

Partial migration in birds: tests of three hypotheses in a tropical lekking frugivore

W. Alice Boyle*†

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

Summary

1. Partially migratory species provide opportunities to understand which ecological factors cause some animals to migrate when others remain resident year round. Partial migration in birds has been explained by the dominance, arrival-time, and body-size hypotheses.

2. Testing these hypotheses has proven difficult due to the similarities of the predictions they make in temperate-breeding long-distance migrants. In tropical altitudinal migrants, however, these hypotheses make different predictions regarding the sex, age, and condition of migrants and residents.

3. Among white-ruffed manakins in Costa Rica, young birds were not more likely to migrate (as predicted by the dominance hypothesis), nor were females more likely to migrate (as predicted by the arrival-time hypothesis). All condition-related variables interacted with sex, together explaining much of the variation in migratory behaviour.

4. I re-articulate the body-size hypothesis in the context of tropical altitudinal bird migration, focusing explicitly on how limited foraging opportunities and differences in individual condition affect fasting ability during torrential rains. Despite ample food, the smallest birds or those stressed by parasites or moult may risk starvation at breeding elevations due to a reduction in foraging time. These results highlight how intrinsic and extrinsic factors may interact to produce observed patterns of within- and among-species variation in migratory behaviour.

Key-words: altitudinal migration, *Corapipo altera*, elevational gradient, manakin, physiological condition, tropical forest

Introduction

Species in all major animal lineages engage in annual migrations. These cyclical, annual movements have profound consequences for the biological communities between which migrants move (Dingle 1996; Greenberg & Marra 2005). Migrants are seen as harbingers of climate change (Peñuelas, Filella & Comas 2002; Jonzen *et al.* 2006) and are acknowledged to require special conservation strategies (Martin & Finch 1995; Powell & Bjork 1995). Because of migrants' importance to both basic and applied ecology, the cause of variation in migratory behaviour has been a topic of debate. Several comparative studies have identified traits associated with the evolution of bird migration (Levey & Stiles 1992; Sol, Lefebvre & Rodriguez-Teijeiro 2005; Boyle & Conway 2007; Møller 2007). Partially migratory species (in which individuals vary in migratory tendency) provide opportunities to corroborate comparative results by identifying traits associated with migration on ecological time-scales. Partial migration may

represent an evolutionary transition between residency and complete migration, and is likely the most common species-level expression of migratory behaviour (Berthold 1999).

Migratory behaviour can be fixed at the individual level (Lundberg 1988; Berthold 2001; 'obligate partial migration' *sensu* Terrill & Able 1988), or can be a condition-dependent strategy varying within individuals over their lifetime (Ketterson & Nolan 1983; Cristol, Baker & Corbone 1999; 'facultative partial migration'). In obligate partial migrants, an individual's migratory behaviour is primarily determined by the genetic makeup of its parents (Lundberg 1988) and thus, age- and sex-related biases in migratory tendency are not expected. In facultative partial migrants, migratory decisions are subject to trade-offs influenced by environment and individual condition. Because condition depends upon competitive abilities, health, and reproductive potential, hypotheses explaining facultative partial migration rely on age- and/or sex-dependent trade-offs between reproduction and survival resulting in condition-dependent biases in migratory tendency.

Three main hypotheses have been proposed to explain facultative partial migration. All assume that food scarcity or physiological intolerance to climatic conditions (or both)

*Correspondence author. E-mail: a Boyle7@uwo.ca.

†Present address: Department of Biology, University of Western Ontario, London, ON, Canada N6A 5B7

limit the abilities of individuals to remain on their breeding grounds during the nonbreeding season. Although the three hypotheses were formulated to explain differences in migratory distance among individuals (differential migration), they have been widely applied to partially migratory species. The dominance hypothesis invokes competition for food (Ketterson & Nolan 1976). According to this hypothesis, dominant (typically older) individuals out-compete subordinates for scarce food resources during winter months; thus, they are able to stay on breeding grounds year round, while subordinates migrate to areas with reduced competition for food. The arrival-time hypothesis (Ketterson & Nolan 1976) predicts that the sex whose fitness is more limited by intra-sexual competition for mates will be more likely to forego food-related benefits of migrating in exchange for enhanced reproductive benefits associated with remaining on the breeding grounds. The body-size hypothesis (Ketterson & Nolan 1976) postulates that inclement weather makes year-round residency a risky strategy, regardless of food availability. Because larger and healthier individuals can fast longer than smaller individuals due to greater fuel reserves relative to their metabolic rates (Calder 1974), only larger individuals should risk starvation during storms, foregoing weather-related benefits of migrating. Thus, identifying if migratory tendency is related to age, sex, and/or condition is critical to determining if migration is a fixed or conditional strategy, may distinguish among condition-dependent hypotheses, and provides insight into the nature of the trade-offs associated with migratory decisions.

