Does food abundance explain altitudinal migration in a tropical frugivorous bird?

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Abstract: Many animals undergo annual migrations. These movements are well studied at proximate levels, but their fundamental causes are poorly understood. Among tropical frugivorous birds, annual migration is thought to have evolved in the context of exploiting reciprocal peaks in fruit abundance among locations and seasons, yet previous tests of this hypothesis have yielded equivocal results. In this paper, I tested whether protein and (or) fruit limitation explain both uphill and downhill migratory movements in a tropical frugivorous bird, the White-ruffed Manakin (*Corapipo altera* Hellmayer, 1906). While White-ruffed Manakins likely migrate uphill to exploit peaks in fruit abundance, I found no evidence that elevational differences in fruit abundance explain the downhill portion of the migratory cycle. This result challenges long-standing ideas regarding the causes of altitudinal migration because it implies that birds seeking to maximize fruit intake should remain sedentary at higher elevations. Data are also inconsistent with the hypothesis that White-ruffed Manakins migrate (either uphill or downhill) to exploit arthropod prey. Future studies should consider how variation in weather, predators, or parasites could help explain altitudinal migrations of birds from breeding areas to nonbreeding areas.

Résumé : Plusieurs animaux entreprennent des migrations annuelles. Ces déplacements sont bien étudiés à l'échelle immédiate, mais leurs causes fondamentalement restent mal comprises. Chez les oiseaux frugivores tropicaux, on croit que la migration annuelle s'est développée afin d'exploiter des pics inversés d'abondance de fruits entre des endroits ou des saisons, bien que des tests antérieurs de cette hypothèse aient donné des résultats équivoques. Ce travail vérifie si les restrictions en protéines et(ou) en fruits expliquent les déplacements de migration vers le haut et le bas chez un oiseau frugivore tropical, le manakin à fraise (*Corapipo altera* Hellmayer, 1906). Les manakins à fraise migrent vraisemblablement en altitude pour exploiter des pics d'abondance de fruits. Il n'y a cependant aucune indication de différences altitudinales d'abondance de fruits pour expliquer la partie descendante du cycle migratoire. Ces résultats remettent en question des idées reçues depuis longtemps concernant les causes des migrations en altitude parce qu'ils laissent croire que les oiseaux qui voudraient maximiser leur apport de fruits devraient demeurer sédentaires aux altitudes plus élevées. Les données sont aussi incompatibles avec l'hypothèse selon laquelle les manakins à fraise migrent (vers le haut ou le bas) pour exploiter des proies arthropodes. Les études futures devraient examiner comment les variations de climat, de prédateurs ou de parasites peuvent aider à expliquer les migrations en altitude des oiseaux à partir de leurs sites de reproduction vers des sites non reproductifs.

[Traduit par la Rédaction]

Introduction

Many species of animals migrate between breeding and nonbreeding areas every year, profoundly affecting the diversity, composition, and biotic interactions of the communities they move between (Dingle 1996; Greenberg and Salewski 2005; Hagan and Johnston 1992). Despite the ubiquity of animal migration and the many hypotheses proposed to explain how (e.g., Joseph et al. 1999; Loxdale and Lushai 1999; Bell 2000) and why (e.g., Cox 1985; Drake and Gatehouse 1995; Alerstam et al. 2003) migratory behaviour evolved, few studies have tested predictions that could

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refute these hypotheses. Much of the difficulty in studying the ultimate causes of avian migration stems from our focus on long-distance temperate–tropical migrants. Short-distance migrations (such as altitudinal migrations) are more tractable systems in which to test hypotheses explaining the evolution of migration owing to the relative ease of linking breeding and nonbreeding ranges and fewer climatic and biotic differences between ranges. Altitudinal migration involves annual, return movements from lower elevation nonbreeding ranges to higher elevation breeding ranges, and seems to be especially common in tropical avifaunas (Loiselle and Blake 1991; Johnson and Maclean 1994; Ornelas and Arizmendi 1995; Hobson et al. 2003).

