

Why do some, but not all, tropical birds migrate? A comparative study of diet breadth and fruit preference

W. Alice Boyle · Courtney J. Conway · Judith L. Bronstein

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Abstract Annual migrations of birds profoundly influence terrestrial communities. However, few empirical studies examine why birds migrate, in part due to the difficulty of testing causal hypotheses in long-distance migration systems. Short-distance altitudinal migrations provide relatively tractable systems in which to test explanations for migration. Many past studies explain tropical altitudinal migration as a response to spatial and temporal variation in fruit availability. Yet this hypothesis fails to explain why some coexisting, closely-related frugivorous birds remain resident year-round. We take a mechanistic approach by proposing and evaluating two hypotheses (one based on competitive exclusion and the other based on differences in dietary specialization) to explain why some, but not all, tropical frugivores migrate. We tested predictions of these hypotheses by comparing diets, fruit preferences, and the relationships between diet and preference in closely-related pairs of migrant and resident species. Fecal samples and experimental choice trials revealed that sympatric migrants and residents differed in both their diets and fruit preferences. Migrants consumed a greater diversity of fruits and fewer arthropods than did their resident counterparts. Migrants also tended to have slightly stronger fruit preferences than residents. Most critically, diets of migrants more closely

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W. A. Boyle (✉)

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA
e-mail: aboyle7@uwo.ca

W. A. Boyle

Department of Biology, University of Western Ontario, London, Ontario N6A 5B7, Canada

C. J. Conway

U.S. Geological Survey, Arizona Cooperative Fish and Wildlife Research Unit, School of Natural Resources and the Environment, University of Arizona, Tucson, AZ 85721, USA
e-mail: cconway@ag.arizona.edu

J. L. Bronstein

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA
e-mail: judieb@email.arizona.edu

matched their preferences than did the diets of residents. These results suggest that migrants may be competitively superior foragers for fruit compared to residents (rather than vice versa), implying that current competitive interactions are unlikely to explain variation in migratory behavior among coexisting frugivores. We found some support for the *dietary specialization* hypothesis, propose refinements to the mechanism underlying this hypothesis, and discuss how dietary specialization might ultimately reflect past interspecific competition. We recommend that future studies quantify variation in nutritional content of tropical fruits, and determine whether frugivory is a consequence or a cause of migratory behaviour.

Keywords Diet · Elevational gradient · Fruit preference · Interspecific competition · Nutrient limitation · Resource variability

Introduction

Migration is among the most complex and impressive of animal behaviours. We know much about migration patterns, proximate causes, and physiological adaptations for migration (Dingle 1996), but the ultimate causes of migration are still poorly understood. This is true even for migratory birds, which have been studied extensively for over a century (Alerstam 1990). Numerous hypotheses have been proposed to explain how and why bird migration evolved (Alerstam et al. 2003), but few of these have been tested empirically. Furthermore, ecologically similar and closely-related sympatric species often differ in migratory tendency, and few hypotheses can account for such differences. Consequently, the question of why birds migrate is more appropriately phrased, “why do some, but not all, bird species migrate?” (Fretwell 1980). Answering this question requires formulating and testing mechanistic hypotheses that explain species-level differences in migratory behavior. Testing alternative hypotheses to address Fretwell’s question forces us to reframe the debate in an explicitly comparative context by focusing on selective pressures that have been important repeatedly in the evolution of migration.

An impediment to answering Fretwell’s (1980) question lies in the difficulty of studying long-distance migrants whose breeding and non-breeding ranges occupy regions that differ dramatically in climate, food, vegetation, competitors, and predators. In contrast, short-distance altitudinal migrations of tropical birds provide relatively tractable systems for examining why bird migration evolved. Altitudinal migrants live in mountains around the globe, and in many tropical areas constitute a major portion of the avifauna (Loiselle and Blake 1991; Johnson and Maclean 1994; Burgess and Mlingwa 2000; Hobson et al. 2003).

Food limitation is the most common ecological process invoked to explain bird migration generally and tropical altitudinal migration specifically (Stiles 1980; Wheelwright 1983; Loiselle and Blake 1991). Many empirical studies examining the causes of tropical altitudinal bird migration have all tested a general hypothesis that birds migrate to elevations where food abundance peaks during the breeding season, and migrate back when food abundance peaks at non-breeding elevations. This hypothesis of reciprocal variation in food abundance has received general acceptance (Alcock 2005) in part because most altitudinal migrants’ diets are broadly similar (predominantly frugivorous or nectarivorous; Stiles 1983), and in part because the abundance of fruit and nectar is assumed to vary among seasons more than does the abundance of insects (Levey and Stiles 1992). Some evidence supports the hypothesis of reciprocal variation in food abundance as an explanation for altitudinal migration (Wheelwright 1983; Solórzano et al. 2000), but the

evidence is inconclusive. For example, the timing and movement patterns of individual species can only partly be explained by seasonal peaks in fruit abundance (Rosselli 1994; Chaves-Campos et al. 2003; Chaves-Campos 2004; Boyle 2010). Most importantly, in all the tropical forests in which species-level studies have been conducted, many sympatric, ecologically similar, and closely-related species do not migrate at all.

We formulate two food-based hypotheses to explain how spatial and temporal variation in food resources could lead to variation in migratory behavior in some tropical frugivorous birds. These two hypotheses differ in how food availability, traits of migrants and residents, and migratory behaviour might be related. The goals of this study are to test predictions of these two hypotheses and, by doing so, shift attention from the level of ecological process (i.e., food limitation) to the level of ecological mechanism (i.e., differences in current competitive abilities or dietary specialization).

The first hypothesis relies on *competitive exclusion* as a mechanism driving migratory behavior which has been proposed to explain the evolution of both long-distance migration (e.g., Cox 1968) and differential migration (e.g., Cristol et al. 1999). This hypothesis could explain differences in migratory tendency if (i) residents out-compete migrants for fruit, and (ii) migrants and residents are subject to different trade-offs in the costs and benefits of migrating. If the fruit not consumed by residents is insufficient to meet the needs of migrants, those migrants will move up- or downhill to elevations where they experience reduced competition. This hypothesis makes no assumptions regarding the causes of differences in competitive abilities, or whether residents reduce fruit availability to migrants via exploitative or interference competition. Previous tropical frugivore studies provide some support for this hypothesis by suggesting that fruit may be limiting during some times of year, and that consequently, competition may structure frugivore communities (Loiselle and Blake 1991).