Previous tests of the dominance, arrival-time, and body-size hypotheses examined territorial birds that breed in temperate or subtropical regions (e.g. Ketterson & Nolan 1976; Lundberg 1985; Belthoff & Gauthreaux 1991; Jenkins & Cristol 2002; Stouffer & Dwyer 2003; Catry *et al.* 2004). Unfortunately, the life histories of most species studied result in the three hypotheses making similar predictions regarding age and sex biases in migratory tendency. For instance, male dark-eyed juncos (*Junco hyemalis*, Linnaeus 1758) are territorial, and are on average 8–10% larger than females. The dominance hypothesis predicts that adult males should be less likely to migrate than females (because females are subordinate) and younger individuals (because young birds are less experienced). The arrival-time hypothesis also predicts that adult males should be less likely to migrate, in this case because they would risk losing breeding territories. Finally, the body size hypothesis also predicts that adult males should be less likely to migrate than smaller females because of the physiological advantages of larger size when fasting or enduring cold-related stress. In the case of juncos, patterns of variation in migratory tendency led to a multi-factor hypothesis in which the relative roles of survival ability, and competition for food and mates varies with sex and age (Ketterson & Nolan 1983). Thus, although females and young birds in temperate regions are often more likely to migrate and migrate farther than males (Cristol *et al.* 1999), such patterns cannot refute any of the three hypotheses. One solution is to study species whose physical attributes and life histories result in distinct predictions under each of these hypotheses.

Tropical, lekking, altitudinal migrant birds such as white-ruffed manakins (*Corapipo altera* Hellmayr 1906, Pipridae) are ideal species for testing the dominance, arrival-time, and body-size hypotheses. Typical of tropical altitudinal migrants, *C. altera* is highly frugivorous, migrates between lower elevation nonbreeding areas and higher-elevation breeding areas on predictable, annual cycles, and is partially migratory with a portion of the population remaining at breeding sites year round (Rosselli 1994; Boyle 2006). Adult (≥ 4 years old) male *C. altera* perform agile solo and multiple-male displays at leks (Rosselli, Vasquez & Ayub 2002), are visited by females to mate, after which females undertake subsequent reproductive behaviour on their own (Stiles & Skutch 1989; Rosselli *et al.* 2002). Females are heavier than males, are not known to defend nesting areas, and neither sex is known to defend food resources. No information exists regarding foraging dominance hierarchies although young birds are presumably less experienced at obtaining food. Thus, the dominance hypothesis predicts that young *C. altera* should be more likely to migrate but does not necessarily predict differences among sexes in migratory tendency. The arrival-time hypothesis predicts that females should be more likely to migrate than males, because females presumably forfeit less by leaving breeding elevations than males who may forfeit lek ownership and social rank if they depart. Finally, the body-size hypothesis predicts that males should be more likely to migrate because they are smaller and would thus be more likely to experience adverse physiological effects of inclement weather during the nonbreeding season. The predictions of each of these hypotheses may be modified by an individual's physical condition which would affect the costs and benefits of migrating in a given year (Ketterson & Nolan 1983).

The objectives of this study were to evaluate three common hypotheses that have been proposed to explain partial migration by capturing *C. altera* individuals over a complete annual cycle at breeding and nonbreeding elevations. I tested predictions of age- and sex-biased migration using capture data of migrant and resident individuals. I also examined how physical condition and diet choices differed among individuals that migrated downhill during the nonbreeding season, and those that remained at breeding elevations year round.

Materials and methods

White-ruffed manakins breed in wet montane forests of southern Central and northern South America (BirdLife International 2004). Atlantic slope populations in Costa Rica breed between 400–900 m during April–June. Unlike Pacific slope populations, many individuals breeding on the Atlantic slope migrate downhill to lowland forests asynchronously during the second half of the year and migrate back uphill in February–March (Loiselle & Blake 1991; Rosselli 1994; Boyle 2006). Sexes are dimorphic in plumage and size, with females being 14% larger than males (mean mass \pm SE: females, 12.4 g \pm 0.08 g; males, 10.9 g \pm 0.05 g). Males resemble the green females during their first 1.5 years, acquiring a black and white mask in their second year and full adult male plumage (iridescent blue-black with a white throat) in their third year.