Tropical altitudinal migrant birds are primarily frugivorous or nectarivorous (Stiles 1983). Consequently, these migrations are widely explained as responses to variation in fruit or nectar abundance (e.g., Stiles and Skutch 1989; Levey and Stiles 1992; Alcock 2005), and several studies have examined the relationship between altitudinal migration patterns and food abundance (Wheelwright 1983; Loiselle and Blake 1991; Rosselli 1994; Solórzano et al. 2000; Chaves-Campos et al. 2003; Chaves-Campos 2004). How-

ever, empirical data have rarely matched the predicted patterns of reciprocal peaks in fruit abundance between breeding and nonbreeding elevations. At best, fruit limitation has been reported to explain uphill (Rosselli 1994; Chaves-Campos et al. 2003) or downhill (Loiselle and Blake 1991) movements alone, but not the whole annual migratory cycle. Nevertheless, recent comparative work suggests that dietary choices (and hence possibly food limitation) likely have influenced the evolution of altitudinal migration in tropical birds (Boyle 2006). Because birds may migrate uphill for different reasons than those for which they migrate downhill (e.g., owing to different energetic or nutritional demands as a result of the seasonality of breeding and moult), a full explanation of altitudinal migration patterns requires accounting for both uphill and downhill phases of the migratory cycle, and articulating mechanistic hypotheses that identify the specific food resources critical in shaping migratory behaviour (Smith and Rotenberry 1990).

If food limitation explains both uphill and downhill movements, then which foods consumed by frugivores would be predicted to vary seasonally and altitudinally? The "fruit-limitation hypothesis" postulates that if more fruits important in the diets of migrant species are available during the breeding season at breeding elevations, then uphill migration could function to track the abundance of those specific fruits. The aggregate energetic requirements of bird populations should be greatest near the end of the breeding season because of the influx of newly fledged young (Both et al. 2006; Visser et al. 2006). Thus, assuming that fruits produced are actually available to foraging birds (Hutto 1990), the fruit-limitation hypothesis makes the following predictions. First, the production of ripe fruits by plants important in the diets of migrants should be higher at breeding elevations during the breeding and postbreeding (fledging) seasons than at nonbreeding (lower) elevations. If true, then one also would predict that fruits abundant at breeding elevations should be particularly common in the diets of recently fledged birds. The fruit-limitation hypothesis could also explain why birds migrate downhill after breeding if the production of ripe fruits important in the diets of migrants is higher at nonbreeding elevations than at breeding elevations during the nonbreeding season.

An alternative to the fruit-limitation hypothesis is the "protein-limitation hypothesis". This hypothesis postulates that birds migrate uphill to exploit elevational differences in arthropod abundance. The increase in protein required by females to lay eggs and feed nestlings may result in protein being more limiting than carbohydrates during the breeding season (Carey 1996). Yet, the morphologies of highly frugivorous species are poorly adapted for the detection, capture, and digestion of arthropod prey (Levey and del Rio 2001). Therefore, frugivores may locate and time protein-intensive activities to exploit the locations and seasons of highest arthropod abundance (Levey 1988; Poulin et al. 1992). The most critical prediction of the protein-limitation hypothesis is that arthropod abundance should be higher at breeding elevations than at nonbreeding elevations during the breeding season. This prediction assumes that arthropod sampling adequately reflects the relative abundance of resources physically and nutritionally available to a foraging

bird (Wolda 1990). Additional predictions of this hypothesis are that the proportion of arthropods in adult diets should be (i) greater in females than in males and (ii) greater in females during the breeding season than in females during other seasons.

The objectives of this study were to test predictions of the fruit-limitation and protein-limitation hypotheses to determine if food abundance can explain both uphill and downhill movements of an altitudinal migrant species. To estimate relative abundance of foods with adequate precision, I focused on a single bird species and the foods it consumes (Blake et al. 1990). The intensive, year-round fieldwork required to test these food-based hypotheses limited the temporal scope of this study to one complete annual cycle. I chose the White-ruffed Manakin (*Corapipo altera* Hellmayer, 1906), a common forest understory bird that migrates between premontane and lowland forests in Central America. Temporal and spatial patterns of migration in this species are typical of other altitudinal migrant frugivores in this region (Stiles and Skutch 1989), and because the species has both migratory and nonmigratory populations, current migratory patterns can safely be assumed to reflect current selective conditions.