The second hypothesis relies on differences between migrant and resident frugivore species in *dietary specialization*; birds may differ in migratory tendency due to differences in foraging ecology (Catry et al. 2004). The dietary specialization hypothesis does not refer to differences among migrants and residents in the extent to which they eat fruit (relative to arthropods) but rather to their extent of specialization on specific fruits (as opposed to being frugivore generalists). This hypothesis could explain differences in migratory strategy if migrants (relative to residents) either (i) have more restricted diets resulting in (on average) fewer fruit types and less food overall being available to them in a given location, (ii) be less likely to switch fruit types due to stronger fruit preferences, or (iii) have equal preference strengths, but prefer fruits of plants that produce fruit more seasonally. This hypothesis also has its roots in previous research on altitudinal migration; Wheelwright (1983) proposed that dependence on fruits in the Lauraceae could explain the direction and timing of Quetzal movements, and Loiselle and Blake (1991) postulated that differences in movement among species of frugivores may reflect differences in the abundance and phenology of preferred fruits. Because differences in traits such as dietary specialization can be the result of past competitive interactions (Schluter 2000), the ultimate process may be similar in both hypotheses (competition for food), but they differ in the mechanism (and the temporal scale) by which the process operates.

We used a comparative approach to distinguish between the *competitive exclusion* and *dietary specialization* hypotheses by testing five predictions regarding differences in realized diets, dietary preferences, and the degree to which diets reflect preferences (Table 1). Similar to all studies that simultaneously test multiple alternative hypotheses, some of the predictions in Table 1 provide greater discriminatory power than others. Because of this variation among predictions, we explore the strength of each in testing the two hypotheses.

Table 1 Summary of the predictions tested to evaluate two food-based hypotheses proposed to explain why some but not all tropical frugivorous birds migrate altitudinally. Our results from tests of these predictions are italicized with the associated *P*-values of each statistical test reported in parentheses

Differences between migrant and resident species in	Hypotheses	
	Competitive exclusion	Dietary specialization
Diet breadth and composition		
(1) Diversity of fruits in diet	<i>Higher in migrants than in residents</i> (Fig. 1a, $P = 0.003$)	Lower in migrants than in residents, or no difference
(2) Relative proportion of fruit vs. arthropods in diet	Residents more frugivorous	<i>Migrants more frugivorous</i> , or no difference (Fig. 1b, $P < 0.0001$)
Fruit preference		
(3) Preferences for fruit types	<i>Preferences shared between migrants and residents</i> (Fig. 3)	EITHER preferences differ between migrants and residents; OR ↓
(4) Strength of preference for preferred fruits	No difference between migrants and residents	<i>Stronger in migrants than in residents</i> (Fig. 2, $P = 0.059$)
Relationship between diet and preference		
(5) Correlation between preferences and realized diets	Weaker in migrants than residents	<i>Stronger in migrants than residents</i> (Fig. 4, $P = 0.043$)

We compared diet breadths of migrant and resident species using both the number of plant species from which birds of each species consumes fruit, and a diversity index that incorporates the relative importance of fruits from different plant species in diets (prediction 1, Table 1). Because under the *competitive exclusion* hypothesis, residents actively out compete migrants for the best fruits available we predicted that residents would consume fewer fruit types in greater proportions than would migrants. Under the *dietary specialization* hypothesis, migrants would either (i) consume a lower diversity of fruits (if migrants restrict their diets to fruits of fewer species), or (ii) not necessarily differ from residents in the diversity of fruits consumed but prefer fruits of plants with different phenologies.

We also quantified the degree to which migrant and resident frugivores diversified their diets with arthropod prey (prediction 2, Table 1). Under the *competitive exclusion* hypothesis, residents' diets should consist of proportionately more fruit (relative to arthropods) because they are capable of competing for their preferred fruits which are sufficient to fill most of their nutritional needs. Although few fruits contain as much protein as arthropods (Wheelwright et al. 1984), arthropods likely impose greater foraging costs on frugivores because (i) arthropod abundance is thought to be low in forest understory (Elton 1973; Janzen 1973) (ii) competition with insectivorous taxa is probably high, (iii) frugivores possess few specialized morphological and behavioral adaptations for efficiently detecting and capturing arthropod prey, and (iv) most arthropods have evolved physical or chemical defenses against predators whereas the function of fruit is to be eaten. Under the *dietary specialization* hypothesis, if residents habitually forage on a broader array of food types, they may be expected to consume a greater proportion of arthropods than migrants (although this prediction is not diagnostic for the dietary specialization hypothesis).

Under the two hypotheses, the expected relationship between migratory tendency and fruit preferences also differ. *Competitive exclusion* for food resources will be most intense if both migrants and residents prefer the same fruits (prediction 3, Table 1), and prefer

them equally strongly (prediction 4, Table 1). In contrast, if *dietary specialization* explains differences in migratory tendency, then either (i) migrants and residents would be expected to prefer different fruits (prediction 3, Table 1), or (ii) if shared, then migrant preferences would be expected to be stronger than residents (prediction 4, Table 1). Whereas shared fruit preferences alone are certainly not sufficient to demonstrate competitive exclusion, lack of shared preferences would indicate that competition is unlikely to occur due to reduced resource overlap. These predictions (3 and 4) expand upon previous studies of the evolution of bird migration which have proposed that tropical frugivores were the evolutionary precursors to long-distance migrants (Levey and Stiles 1992), that degree of frugivory among species is associated with short-distance migration (Boyle and Conway 2007), and that resident birds are morphologically more adept at capturing arthropods compared to their migratory counterparts (Greenberg 1981).