C. altera was studied at three sites spanning breeding and non-breeding elevations in the Braulio Carrillo National Park (BCNP) region of north-east Costa Rica. The highest-elevation site at 750 m (Rara Avis Reserve, 10°17'3"N, 84°02'47"W) lies in the middle of breeding elevations in this region. Forests at this site receive 8279 mm (\pm SE 263 mm) of rain annually. *C. altera* was also studied at two sites below breeding elevations: (i) La Selva Biological Station at ~100 m (10°24'59"N, 84°01'55"W), and (ii) BCNP, near the 'Cantarrana' refuge at 300 m (10°22'16"N, 84°02'45"W). The lowland forests at La Selva receive 4260 mm (\pm SE 100 mm) of rainfall annually and rainfall at Cantarrana is estimated to be ~6845 mm based on data collected during 2004. Cantarrana is located roughly equidistant (~7 km) in between the other two sites. In terrain, forest structure, and species composition, Cantarrana is transitional between the lower- and higher-elevation sites. Seasonal patterns of rainfall are similar along the gradient. On average, May–July and December are the rainiest months and February–April the least rainy, with roughly 2.5 times as much precipitation falling during the second half of the year as the first half. Mean annual temperatures range from 25.3 °C at 100 m to 22.3 °C at 750 m and temperature varies little over the course of the year (meteorological data; Rara Avis, La Selva, Instituto Costarricense de Electricidad, W. A. Boyle, unpublished).

C. altera were captured in 6–16 mist nets (12 m wide \times 3 m tall, 38-mm mesh) open 06:00–12:00 (or until rain began) for five to seven consecutive days at each site during each month of 2004. Nets were placed in the same locations in successive months in the understorey of old-growth forest. Nets were checked every 20 min and faecal samples collected for dietary analyses. Wing chord (millimetres) and body mass were measured (to the nearest 0.01 g using digital scales accurate to 0.001 g). In addition, sex (based on plumage, body mass, and presence of a brood patch or cloacal protuberance), and indices of subcutaneous fat (0–5; Helms & Drury 1960), ectoparasite infestation (0–3), and feather moult (0–3) were recorded for each individual. Hatch-year birds were not sexed but were generally distinguishable from adults by differences in moult limits, plumage colouration, and feather shape. Ectoparasite scores reflected both the number of ectoparasite types found on each individual as well as the intensity of infestation for each type (none, low, medium, high). Moult was classified as either none (0), light (1; body feathers only), moderate (2; some flight feathers, sometimes with some concurrent body moult), or high (3; extensive flight feather and body moult). Decimal values for parasite and moult indices reflect mean values of this numeric index. Seeds in faecal samples were identified (Boyle 2003) and the proportion of each sample that consisted of arthropod vs. fruit/seed remains was estimated (see Boyle 2006 for detailed description of diet methods and complete diet composition data). The relationship between migratory tendency and the relative proportion of fruits and arthropods in diets was examined because previous work showed that this component of diet is an important correlate of variation in migratory behaviour at the species level in the region (W.A. Boyle, C.J. Conway & J.L. Bronstein, unpublished).

The following four 'seasons' in the annual cycle of *C. altera* were defined based on capture rates, presence of brood patches or cloacal protuberances, and moult: (i) breeding (April–June), characterized by no *C. altera* at 100 m or 300 m and a high incidence of active brood patches; (ii) post-breeding (July–September), characterized by recruitment of hatch-year birds, initiation of moult in adult birds, and most captures at 750 m but a few at 300 m; (iii) nonbreeding (October–January), characterized by continued moult, gradual decline in captures at 750 m, and increases in captures at both 100 m and 300 m; and (iv) uphill migration (February–March), character-

ized by dramatic increases in captures at 750 m and disappearance of all *C. altera* from 100 m and 300 m. Residents were defined as those birds captured during October–January at 750 m and migrants as those captured at 100 m and 300 m during the same months.