Materials and methods

Focal species and study sites

White-ruffed Manakins are small (10–12 g) understory frugivorous birds that inhabit wet forests of southern Central America and northern South America (Snow 2004). Populations on the Atlantic slope of Costa Rica breed between 400–900 m elevation primarily during Apr.–June, and are partially migratory (some unknown proportion of the individuals descend to lower elevation forests for the nonbreeding season; Loiselle and Blake 1991; Rosselli 1994; Boyle 2008a). Male White-ruffed Manakins display at leks that females visit where they copulate with males (Rosselli et al. 2002). Females alone build nests, incubate, and feed young (Stiles and Skutch 1989). Based on Rosselli (1994), I defined the following four "seasons" in the annual cycle of White-ruffed Manakins: (1) "breeding" when all individuals are at higher elevations (Apr.–June), (2) "postbreeding" when most individuals remain on breeding grounds and initiate moult (July–Sept.), (3) "nonbreeding" when many individual migrate downhill (Oct.–Jan.), and (4) "uphill migration" when migrants return to breeding elevations (Feb.–Mar.).

I studied White-ruffed Manakins at three old-growth forest sites in the vicinity of Braulio Carrillo National Park (BCNP) in northeastern Costa Rica. The highest elevation site (Rara Avis Reserve; 10°17′3″N, 84°02′47″W) at 750 m lies in the middle of breeding elevations for White-ruffed Manakins in this region. Forests at Rara Avis are classified as premontane pluvial (Holdridge 1967), and receive a mean (SE) annual rainfall of 8279 ± 263 mm. Two lower elevation sites below the breeding range were (1) BCNP near the "Cantarrana" refuge at 300 m (10°22′16″N, 84°02′45″W) and (2) La Selva Biological Station at 100 m (10°24′59″N, 84°01′55″W). Forests at La Selva are classified as lowland tropical wet (Holdridge 1967) and receive a mean (SE) annual rainfall of 4260 ± 100 mm). By interpolating daily

rainfall data collected during days I worked at Cantarrana, I estimated mean annual rainfall to be 6845 mm. Hereafter I refer to these sites by their elevation. Temperature is virtually aseasonal in the region, and seasonal rainfall patterns are similar along the gradient. On average, May–July and Dec. are the rainiest months at all elevations and Feb.–Apr. are the least rainy, with substantially more precipitation falling during the second half of the year than the first. The seasonality of rainfall during 2004 was similar to long-term patterns (meteorological data from Rara Avis and La Selva Biological Station).

Manakin capture and dietary data

I spent 5–7 days at each elevation during each month of 2004, visiting sites in sequence every month. I captured White-ruffed Manakins in 6–16 mist nets (12 m wide × 3 m tall, 38 mm mesh) placed in the same forest understory locations in successive months. I opened mist nets at 0600, keeping them open until noon or until rain began, checking nets every 20 min. Capture rates may not directly reflect relative abundance because of seasonal changes in activity or behaviour. However, I controlled for many potential sources of error by basing predictions on comparisons of within-season capture rates (Remsen and Good 1996). Furthermore, mist nets currently provide the most feasible means of estimating relative abundance of understory birds and yield data directly comparable with those reported in many related studies (e.g., Blake and Loiselle 1991; Rosselli 1994; Herrera 1998). I collected fecal samples by placing birds in cages for 30 min and collecting all regurgitated and fecal matter voided during this time. I banded each bird with a numbered aluminium leg band and recorded sex (based on plumage and presence of a brood patch or cloacal protuberance) and feather moult. Animals were cared for in accordance with guidelines in Olfert et al. (1993) and protocols were reviewed and approved by the Institutional Animal Care and Use Committee of the University of Arizona. I immediately released individuals captured earlier the same day, but resampled individuals captured on previous days. I used capture data to confirm the "seasons" previously defined in the annual cycle of White-ruffed Manakin breeding and migration.

I preserved fecal samples in 70% alcohol and subsequently examined contents under a 40× microscope. I matched seeds found in fecal samples to a reference collection of seeds of plants collected in the region (Boyle 2003), and used presence or absence of seed types found in samples to characterize diets of White-ruffed Manakins. I estimated the proportion of each fecal sample consisting of arthropod remains (identified to family or order when possible) relative to fruit pulp and seeds by inspecting arthropod remains in each of 12 quadrants of each fecal sample, averaging estimates from all quadrants. This method may not accurately represent the volume or mass of arthropods in diets, but it provides a quantitative index of the relative importance of arthropods and fruit in diets, and is similar to the methods

used in other studies of frugivorous birds (Herrera 1998). In addition to comparing the proportion of arthropods in samples, I also compared the proportions of samples containing zero vs. some arthropod remains.[2]

