary versus pair or group foraging influences the efficiency of resource acquisition.

What can we infer about the evolutionary precursor hypothesis? Our results imply that simple direct associations between either habitat or diet and the evolution of migration do not exist. Not only are the associations of these traits among extant species more complex than previously suggested, but results of our migratory distance analyses imply that different traits are associated with different types of migratory behavior. Short-distance migrant frugivores may not be precursors of long-distance migratory lineages in the sense of representing an evolutionary bridge between sedentary species and long-distance migratory species but may instead represent a distinct evolutionary response to a different set of selective pressures.

### *Resource Variability Hypothesis*

Results of this study suggest that the evolutionary precursor hypothesis as previously stated must be refined. We hope that by restating this hypothesis explicitly in terms of resource variability instead of presumed surrogates for resource variability, we will stimulate tests of critical predictions of this and other hypotheses explaining the evolution of migration. We propose a resource variability hypothesis that states that species living in areas where fluctuation in food resource availability is large will be more likely to initially evolve migratory behavior than species depending on less seasonal resources, regardless of where those areas are located (i.e., habitat) or what type of food resources the species depend on (i.e., diet). Once migration has evolved, factors associated with the extension and modification of this behavior will not necessarily be the same as factors associated with the initial steps toward becoming migratory. Additionally, migration appears to somehow constrain the ability of species to forage with conspecifics; group foraging may in turn be an alternative strategy to migration, allowing sedentary species to overcome some of the difficulties associated with variation in resource availability.

The resource variability hypothesis and results of this study make testable predictions regarding the seasonal patterns of resource variation expected between habitats for tropical insectivores and frugivores. If habitat-specific variation in resources promotes migration, then the extent of food limitation should be more temporally variable (or

more severe) for insectivores in open areas than for insectivores in forests, but the extent of food limitation for frugivores should be similar across habitats. Furthermore, food should be more limiting for birds of open habitats than for forest-dwelling species. We do not know whether the overall magnitude of temporal variation in resources, a drop in resource abundance below some critical threshold, or an interaction between resource availability and resource quality is the critical factor influencing whether a species embarks on the evolutionary pathway to migration. We recommend an empirical approach to resolving these questions. Only by carefully quantifying community-level production rates of fruits and insects in forested and open habitats can we infer that habitat is indeed a good surrogate for resource variability.

Species-level phylogenetically explicit comparative studies are a powerful approach in addressing questions related to the evolution of avian migration. Although our inferences are limited to the Tyranni, we believe the discrepancies between results of this study and those of previous studies form a compelling argument for more research on the species-level correlates of migration, particularly studies focusing on migration systems in other parts of the world. Ideally, future studies will better capture the detail and continuous nature of the variation in both food resource variability among habitats and the variation in migratory behavior across species. Phylogenetically explicit comparative studies could greatly advance our understanding of the processes contributing to the evolution of migration in systems very different in their ecology. The evolutionary precursor hypothesis is one of many hypotheses proposed to explain variation in migratory behavior among species that have rarely (if ever) been empirically tested. Yet all of these hypotheses make predictions regarding species-level correlates of migratory behavior. We encourage other researchers to take advantage of the ever-increasing number of phylogenies being published to test predictions of alternative hypotheses explaining the evolution of migration.

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