To determine if birds of different ages differed in migratory tendency as predicted by the dominance hypothesis, comparisons were made between the ratios of hatch-year to adult birds among migrants and residents. To determine if birds of different sexes differed in migratory tendency as predicted by the arrival-time and body-size hypotheses, comparisons were made between the ratios of males to females captured at low elevations during the nonbreeding season relative to (i) 750 m during the breeding season, and (ii) 750 m during the nonbreeding season. Fisher's exact tests were used to detect differences in age and sex ratios. Birds of unknown age were excluded for analyses of age bias, and hatch-year birds and birds of unknown sex were excluded for analyses of sex bias. Recapture data on individuals captured repeatedly within seasons were excluded for age- and sex-bias analyses.

To further explore correlates of migratory tendency, a multiple logistic regression framework was used to model the likelihood of migrating as a function of age, sex, mass:wing chord ratios, fat scores, moult scores, diet choices, and ectoparasite scores. Month that measurements were taken on each bird was included as a covariate to control for temporal fluctuations in condition during the nonbreeding season unrelated to migratory status. Because of the results of the sex-bias analysis (see Results), models were evaluated that included interactions between sex and each of the other variables. Akaike's information criterion (AIC; Burnham & Anderson 2002) was used to evaluate among competing models. To interpret interaction terms in this model, means of the four sex and migration categories of each condition-dependent variable were plotted. The correlates of migratory tendency were modelled using two data sets: (i) including recapture records when those captures occurred in different months (excluding within-month recapture data), and (ii) a subset of those records, excluding all but the first capture record for each individual within a season. Results of these two analyses were qualitatively identical, so results of only the first set of analyses are presented.

Results

A total of 251 *C. altera* were captured during 13 321 mist net hours at the three elevations during 2004. Sixty-five individuals were captured more than once, and recaptures accounted for 139 of the 390 records. Three birds were recaptured at different elevations from their initial capture location providing direct evidence for altitudinal migration in this population. Fifteen birds captured between March and August at 750 m were still present during the nonbreeding season, implying that some individuals do remain at their breeding sites year round and are not being displaced by individuals migrating downhill from higher elevations.

The ratio of young (hatch year) to adult *C. altera* captured at low elevations (100 m and 300 m; 15:22) was no greater than the ratio of young birds captured at breeding elevations (750 m; 20:25) during the nonbreeding season (October–January; one-tailed Fisher's exact test, $P = 0.719$). Among adult (after-hatch-year) *C. altera*, the ratio of males to females at 750 m did not differ between breeding (April–June; 17:22) and nonbreeding seasons (13:11; two-tailed Fisher's exact test, $P = 0.447$). Males and females did not differ statistically

in their tendency to migrate (two-tailed Fisher's exact test, $P = 0.233$). However, trends in these data suggest that if anything, males were more likely to migrate than females, not the reverse as predicted by the arrival time hypothesis; during the nonbreeding season, males accounted for 73% of migrant captures whereas they accounted for only 54% of resident captures.

The model that best explained variation in migratory tendency included all main effects and three interactions: sex \times age, sex \times mass:wing chord, and sex \times moult score interactions (whole model, $\chi^2 = 53.7$, d.f. = 19, $P < 0.0001$). The only other model within two AIC values of the best model included an additional interaction term (sex \times fat score). Although residents had slightly higher mean fat scores and consumed proportionately more arthropods, after accounting for variation in migratory tendency associated with other factors, individual effect tests for fat score and diet were not statistically significant (Table 1). On average, a 1-unit increase in ectoparasite score was associated with a 3.6-fold increase in the odds of migrating.

The nature of the relationship between migratory tendency and age depended upon the sex of the bird (sex \times age interaction, $P = 0.001$; Table 1). Among females, the proportion of adult birds was very similar between migrants (66.7%) and residents (61.1%). However, among males, adults were more likely to migrate than younger birds; 82.6% of migrant males were adults whereas only 60.9% of resident males were adults. To further explore the relationship between age and migratory tendency in males, adults were separated into two groups by classifying all males according to plumage at the time of capture: immature (all green), full adult, or an intermediate plumage (masked plumage or moulting into adult plumage). Birds in these different age- and plumage stages likely experience different predation-related trade-offs due to differences in conspicuousness, and differ in the reproductive benefits they could accrue by remaining near leks year round. Adult-plumage males were the most likely to migrate, whereas intermediate-plumage males were the least likely to migrate with all-green birds being roughly equally represented among migrant and resident captures (Fig. 1).