Finally, the relationship between diet and fruit preference should differ as a consequence of migratory strategy (prediction 5, Table 1). A key prediction that, if false, would refute the *competitive exclusion* hypothesis is that resident species' diets in the wild (i.e., realized foraging niches) should more closely resemble their dietary preferences (i.e., fundamental foraging niches) than in migrant species (at the time that birds initiate migration) due to superior competitive abilities. However, if *dietary specialization* explains differences in migratory strategy, then diets of migrants would be expected to more closely reflect their preferences than would diets of residents because migrants would leave when their preferred foods become scarce. By clearly predicting opposite relationships between diet and preference in migrants and residents, this prediction is the strongest of the five with which to differentiate the two hypotheses.

We compared these components of diet and preference in a community of frugivorous birds in Costa Rica by pairing seven altitudinal migrant species with their most-closely-related resident sympatric counterpart. This approach controls for confounding effects of shared evolutionary history (Harvey and Pagel 1991) and provides a conservative test of correlated trait evolution when the phylogenetic relationships among all taxa are not known (Ackerly 2000) as is the case for the majority of the taxa we studied. Consistent results across several species-pairs would imply that similar selective pressures have been repeatedly important in the evolution of migration.

Materials and methods

Spatial and temporal scope

We studied birds at 700–800 masl on the Atlantic slope of Costa Rica at Rara Avis (10°17'3" N, 84°02'47" W). This site is located along an altitudinal gradient of protected forest extending from 30 to 2,900 m elevation. Rara Avis has a mean annual temperature of 23°C and receives 8,279 mm (\pm SE 263 mm) of rain annually. Approximately 25% of the bird species breeding on the Atlantic slope migrate altitudinally (Stiles 1983). We collected dietary data during June–July 2001, 2002, and 2004. The months of Jun–Jul mark the end of the breeding season for both residents and migrants and the beginning of down-hill migration (Stiles and Skutch 1989; Boyle 2006). Migrants include species that migrate from this site to lower non-breeding elevations as well as species arriving from higher breeding elevations to spend the non-breeding season. This aspect of our study design allowed us to essentially sample both ends of the migratory journey (for different species) at a single location. We intentionally restricted our study to a single time of year

(June–July) and a single elevation to control for variation in diets due to seasonality in fruiting phenology of food plants (residents), differences in plant community composition among elevations (migrants), and shifts in diet due to changing nutritional needs related to reproduction and moult (all birds) (Carnicer et al. 2008). By doing so, we were able to examine whether and how species with different migratory strategies differ in their diets and preferences (during the migratory period) given the very same foraging opportunities. Fruiting phenology appeared to be consistent among years based on 6 years of observations and plant collections in the region.

Bird capture and fecal sample collection

We placed 6–16 understory and three canopy mist nets (12 m × 3 m, 38-mm mesh) for 4–7 days in 15 different old-growth or selectively logged forest locations. We opened mist nets from 600–1,200 or until rain began, checking them every 20 min. We collected fecal samples from all captured birds belonging to primarily frugivorous lineages: trogons (Trogonidae), toucanets (Ramphastidae), manakins (Pipridae), cotingas (Cotingidae), tityras and becards (uncertain familial affinities), thrushes (Turdidae), tanagers (Thraupidae), and the genus *Mionectes* (Tyrannidae). We placed individual birds in small bird cages covered with cloth which were lined below with plastic wrap. During the ~30 min that birds remained in cages, they voided seeds either via defecation or regurgitation (hereafter “fecal” samples). We collected fecal samples from cages and bird bags and preserved them in 70% ethanol. We washed bird bags and replaced plastic cage lining after every use.

Seed reference collection and characterization of diets

Because no published references were available with which to identify seeds of plants at our site, we made botanical collections of trees, lianas, and epiphytes fruiting on or near the site during 19 months of field work. We prepared herbarium specimens from fruiting branches collected within 14 m of the ground and preserved seeds in 70% ethanol to build a seed reference collection (Boyle 2003). We identified botanical specimens using published materials, by matching with herbarium collections, and with help from local botanists. When we found seeds in fecal samples not found in our reference collection, we assigned the seed a unique morphospecies name, added it to the collection, and often later identified seeds based on subsequent collections.

We examined each fecal sample under a 40× microscope on a filter-paper-lined Petri dish divided into 12 quadrants of similar area. We searched for seeds and arthropod pieces in each quadrant using forceps. Seed size influences the time that seeds are retained in the digestive tract of birds (Martínez del Rio and Restrepo 1993), thus biasing estimates of the relative importance of different fruits in diets based on seed abundance in fecal samples. Hence, we used presence or absence of seeds from each plant species to characterize diets. We analyzed 207 fecal samples and identified seeds from 82 plant species or morphospecies in samples (Appendix). Of those, 62 seed types (76%) could be matched to one of the 144 species of plants we collected in the region. The proportion of unidentified seeds did not differ between migrants and residents (Fisher’s exact test, $P = 0.454$).

We estimated the proportion of each fecal sample consisting of arthropod remains by estimating the amount of arthropod pieces in each quadrant relative to the amount of all fruit pulp and seeds, averaging estimates among quadrants within a sample. Separating and weighing arthropod remains was not possible due to the small size of most arthropod

fragments. Although this method may not accurately represent the volume or mass of arthropods in diets, it provides a quantitative index of the relative importance of arthropods when comparing diets among species, and is similar to methods used in other frugivorous bird studies (Herrera 1998). When possible, we noted the orders of arthropod remains found in samples (Appendix).

Pairing of migrant and resident species for dietary comparisons

We categorized all frugivorous species we captured as either altitudinal migrants or residents. We relied primarily upon Stiles and Skutch (1989) and Loiselle and Blake (1991) for categorization of each species' migratory status in the region. Migratory status for two of 19 species was ambiguous; Stiles and Skutch (1989) do not mention altitudinal movements for *Pipra pipra* Linnaeus or *Mionectes oleagineus* Lichtenstein, but Loiselle and Blake (1991) categorize these species as complete and partial altitudinal migrants, respectively. We resolved the classification of these two species (and verified classifications of all species) by examining seasonal patterns of capture rates from 2001 to 2004 from four study sites that varied in elevation (100 m, 300 m, Rara Avis, and 1,100 m, W. A. Boyle unpublished data). These data strongly suggest that *Pipra pipra* is an altitudinal migrant breeding at higher elevations than Rara Avis, and that most *Mionectes oleagineus* at Rara Avis do not migrate.