Fruit production rates

To test the prediction that production rates of fruits important in the diets of migrant species are higher during the breeding and postbreeding seasons and lower during the nonbreeding season at breeding elevations (relative to lower elevations), I monitored the phenology of 226 individual plants belonging to 35 species. I compared relative abundance of fruits between elevations using estimates of production rates rather than standing crop because differences in underlying ripe fruit production rates between regions is what potentially influences the evolution of behaviours such as migration. To quantify fruit abundance for manakins as accurately as possible, instead of sampling fleshy fruits produced by the entire community, I sampled plants in the Melastomataceae and Rubiaceae likely to be important in the diets of White-ruffed Manakins. I chose plant species based on preliminary fecal sample analyses, fruit morphology, and previously reported dietary data (Rosselli 1994). I marked plants, measured their diameter at breast height (DBH), their basal diameter, and visually estimated their height to the nearest 0.5 m to determine the minimum size at which each species typically became reproductive. After analyzing fecal samples, I chose to restrict estimates of fruit production to 18 of the 35 species whose seeds were among the 76 plant species found in fecal samples collected from White-ruffed Manakins during 2004 (173 individual plants: 73 at 750 m, 43 at 300 m, and 57 at 100 m). Calculating the absolute contribution of these species to the manakins' diet was not feasible because of differences among species in seed size; because small seeds remain in a bird's digestive tract longer (del Rio and Restrepo 1993), estimating relative consumption of fruits based on relative abundance of seeds underestimates the dietary importance of large-seeded fruits (Rosenberg and Cooper 1990). These 18 species accounted for 44.9% of the seed records in fecal samples. Of the 15 most common seed types in fecal samples, only 4 were not among the 18 plant species monitored.

I visited each marked plant at the beginning of a week's sampling period. I noted phenological stage, and counted the total number of ripe fruits and infructescences on each plant. Counting ripe fruits permitted a comparison of fruit abundance in 2004 with the results of other studies based on standing crop. I also marked and counted fruit on 1–11 infructescences for each plant bearing fruit. The number of marked infructescences varied due to infructescence accessibility, number of infructescences per plant, and number of fruits per infructescence (mean = 4.1 infructescences/plant). I marked plants with small pieces of green flagging tied below the infructescence. Flagging appeared not to deter avian foraging, as I observed birds consuming fruits from marked infructescences on several occasions. On each marked in-

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[2] Contents of all fecal samples are presented in supplementary Table S1, which is available on the journal Web site (http://cjz.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5344. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html.

fructescence, I counted all ripe, unripe, parasitized (unripe fruits attacked by pathogens or seed predators), and rotten (ripened, but attacked by pathogens) fruits, removing parasitized and rotten fruits on each visit. I recounted fruits on marked infructescences at the end of the sampling week (mean = 4.9 days between checks) and estimated the per-infructescence production of ripe fruits as (*n* unripe at 1st check) – (*n* unripe at 2nd check) – (*n* parasitized at 2nd check). I estimated daily production rates of ripe fruit for each individual during each month as (mean per-infructescence production) × (*n* infructescences bearing fruit that month) / (*n* days between checks).

To calculate monthly rates of fruit production at the species level, I estimated the density of individual plants per hectare (for each species) by surveying 10 (at 300 m and 750 m) or 15 (at 100 m) 0.01 ha belt transects (2 m × 50 m) systematically spaced ≥100 m apart surrounding the bird capture locations. I identified all plants in the Melastomataceae or Rubiaceae that were ≥1 m tall, recorded reproductive status, and measured the DBH and basal diameter. Vouchers of each plant species from each elevation are deposited at the Museo Nacional de Costa Rica, the Instituto Nacional de Biodiversidad (CR), and the Missouri Botanical Garden. Using marked individuals and those in transects, I estimated the minimum size at which each species reached reproductive maturity. I used the number of individuals in transects greater than or equal to this size to estimate the density of potential fruit-producing individuals per hectare at each elevation.