Table 1. Factors associated with variation in migratory tendency among 81 individuals of *Corapipo altera* captured during the nonbreeding season on the Atlantic slope of Costa Rica

	Likelihood ratio χ^2	d.f.	P
Whole model	53.7	19	< 0.0001
Age	3.9	2	0.143
Sex	< 0.01	2	1.000
Mass:wing chord	0.5	1	0.487
Fat score	0.3	1	0.618
Moult score	0.6	1	0.428
Diet	1.5	1	0.222
Ectoparasite score	8.7	1	0.003
Month	20.2	3	< 0.001
Sex \times age	15.7	3	0.001
Sex \times mass:wing chord	9.8	2	0.007
Sex \times moult score	11.5	2	0.003

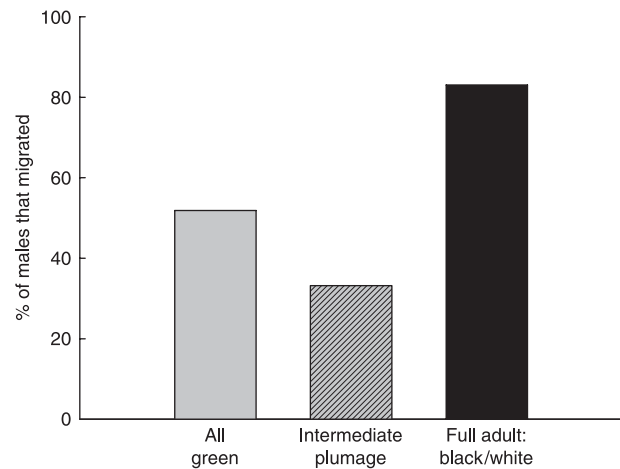


Fig. 1. Migratory tendencies of male white-ruffed manakins (*Corapipo altera*) of different age classes. Females of different ages were similar in their tendency to migrate but males differed according to age (sex \times age interaction term in multiple logistic regression model, $P = 0.001$; Table 1). This figure further explores the role of age (grouped according to plumage classes) in male migratory tendency. The percentage of ≥ 4 -year-old males (full adult plumage) that migrated was higher than the percentage of younger birds that migrated, and males acquiring adult plumage were less likely to migrate than all-green younger birds.

Physical condition affected migratory tendency differently for males and females (sex \times mass:wing chord ratio, $P = 0.007$; sex \times moult score, $P = 0.003$; Table 1). Among females, migrants were on average 4.8% lighter for their body size than residents. However, males differed little in this index of body condition; in fact, migrants tended to be slightly heavier for their size than residents (Fig. 2a). Overall, females were 11.6% heavier than males of the same wing length. Trends in the associations between migratory tendency and fat score (although not statistically significant) mirrored associations between migratory tendency and mass:wing chord ratios: average resident female fat scores were 0.6 higher than in migrant females, average resident male fat scores were 0.2 lower than in resident males, and average male fat score was 0.6 lower than in females (fat score, $P = 0.618$; Table 1). The association between moult and migratory tendency also differed between sexes. Residents had similar moult scores, independent of sex. In contrast, female migrants had average moult scores that were 2.2 times higher than female residents, whereas the moult score of male migrants averaged a little less than that of male residents (Fig. 2b). Overall, females were more likely to moult during the nonbreeding season than males; between October and January, mean moult scores of females more than doubled those of males.

Discussion

Patterns of variation in migratory tendency among *C. altera* suggest that individuals make migratory decisions associated with sex-related trade-offs in the costs and benefits of year-round residency. The correlates of migration were sex-dependent in ways that are consistent with the body-size hypothesis. The