We collected data from eight migratory and 11 resident species. Six of the eight altitudinal migrant species could be paired with resident species in either the same genus or family. We paired a seventh migratory species (*Corapipo altera* Hellmayr) with *Schiffornis turdina* Wied-Neuwied. *S. turdina* was removed from the Pipridae, placed in the Cotingidae (Snow et al. 2004), then placed in a clade of uncertain affinities within the Tyranni, and now is placed in the new Tityridae, sister group to Cotingids (Remsen et al. 2009). Species-pairs (with authorities; *n* fecal samples) used in diet comparisons are as follows with the migrant listed before the resident for each pair (names follow the American Ornithologists' Union 1998, 2005): manakin1 = *Corapipo altera* (89), *Schiffornis turdina* (8); manakin2 = *Pipra pipra* (13), *Manacus candei* Parzudaki (7); flycatcher1 = *Mionectes olivaceus* Lawrence (9), *M. oleagineus* (11); thrush1 = *Myadestes melanops* Salvin (10), *Catharus mexicanus* Bonaparte (10); thrush2 = *Turdus obsoletus* Lawrence (12), *T. grayi* Bonaparte (5); tanager1 = *Tangara icterocephala* Bonaparte (11), *Tachyphonus delatrii* Lafresnaye (15); tanager2 = *Tangara florida* P. L. Sclater & Salvin (3), *Chlorospingus ophthalmicus* Du Bus de Gisignies (4). Body mass of migrants and residents did not consistently differ (paired-sample *t*-test, $t = 0.4$, $df = 6$, $P = 0.718$), nor did bill length, bill width, or the ratio of bill length:width (paired-sample *t*-tests; $t_{\text{length}} = 1.5$, $df = 6$, $P = 0.197$; $t_{\text{width}} = 1.2$, $df = 5$, $P = 0.296$; $t_{\text{ratio}} = -1.3$, $df = 5$, $P = 0.246$). This lack of clear morphological trends combined with the fact that we captured all species in nets placed at the same height within the forest and observed most of these species foraging together in mixed-species flocks underscores the ecological similarity of species within our pairs. More detailed ecological data is available in Stiles and Skutch (1989) and del Hoyo et al. (1992).

Fruit preference trials

We conducted all preference trials in 2002 using as many of the same species from which we collected dietary data as possible. Due to the refusal of approximately 20% of birds to acclimate to captivity (Boyle 2009), we conducted preference trials with 38 individuals of

eight bird species (n individuals) with migrant listed before the resident for each species pair: manakins = *Corapipo altera* (10), *Manacus candei* (5); flycatchers = *Mionectes olivaceus* (6), *M. oleagineus* (2); thrushes = *Myadestes melanops* (8), *Catharus mexicanus* (2); and tanagers = *Tangara icterocephala* (3), *Tachyphonus delatrii* (2). Of these, 10 individuals consumed no fruits during trials, including all *C. mexicanus* and *T. icterocephala*. Because thrushes and tanagers are more closely related to each other than either family is to manakins or flycatchers (Sibley and Ahlquist 1990), we paired *M. melanops* with *T. delatrii* for analyses of fruit preference (predictions 3 and 5, Table 1). *Corapipo* was paired with *Manacus* for analyses of fruit preference because we lacked preference data for either *Schiffornis* or *Pipra*.

To avoid preference data being influenced by the type of fruits consumed immediately before trials, we fed birds an artificial diet (Denslow et al. 1987) for at least 24 h (typically 2–3 days) while housed under ambient temperature and light conditions. We removed food from cages 1 h prior to conducting trials. We conducted trials in a 3 m × 2 m × 2 m cloth flight cage with one end containing a door and a 5-cm-diameter mesh panel through which an observer recorded bird foraging. The cage was roofed by translucent mesh that lit the interior with natural light and was positioned so that birds could see no landscape features. The center of the cage contained one 1.3 m tall bamboo perching structure. At ~40 cm from the back wall of the cage we located seven bamboo perches placed ~25 cm apart and secured by cord on which birds readily perched.

We offered birds fruits of up to seven plant species during 45-min trials. Arrays of fruits used during trials differed among the species-pairs from different families. When possible, we offered all individual birds within a species-pair the same arrays of fruits. However, because the fruiting period of some plant species ended before trials were complete, fruits of a few plant species were not offered to all individuals. We chose fruits based on published dietary information, presence of seeds in 2001 fecal samples, and availability of fruit at our site. Not all fruits available to a wild-foraging bird were available during trials; thus, we can not be certain whether we neglected to include a preferred fruit type. Consequently, preference data represent relative indices comparable between species-pairs.

We did not manipulate the number of fruits on infructescences for two reasons. First, we sought to preserve as many visual morphological cues as possible. Thus, we also left a pair of leaves subtending each infructescence. Second, due to unequal size, structure, and nutritional composition among fruits of different species, reducing the number of fruits/infructescence to a common denominator would not result in infructescence of equal attractiveness to a foraging bird. We assigned plant species randomly to perches and mounted infructescences to perches with fruits oriented toward the center of the cage in ways that mimicked their presentation in nature (e.g., upright, pendulous, etc.). All birds actively inspected the full array of fruits and moved freely around the cage, interspersing foraging bouts with preening and other behaviours. Birds frequently consumed all ripe fruits of one or a few species, but never consumed all the fruits available to them. We aborted the trial if the bird appeared distressed or did not forage. We fed and released birds following trials.

Analyses

We compared the breadth of fruits in migrant and resident diets in two ways. First, we compared dietary fruit diversity using Fisher's α diversity index based on presence-absence matrices of seeds in fecal samples. We chose Fisher's α to incorporate both data

on the total number of plant species from which a bird species foraged, as well as the evenness of those species among samples. Furthermore, Fisher's α permits a comparison of fruit diversity in diets of different species represented by unequal numbers of fecal samples (Magurran 1988). Second, we counted the number of plant species (seed types) found in fecal samples (all individuals pooled) within a species. To correct for differences among species (within a pair) in the number of fecal samples available for analysis, we rarefied the number of fecal samples of the species with more samples to the number of fecal samples of the species with fewer samples. We compared diversity indices and number of plant species consumed using paired-sample t -tests (prediction 1, Table 1). We compared the relative predominance of fruits vs. arthropod prey in migrant and resident diets using the proportion (arcsine square-root transformed) of arthropod remains in each fecal sample (prediction 2, Table 1), analyzed using a linear mixed-model with migratory tendency as a fixed effect and species pair as a random effect. We evaluated predicted differences between migrants and residents based on effect tests for migratory tendency.