To estimate fruit production rates at each elevation, I multiplied the mean per-individual fruit production rate in a given month by the number of reproductively sized individuals per hectare for each species. Of the 18 plant species important in the diets of manakins, 4 (at 100 m) or 1 (at 300 m and at 750 m) of those species did not occur in any of the 10 (or 15) transects. I arbitrarily assigned these plant species densities of two individuals per hectare to estimate fruit production rates by elevation and month. Two individuals per hectare represents a conservative estimate of rarer species' abundances, which is >0/ha (marked individuals do occur within the study area) but <10/ha (not found in transects). Finally, I summed the monthly fruit production rates for all 18 species at an elevation to obtain overall fruit productivity estimates per month at each elevation. Because the data from Jan. were incomplete, I compared fruit abundance among elevations from Feb. to Dec.[3]

Arthropod abundance

To test the prediction that manakins migrate uphill to exploit elevational differences in arthropod abundance, I sampled the abundance of understory arthropods at up to 10 sampling points at each of the three elevations every month (monthly mean = 8.1 samples/elevation). I used sweep nets to sample foliage-dwelling arthropods between 0.2 and 2.5 m above the ground. White-ruffed Manakins typically forage by sallying from understory and midstory (≤6 m) perches to snatch prey from foliage (Stiles and Skutch 1989; W.A. Boyle, personal observation). While no perfect method of arthropod sampling currently exists, sweep sampling is a more appropriate method for sampling foliage-dwelling prey than pitfall traps or sticky traps that are biased toward terrestrial substrates and aerial taxa, respectively (Cooper and Whitmore 1990). To evaluate visual inspection of foliage (e.g., Jones et al. 2003) as an alternative to sweep sampling, I paired adjacent 5 m × 5 m plots on which to conduct both methods. Visual samples tended to contain more arthropod individuals (paired-sample *t* test, $t_{[4]} = -2.4$, $P = 0.074$). However, the increase in prey numbers was primarily attributable to ants, adult Lepidoptera, and flies. Thus I chose sweep samples because (*i*) increased arthropod abundance in visual counts consisted of taxa rarely consumed by manakins, (*ii*) the patterns of relative abundance among the five plots was identical using both methods, and (*iii*) my field crew felt that sweep sampling was less prone to variation in observer error. The last was an important consideration because 10 technicians helped collect arthropod samples during the year. All 10 sweep-net sampling points were ≥100 m apart and consisted of a 50 m radius circle within which I randomly located one 5 m × 5 m square of vegetation to sample each month. On each sampling occasion, I conducted a 4 min sweep between the hours of 1100 and 1700 and did not sample when rainfall exceeded a light drizzle.

I examined all surfaces of every piece of leaf and twig in the sweep sample to separate arthropods (visible to the naked eye, approximately ≥1 mm) from plant debris. I measured body length (mm) and identified each arthropod to order. I weighed the combined wet mass of arthropods, and preserved samples in 70% alcohol. I excluded taxa inhabiting rotting wood or soil (Isopoda, Annelida, Zoraptera, Psocoptera), as these taxa likely entered into samples when the net broke open rotting twigs. I also excluded ants and termites from analyses because, like the above taxa, they are not known from diets of White-ruffed Manakins (Rosselli 1994). Finally, I excluded arthropods >30 mm long from the analyses because I assumed that prey >30 mm were too difficult for White-ruffed Manakins to successfully capture and handle. Dietary analyses verified this assumption; the maximum dimension of arthropod pieces or fruit from which I found seeds in fecal samples never exceeded 30 mm.[4]

Analyses

I used capture data to confirm previously reported seasonal and spatial patterns of White-ruffed Manakin migration, breeding, and moult. To evaluate the fruit-limitation hypothesis, I examined the relative rates of fruit production

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[3] Detailed plant fruiting data are presented in supplementary Table S2, which is available on the journal Web site (http://cjz.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5344. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html.

[4] Contents of sweep samples summarized by elevation and month are presented in supplementary Table S3, which is available on the journal Web site (http://cjz.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5344. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html.

at each of the three elevations throughout the annual cycle of White-ruffed Manakins. I compared mean monthly (ln-transformed) fruit production rates within seasons among elevations using ANOVA models, and tested the predictions of greater relative fruit production at breeding elevations during breeding and postbreeding seasons at breeding elevations, and lower relative fruit production during the non-breeding season at breeding elevations by conducting planned linear contrasts between breeding and nonbreeding elevations. I determined whether (ln-transformed) fruit production rates differed among elevations using a two-way ANOVA (elevation and month). To compare results based on fruit production with results of previous studies, I reran these models substituting fruit production rates with (ln-transformed) standing crop. To verify that fruits of marked plant species comprised a similar proportion of the diet throughout the year, I examined whether the proportion of seed records in fecal samples corresponding to the 18 marked plant species differed among seasons using a likelihood ratio test.