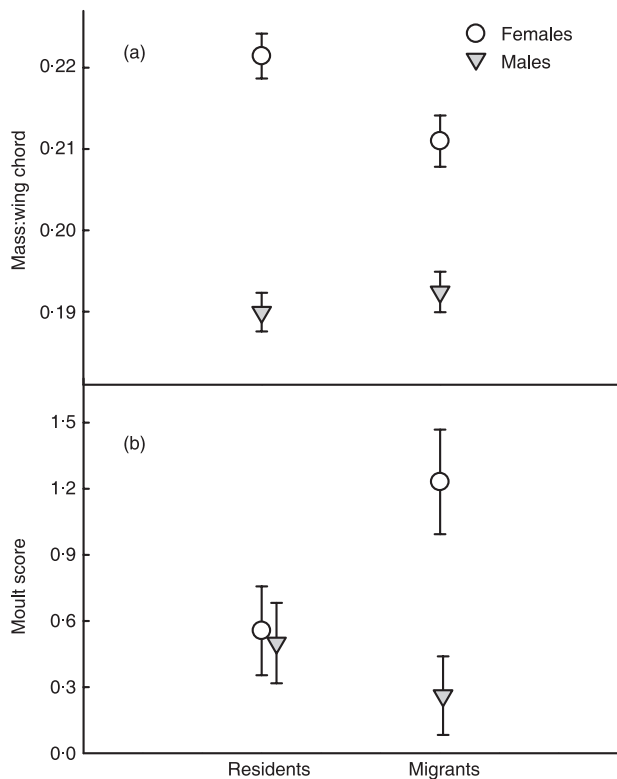


Fig. 2. The relationship between migratory tendency and two indices of individual condition. Mass:wing chord ratios (panel a) and moult scores (panel b) of *Corapipo altera* both interacted with sex in their association with migratory tendency. White circles represent mean female values and grey triangles represent mean male values with error bars representing one SE of the mean.

smaller sex (males) tended to be more likely to migrate than the larger sex (females), and among females, migrants were lighter for their size than residents (Fig. 2a). In contrast, I found no support for either the dominance or arrival-time hypotheses. Migratory tendency did not differ between age classes in ways that suggest that dominant individuals were forcing subordinates to be migratory; young and adult females were equally likely to migrate, and older males were more likely to migrate than younger ones. Migratory tendency also did not differ between sexes in ways consistent with the arrival-time hypothesis; females were not more likely to migrate, and trends in the data suggest the reverse may be true. Additional evidence undermining both the dominance and arrival-time hypotheses lies in spatial and temporal patterns of fruit availability (Boyle 2006). Fruits consumed by *C. altera* remain more abundant at breeding elevations throughout most of the post-breeding and nonbreeding seasons. These data refute an assumption common to both the dominance and the arrival-time hypotheses by suggesting that competition for food should be *lower* at breeding elevations than in the lowlands.

Year-round mild temperatures in wet tropical premontane forests may seem unlikely to present severe weather-related risks that could threaten survival. However, rainstorms lasting 3 or 4 days occur regularly between May and January in Central America. Although all elevations are affected by storms,

lowland forests receive less than half the precipitation of breeding elevations where as much as 292 mm of rain can fall in one day (Rara Avis, unpublished). Prolonged downpours during such storms could limit a small bird's foraging opportunities to the point of starvation, reducing the likelihood of survival for birds that remain resident year round. Increases in the allostatic load (McEwen & Wingfield 2003) due to severe rainfall events would only be exacerbated by the increased metabolic demands imposed by the slight (3 °C) reduction in mean temperature relative to lower elevations. For birds at the limits of their physiological capacities, increases in allostatic load due to unpredictable stressors (i.e. storms) would result in a deficit of energy intake relative to energetic demands (McEwen & Wingfield 2003). This imbalance would be predicted to activate hormonal and other physiological responses to stress that would result in allostatic overload and expression of behavioural responses such as downhill migration to alleviate the energetic imbalance (Wingfield 2003).

I propose that limited foraging opportunities could explain downhill migration in a manner consistent with both data presented here and several additional lines of evidence. This hypothesis is based on the body-size hypothesis but shifts attention explicitly towards the mechanisms through which diet, body size, and weather could explain inter- and intra-specific variation in migratory tendency in tropical birds. Females, especially larger individuals, may be less likely to migrate because they have the metabolic capability to fast for longer periods than do smaller males. Females that gamble successfully on year-round residency can forage on abundant food resources when weather conditions permit. Thus, females that survive may begin their next reproductive season in better condition than females that migrate. Females that initiate moult late or whose moult is more protracted would be less capable of fasting due to the demands of feather growth (Murphy 1996) making residency a riskier strategy. Because males initiate moult 2 months earlier than females (Boyle 2006), moult-related differences would play a smaller role in the migratory decisions of males than females. Resident males are likely to experience greater risks associated with fasting than females due to their smaller size. Differences in migratory tendency among males of different age classes could reflect either differences in the costs of carrying more fat or differences in the reproductive benefits of residency. Heavier birds (relative to wing area) are less able to escape predation (Lima 1986), and conspicuous adult plumage would only exacerbate this risk relative to drab green young males. Therefore, if the limited foraging opportunities associated with residency can be offset by carrying more fat, young males may be more likely to adopt this strategy than adult males. Alternatively, younger birds (especially those soon competing for mating opportunities) may benefit from the departure of older males as they prospect for lek sites. Across all individuals, poorer body condition due to ectoparasitism would increase the incidence of allostatic overload and the likelihood of migrating downhill (Proctor & Owens 2000).