We estimated the relative strength of fruit preferences by calculating the number of plant species upon which an individual foraged during preference trials. We assumed that birds with strong fruit preferences would consume fruits of few plant species, and that birds with weak fruit preferences would consume fruits of many plant species. We compared relative preference strengths using a linear mixed-model with migratory tendency as a fixed effect and species pair as a random effect (prediction 3, Table 1). To ensure that preference results were not biased by slight differences in arrays of fruits offered to individuals, we analyzed preferences twice: (1) using all data, and (2) restricting analyses to only those fruits offered to all individuals within a species pair (migrant vs. closely related resident). Results did not differ between these two analyses so we present only the results based on data from all trials.

To determine the extent to which species within pairs shared fruit preferences and the extent to which realized diets reflected fruit preferences, we calculated fruit preference ranks for each individual bird based on the order that fruits were consumed in trials for the flycatcher and manakin pairs (prediction 4, Table 1). We did not test this prediction with the tanager-thrush pair because the arrays of fruit presented to birds of these two species were not the same. To estimate species-level fruit preferences, we summed ranks for each plant species from all individuals of each bird species. Alternative methods of ranking fruit preference were all highly correlated (Boyle 2006). Thus, we present results based on a single ranking method. We determined that differences among infructescences in the number of fruits available did not affect preference results by analyzing the relationship between the number of fruits presented of a given plant species and its preference rank by an individual bird. To investigate how similarly migrant and resident species (within pairs) rank fruits, we used non-parametric Spearman rank correlations to compare fruit preference ranks between pairs of migrant and resident species. Finally, we calculated the proportion of fecal samples collected from a given bird species containing seeds of each plant species. Using these proportions, we constructed diet ranks for plant species also offered in preference trials. We examined whether rankings based on dietary data reflected rankings of those same plant species based on preference data using Spearman rank correlations (diet rank vs. preference rank) for each bird species. We then compared correlation coefficients of migrant and resident species-pairs using a paired-sample t -test (prediction 5, Table 1). In cases where our *a priori* predictions were directional (i.e., $A > B$), we used 1-tailed statistical tests (Rice and Gaines 1994).

Results

Diet comparisons

Diet breadth differed between migrants and residents. The Fisher's α score of seed types in fecal samples for resident species was on average half the score of their migrant counterparts (Fig. 1a) indicating that resident species consumed a lower diversity of fruits than did closely related migrant species. All species-pairs but one (tanager1) were consistent in the direction of this association. Higher fruit diversity in the diets of migrants is consistent with the *competitive exclusion* hypothesis ($t = 4.3$, $df = 6$, $P = 0.003$). Additionally, migrant species consumed fruits from an average of 23.5% more plant species than did their resident counterparts, although this trend was only

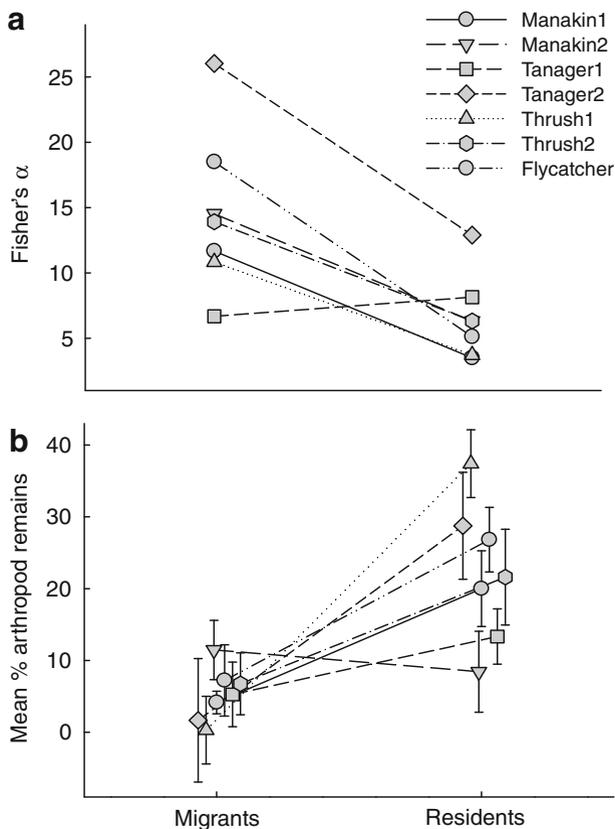


Fig. 1 Differences in the diet of altitudinal migrant birds and closely related sympatric resident species based on **a** Fisher's α index calculated using presence of seeds of different plant species within fecal samples, and **b** mean proportions (± 1 SE) of arthropod remains within fecal samples. Species and sample sizes for species-pairs involved in dietary analyses are as follows (in all cases, the migrant species is followed by the resident in a pair): manakin1 = *Corapipo altera* (89), *Schiffornis turdina* (8); manakin2 = *Pipra pipra* (13), *Manacus candei* (7); flycatcher1 = *Mionectes olivaceus* (9), *M. oleaginous* (11); thrush1 = *Myadestes melanops* (10), *Catharus mexicanus* (10); thrush2 = *Turdus obsoletus* (12), *T. grayi* (5); tanager1 = *Tangara icterocephala* (11), *Tachyphonus delatrii* (15); tanager2 = *Tangara florida* (3), *Chlorospingus ophthalmicus* (4)

marginally significant ($t = 1.5$, $df = 6$, $P = 0.087$). In contrast, residents consumed proportionately more arthropods than did migrants (whole model, $F_{7, 199} = 10.1$, $P < 0.0001$; Fig. 1b) which is consistent with the *dietary specialization* hypothesis. Fecal samples collected from migrant birds contained on average 5.0% ($\pm 1.8\%$ SE) arthropod remains, whereas samples from resident birds contained on average 21.9% ($\pm 2.1\%$ SE) arthropod remains. All species-pairs but one (manakin 2) were consistent in the direction of this association.