To evaluate the prediction of higher arthropod abundance at breeding elevations relative to nonbreeding elevations during the breeding season, I constructed ANOVA models using both the number of arthropods in samples and the total mass of arthropods in samples as response variables. I tested for an interaction between elevation and season (uphill migration, breeding, postbreeding, and nonbreeding) using the 277 sweep samples as the units of replication. I constructed richer models including weather conditions at the time samples were collected ($n = 252$ samples for which I noted whether it was sunny, overcast, or damp or drizzling), and interactions between weather, elevation, and season. To test the predictions of increased protein consumption for (*i*) adult females relative to adult males and (*ii*) females during the breeding season relative to females during other seasons, I tested for differences in the proportion of fecal samples containing any arthropod remains using one-tailed Fisher's exact tests. Additionally, I compared the mean proportions of arthropod remains in fecal samples between sexes using a Student's *t* test.

Results

I captured 252 individual White-ruffed Manakins, and recaptured banded individuals 138 times during a total of 13 311 mist-net-hours. From these 390 captures, I collected 345 fecal samples and analyzed the contents of 257 samples (Table S1).[2] I recaptured three individuals at different elevations from their initial capture location, thereby documenting movements of marked individuals among all three of the elevations I sampled. The timing of White-ruffed Manakin migration, breeding, and moult during 2004 was consistent with patterns previously described for this species (Fig. 1A; Rosselli 1994). I did not capture any White-ruffed Manakins at 100 m between Apr. and Oct., or at 300 m between Mar. and June, suggesting that individuals rarely (if ever) remain at low elevations during the breeding season. Peak breeding occurred between Apr. and June; 100% of females captured in May had brood patches, and hatch-year birds increased from 0% to 61% of captures between May and July. Males initiated moult toward the end of the breed-

ing period (May–June), whereas most females initiated moult in July–Aug. A few individuals moved downhill beginning in the postbreeding period (July–Sept.) with migrants increasing at the two lower elevations through the nonbreeding season (Oct.–Jan.) during which period capture rates gradually declined at 750 m (Fig. 1A).

Fruit-limitation hypothesis

Elevational patterns of fruit production were consistent with the hypothesis that White-ruffed Manakins migrate uphill to exploit higher fruit production at breeding elevations relative to lower elevations (Fig. 1B). Consistent with predicted patterns, more fruit was produced at 750 m than at lower elevations later when young White-ruffed Manakins fledge and throughout the postbreeding season (July–Sept.; $F_{[2,6]} = 7.4$, $P = 0.024$; linear contrast, $F_{[1,6]} = 14.2$, $P = 0.009$). During July, fruit production rates were 81% lower (at 100 m) and 91% lower (at 300 m) than the fruit production rate at 750 m. However, elevations did not differ significantly in their fruit production rates during uphill migration (Feb.–Mar.; $F_{[2,3]} = 2.6$, $P = 0.221$) or when birds breed (Apr.–June; $F_{[2,6]} = 0.1$, $P = 0.942$), thus yielding partial support for fruit-limitation explaining the uphill portion of the migratory cycle. Overall, fruit production rates varied >100-fold between elevations and seasons. After accounting for monthly variation, mean fruit production rates differed among the three elevations (whole model, $F_{[13,20]} = 2.2$, $P = 0.057$; effect test for elevation, $F_{[2,20]} = 8.2$, $P = 0.003$); mean (SE) daily fruit production rates at 750 m (3061 ± 473 fruits/ha) nearly doubled those at 300 m (1715 ± 514 fruits/ha), and tripled those at 100 m (949 ± 514 fruits/ha).

Fruit production rates were never higher at 300 m or 100 m compared with 750 m during the postbreeding and nonbreeding seasons (Fig. 1B). Although elevations differed in fruit production rate during the nonbreeding season (Oct.–Dec.; $F_{[2,7]} = 6.2$, $P = 0.028$), patterns were opposite to those predicted if fruit limitation explains downhill movements. Lower elevations did not produce more fruit than at 750 m (linear contrast, $F_{[1,7]} = 2.3$, $P = 0.169$). Patterns of relative fruit abundance estimated from standing crop were extremely similar to the patterns estimated using fruit production rates. Standing crop did not differ among elevations during uphill migration ($F_{[2,3]} = 0.8$, $P = 0.512$) or breeding ($F_{[2,6]} = 0.1$, $P = 0.898$) seasons. Standing crop tended to be higher at 750 m relative to lower elevations during postbreeding ($F_{[2,6]} = 2.3$, $P = 0.179$; linear contrast, $F_{[1,6]} = 4.2$, $P = 0.087$) and tended to differ among elevations during the nonbreeding season ($F_{[2,7]} = 4.7$, $P = 0.051$). However, fruit was not more abundant at lower elevations than at 750 m during the nonbreeding season (linear contrast, $F_{[1,7]} = 2.5$, $P = 0.155$).