Several lines of evidence are consistent with this foraging-limitation hypothesis. First, post-breeding birds at breeding

elevations generally have very low fat indices (mean fat score = 0.66). Second, death by starvation resulting from fasts during successive days with heavy downpours is plausible given the high food intake rates maintained by small frugivorous birds. Captive male *C. altera* consumed their body mass in fruits in < 1.5 h, and individuals that failed to learn to eat artificial diet within 4 h in captivity died the following night (W. A. Boyle, unpublished). Third, differences in migratory strategy between Costa Rican Atlantic slope populations (partially migratory) and Pacific slope populations (nonmigratory) parallel differences in weather regimes. Breeding elevations of *C. altera* on the Pacific slope receive less than half the annual rainfall (~4000 mm) of breeding elevations on the Atlantic slope. Fourth, the highly asynchronous nature of downhill migration (unlike uphill migration) in manakins and other altitudinal migrants suggests that individuals make condition-dependent migratory decisions, perhaps only moving downhill when energy demands outstrip food intake. Fifth, storms have been credited with causing short-term facultative altitudinal movements in other tropical avifaunas (O'Neill & Parker 1978; Winker *et al.* 1997). Sixth, expert naturalists in the lowlands report seeing more altitudinal migrants during years of particularly heavy rains (J. Alvarado, personal communication). Finally, intact *C. altera* carcasses have been found immediately following severe rainstorms at lowland sites (S. Woltman, personal communication).

The foraging requirements of birds feeding on carbohydrate-rich fruits may be similar to nectarivores (the only other guild of tropical birds that regularly migrate altitudinally; Stiles 1988) that must maintain high intake rates to maintain energy balance (Martínez del Río *et al.* 2001). The nutritional content of watery carbohydrate-rich fruits more closely resembles nectar than lipid- or protein-rich foods such as arthropods, vertebrate prey, or fruits of certain plant taxa such as palms or Lauraceae (Wheelwright *et al.* 1984). Fruits consumed by *C. altera* contain an average of ~6.5% sugar (H. A. Lumpkin and W. A. Boyle, unpublished), which is well below typical sugar concentrations of hummingbird nectar (Baker, Baker & Hodges 1998).

The limited-foraging-opportunities hypothesis is also consistent with species-level correlates of migration. Diets differ among migrant and resident species in both large-scale comparative analyses (Levey & Stiles 1992; Boyle & Conway 2007), and in species-pair comparisons of frugivorous tropical birds (Boyle *et al.* in review) in ways that parallel trends in diet choices of individual *C. altera*. Associations between a frugivorous diet and short-distance tropical migrations have been interpreted as evidence that variation in food abundance promotes migratory behaviour. The limited-foraging hypothesis suggests an alternative interpretation; foraging choices may influence the physiological attributes of frugivores and nectarivores such that their responses to environmental variation differ from those of birds in other foraging guilds. While food abundance may explain uphill movements, fasting ability may explain why highly frugivorous and nectarivorous birds often migrate downhill.

If we are able to directly link short-distance migrations of tropical birds to variation in weather, then we will come tangibly

closer to understanding the consequences of climate change on the long-term persistence of altitudinal migrant populations. Tropical storms are predicted to increase in frequency and severity (Albritton *et al.* 2001). In addition to the effects such storms may have on food production, increases in the frequency or duration of storms could lead to increased risks associated with year-round residency. Stability of altitudinal migrant populations would thus depend on whether the ever-diminishing patches of Central American lowland forest (Sanchez-Azofeifa, Harriss & Skole 2001) are sufficient to sustain increasing numbers of altitudinal migrants during their nonbreeding season. The extent to which we can generalize results based on a lekking species such as *C. altera* to other partially migratory species is not yet clear. In addition, because individual condition was measured after migration occurred in this study, differences in condition could be consequences rather than causes of migration. Thus, broader inferences must be tentative until we test the foraging-limitation hypothesis in other species and examine how storms affect physiological condition in more detail. At present, however, these results suggest that both intrinsic and extrinsic factors must be taken into consideration when explaining why some animals migrate and others do not. Food availability likely interacts in important ways with climate and an individual's physiology and nutritional needs to shape the diversity of migration patterns we see within and among species.

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