Preference comparisons

Fruit preferences tended to be slightly stronger in migrant species compared to resident species; residents consumed a broader array of fruits (whole model, $F_{3, 24} = 5.5$, $P = 0.005$; Fig. 2) consistent with the *dietary specialization* hypothesis ($F_{1, 24} = 2.6$, $P = 0.059$). Migrants consumed fruits from an average of 0.82 (11.4%) fewer plant species during preference trials than did their resident counterparts. This (statistically marginal) difference was not due to migrants eating more individual fruits during trials; the total number of fruits consumed was not related to migratory tendency (whole model, $F_{3, 24} = 2.6$, $P = 0.007$; effect test for migratory status, $F_{1, 24} = 0.02$, $P = 0.880$). The number of fruits offered on each infructescence did not affect fruit rankings ($F_{1, 107} = 1.1$, $P = 0.295$). Although migrants tended to consume fruit from fewer plant species, species-pairs shared the same fruit preferences; the ranking of fruit preferences between migrants and residents within a species-pair was very similar (flycatchers, $r = 0.932$; manakins, $r = 0.901$; Fig. 3). These findings are consistent with the *competitive exclusion* hypothesis ($P < 0.0001$ and $P = 0.003$ for flycatchers and manikins', respectively). Fruit rankings based on preference trials were more similar to each other than were fruit rankings based on diet (flycatchers diet ranks, $r = 0.843$, $P = 0.002$; manikins' diet ranks, $r = 0.181$, $P = 0.698$).

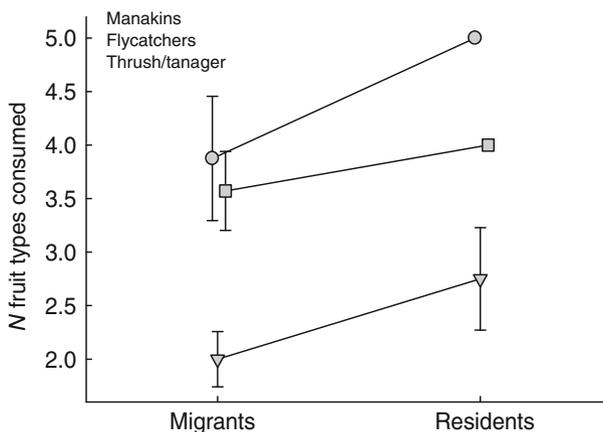


Fig. 2 Strength of fruit preference by altitudinal migrant birds and closely related sympatric resident birds based on the mean (± 1 SE) number of plant species from which individual birds consumed fruits during preference trials. Species and sample sizes for species-pairs involved in dietary analyses are as follows (in all cases, the migrant species is followed by the resident in a pair): manakins = *Corapipo altera* (8), *Manacus candei* (2); flycatchers = *Mionectes olivaceus* (6), *M. oleagineus* (4); thrush/tanager = *Myadestes melanops* (7), *Tachyphonus delatrii* (1)

Fig. 3 The similarity of fruit preferences (based on preference trials) between migrants and residents within species-pairs (manakins = *Corapipo altera* and *Manacus candei*; flycatchers = *Mionectes olivaceus* and *M. oleagineus*). Values on x- and y-axes represent rank order of the bird's preference for the fruit of a particular plant (low values are most preferred), and dots represent plant species used in preference trials. Plant codes are: CaveComp, *Cavendishia complectans*; CaveEndr, *Cavendishia endresii*; ClusGrac, *Clusia gracilis*; ClusSten, *Clusia stenophylla*; ColuParv, *Columnnea parviflora*; ConoMicr, *Conostegia micrantha*; DoliMult, *Doliocarpus multiflora*; HedyBonp, *Hedyosmum bonplandianum*; MarcCaud, *Marcgravia caudata*; MicoCent, *Miconia centrodesma*; MicoLore, *Miconia loreyoides*; OssaMicr, *Ossaea micrantha*; PscBuch, *Psychotria buchtienii*; ShefSyst, *Schefflera systyla*

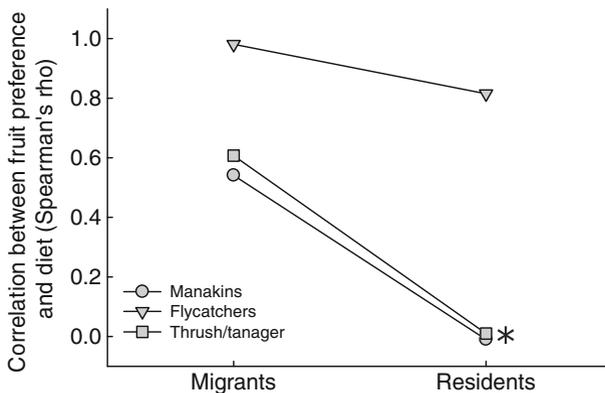
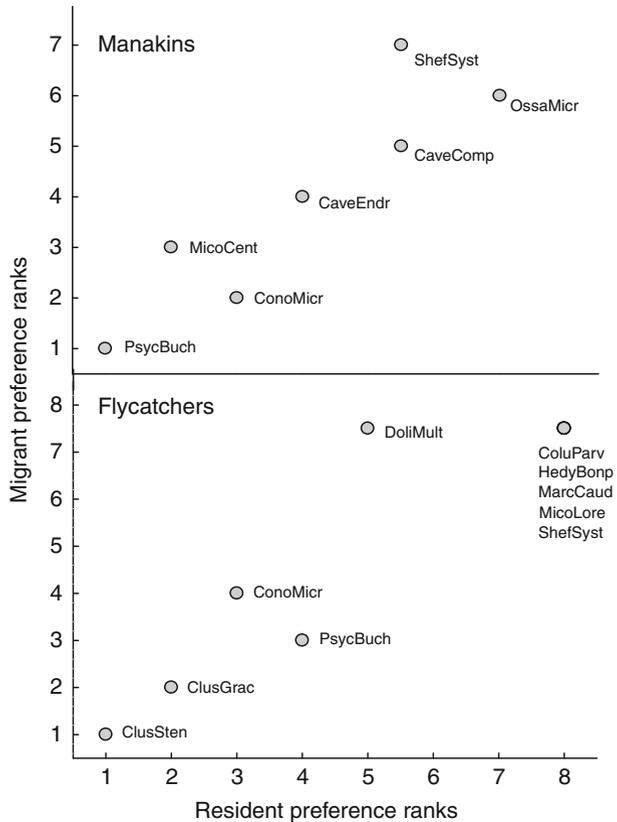


Fig. 4 Extent to which the preferred fruits (based on preference trials) were actually eaten by birds in the wild is depicted by the correlation between ranks of fruits eaten based on frequency of seeds in fecal samples and ranks of fruit preference based on experimental preference trials. Correlation coefficients marked with an asterisk (*Tachyphonus delatrii* and *Manacus candei*) were indistinguishable from zero. *P*-values of other correlations were: *Mionectes oleagineus*, *P* = 0.004; *M. olivaceus*, *P* < 0.0001 (flycatchers); *Corapipo altera*, *P* = 0.069 (manakin); *Myadestes melanops*, *P* = 0.083 (thrush). Species and sample sizes for species-pairs are the same as in Fig. 2

Relationship between diet and preference

Diets of migrant species (based on fecal samples) more closely resembled their preferences (based on preference trials) than did those of their resident counterparts (Fig. 4). The correlation coefficient between diet rank and preference rank was not weaker in migrants relative to their resident counterparts as predicted by the *competitive exclusion* hypothesis; indeed, diet and preference ranks were more similar in migrants than in residents, consistent with the *dietary specialization* hypothesis ($P = 0.043$). Despite the few pairs of species for which we were able to make this comparison, all species-pairs were consistent in the direction of this effect.

Discussion

Migrant and resident frugivores consistently differed in their diets and their fruit preferences, with results providing some support for each hypothesis (Table 1). The *competitive exclusion* hypothesis postulates that differences in migratory behavior between sympatric frugivore species are attributable to residents having competitive foraging advantages over their migrant counterparts. The *dietary specialization* hypothesis, in contrast, postulates that differences in foraging choices (i.e., diet breadth of fruits eaten) among frugivores explain differences in migratory behaviour between species. Consistent with the *competitive exclusion* hypothesis, the diversity of fruits in diets was higher in migrant species than in resident species (Fig. 1a), suggesting that residents are able to fill more of their dietary needs with their most preferred fruits, and that migrants may be forced to sample from a broader array of fruits (prediction 1, Table 1). Migrants and closely related residents also shared fruit preferences to a remarkable degree (prediction 3, Table 1), indicating that opportunities do exist (i.e., a necessary condition but not diagnostic) for interspecific competition for the most sought-after fruits. This result also suggests that different fruit preferences do not explain species-level differences in migratory behaviour. However, the results of predictions 2, 4, and 5 (Table 1) challenge the *competitive exclusion* hypothesis and are consistent with the *dietary specialization* hypothesis. Our comparison of the relative importance of fruits vs. arthropods in diets suggests that residents more often include arthropod prey in their diet. In this sense, residents have less restricted diets than migrants. Furthermore, preference trial results suggest that despite sharing preferences for the same fruits, migrants tend to exhibit stronger preferences (although sample sizes are low and the differences small and of marginal statistical significance), which would be expected under the *dietary specialization* hypothesis but not the *competitive exclusion* hypothesis. Most importantly, the degree to which the diets of residents reflect their preferences suggests that current interspecific competition is insufficient to explain differences in migratory strategy among species. Interestingly, this result is consistent with results of recent intraspecific studies where age-related dominance appears not to be associated with migratory strategy (Boyle 2008), but contrasts with those of some temperate birds where resident individuals outcompete migrants for prime wintering territories (Pérez-Tris and Tellería 2002). The strong correlations between migrants' diets and fruit preferences imply that the broader diversity of fruits in migrant diets is not caused by migrants being outcompeted by residents for the most-preferred fruits.

The relationship between diet breadth and migratory behavior differed depending on which of the two measures of diet breadth (fruit diversity or balance between fruit and arthropods) we used. Consequently, we suggest that future studies carefully examine how

each of these two components of diet breadth might be constrained. Our data does not indicate that migrants eat fruits of fewer plant species, but migrants do appear to have diets more restricted to fruit relative to other food types. This result mirrors the positive relationship found between dietary fruit diversity and degree of frugivory in other frugivorous bird communities (Jordano 1987; Carnicer et al. 2009). As a consequence of foraging more exclusively on fruit, migrants may be obliged to sample more broadly from the fruits produced by the plant community. Most fruits are low in protein (Wheelwright et al. 1984) relative to arthropod prey, and the low protein content of fruits can present a nutritional limitation (Witmer 1998). Sampling broadly from the fruits available may thus be necessary in order to complete the nutritional needs of an obligate frugivore. In at least a few species of frugivores, fruits apparently fill the total protein requirements of individuals (Bosque and Pacheco 2000; Herrera et al. 2009). Yet dietary choices can be influenced by small changes in protein levels, supporting the idea that fruit choices result from an interaction between the endogenous state of an individual and the morphological and chemical traits of fruits (Bosque and Calchi 2003; Schaefer et al. 2003). Interpretation of our results will be enhanced by a better understanding of: (i) the role that arthropods play in fulfilling a frugivore's nutritional needs during the non-breeding season, (ii) temporal and interspecific variation in the nutrient content of tropical fruits, and (iii) how foraging on a diverse assemblage of fruits might mediate a bird's need to forage for arthropods.

Our finding of similar fruit preferences between pairs of migrant and resident species (prediction 3, Table 1) does not refute the *dietary specialization* hypothesis as a whole, but suggests how to refine the mechanism underlying this hypothesis. In particular, high fruit diversity in migrants' diets suggests that most are unlikely to be tracking the phenology of a single family or genus of plant over their migratory cycle (but see Wheelwright 1983). However, birds might migrate in response to the changing nutrient profiles of fruits at different elevations over the course of the year. Possibly, migrants seek plant communities producing fruits with complementary chemical compositions (Whelan et al. 1998; Schaefer et al. 2003) as has been suggested in nutrient-balancing models of insect foraging (Raubenheimer and Simpson 1993). Interestingly, analysis of the diet of one of the species involved in this study reveals that over the course of a whole year and the elevations frequented during migration, dietary profiles remain remarkably constant with only small shifts in the consumption of arthropod prey or characteristics of the fruits consumed (Boyle 2006, 2010).

It is useful to compare and contrast the *competitive exclusion* and *dietary specialization* hypotheses and examine whether their similarities affect our ability to distinguish between them. We made no assumptions regarding the underlying causes of putative differences among species in when formulating these hypotheses. A potential cause of differences in dietary specialization is past interspecific competition; on evolutionary time-scales, overlapping resource use is thought to select for morphological and behavioural differences among taxa that result in reduced competition on ecological time-scales. If this "ghost of competition past" (Connell 1980) has led to differences in dietary specialization, which in turn affects migratory behaviour, then the ultimate process underlying both hypotheses might be the same, differing only in the mechanism and the temporal scale by which interspecific competition acts. The *competitive exclusion* hypothesis posits that active competition for food mediates individual interactions, whereas the *dietary specialization* hypothesis posits that differences between coexisting species in migratory tendency are not caused by ongoing competitive interactions but rather are the result of adaptations shaped by past interactions. In addition, differences in dietary specialization could reflect strategic differences (*sensu* Sherry 1990) among species caused by morphological, physiological,

behaviorial, or cognitive constraints, or tactical differences between species in the degree to which a species' realized niche reflects its fundamental niche.

The fact that interspecific competition may underly both of these hypotheses does not make them synonymous, however. Many alternative research hypotheses are based on the same ecological process (but differ in mechanism) and they frequently make similar predictions (Wiens 1989). The key is to find predictions that allow us to differentiate among them. The literature on avian migration continues to be dominated by theoretical and synthesis papers that present a wide array of hypotheses, many of which partially overlap with one another and whose mechanisms are only vaguely defined (e.g., Alerstam et al. 2003; Bell 2005; Salewski and Bruderer 2007; Bruderer and Salewski 2008). Only via side-by-side tests of alternative, mechanistic hypotheses can we distinguish between explanations, and thereby identify the underlying causes of ecological patterns in the natural world (Oksanen 1991; Krebs 2006).

Predictions tested in this study represent expected differences between migrant and resident species at a single point in time, and do not consider the temporal dynamics of dietary choices. Recent work has demonstrated how the temporal dynamics of dietary switching between fruits and arthropods in birds can reduce competition between species and how switching is related to diet breadth (Carnicer et al. 2008). Interestingly, because more dietarily specialized taxa (insectivores in Carnicer et al. 2008) were slower to switch food types following a change in the relative abundance of fruits and insects, both the dynamic models (Abrams 2006) and the empirical data predict that in a community “snapshot”, dietarily specialized species would have narrower diet breadths and exhibit stronger preferences for their primary food source than generalist species.

The results of this study demonstrate that previously-noted correlations between frugivory and migration are apparent even when comparing closely related species within lineages of primarily frugivorous birds. Whereas Levey and Stiles (1992) correlated both general dietary category (346 species of Costa Rican forest birds) and a three-level degree of frugivory/insectivory (61 species of flycatchers) with short-distance migration, and Boyle and Conway (2007) correlated degree of frugivory/insectivory using a four-level qualitative scale (among other factors) with migration tendency across 379 Tyrannid species in a phylogenetic context, this study focuses exclusively on “primarily frugivorous” birds. Here, we also incorporate a phylogenetic control and characterize diet choices much more thoroughly via direct measurement rather than by characterizations based on written descriptions in published works. The results reveal that even within frugivorous birds, there is a positive association between degree of frugivory and short-distance migration. Thus, our findings provide further support for the idea that food limitation plays a role in causing some birds to migrate. Gaining a more thorough understanding of the mechanisms by which food limitation has influenced the evolution of bird migration remains a challenge.

To further our understanding of the causes of variation in migratory behavior, we suggest that the *dietary specialization* hypothesis be tested against hypotheses that do not rely upon food limitation. Under such alternatives, the direction of the causal arrow between diet and migration could be reversed, whereby observed differences in diet between migrants and residents are caused by migration itself. For example, if migration is actually caused by spatial and temporal variation in weather (Boyle 2008) or predation risk, migrants could be constrained to eat foods that are easiest to find following migration to a new location. Tropical forests are believed to be places of intense competition for arthropod prey (Janzen 1973; Sherry 1984), contrasting with the view that fruits and flowers (unlike most other food resources) “want” to be eaten (Snow 1971). Distinguishing

whether dietary differences between species are a cause or a consequence of migration would require manipulating diet and determining whether changes in migratory tendency ensue, an approach that thus far has been logistically impractical. Future research could, however, explicitly examine if competition is higher for insects than for fruits. Additionally, because in comparative studies of migratory behaviour, sample size is limited by the number of migrant species in the community, the inferences that can be drawn from this study are restricted. Thus, future work should also replicate this study with other migrant-resident species-pairs in other tropical regions.

Ours is the first empirical study to compare diet preferences between sympatric migrant and resident birds using preference trials in wild birds, and is one of the few studies to quantify the correlation between frugivorous birds' diets (realized foraging niche) and their preferred foods (fundamental foraging niche) (but see McPherson 1988; Whelan and Willson 1994). Our results call into question the mechanism of ongoing competitive exclusion to explain why some, but not all, tropical birds migrate altitudinally. This study is the first to reveal associations between realized diet, dietary preference, and migration within several lineages of passerine birds with similar diets, implying that ecological factors acted similarly on multiple taxa in the evolution of altitudinal migration. These results lend new support to hypotheses suggesting that food limitation has influenced the evolution of bird migration and help focus attention on mechanisms that underly this relationship.

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