The proportion of seed records in fecal samples corresponding to marked plant species differed among seasons (likelihood ratio test, $\chi^2 = 24.8$, $P < 0.001$). More seed records in fecal samples corresponded to marked plant species during the postbreeding (62%) and nonbreeding seasons (44.5%) than during the breeding (30.7%) and uphill migration seasons (31.9%).

The spike in fruit production during the early postbreeding season at 750 m was primarily attributable to the fruiting
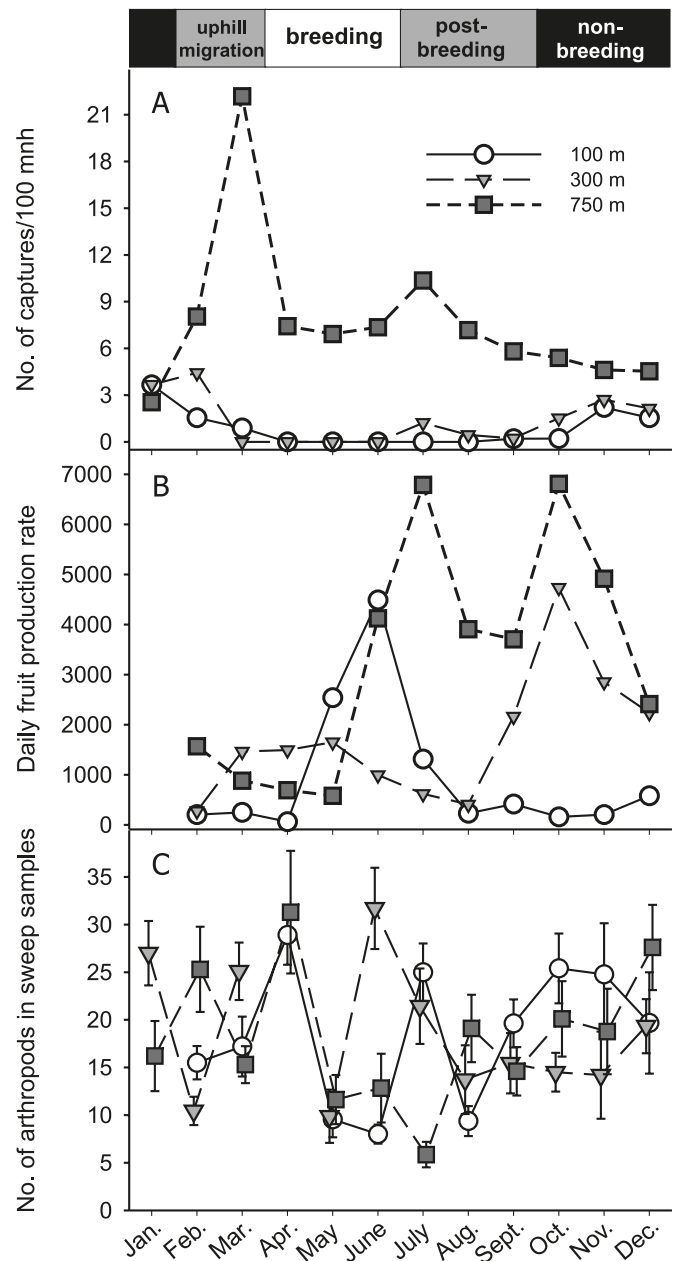
Fig. 1. (A) Monthly capture rate of White-ruffed Manakins (*Corapipo altera*) per 100 mist-net-hours (mnh), (B) the daily number of ripe fruits produced per hectare, and (C) mean (SE) number of arthropods captured in sweep samples during each of 12 months at each of three elevations in northeastern Costa Rica during 2004. The bar above A provides a reference for the four "seasons" relevant to the annual cycle of breeding, moult, and migration of White-ruffed Manakins. Downhill migration primarily occurs during the last 3 months of the year, but some individuals depart as early as July when most individuals are moulting on the breeding grounds. Capture rates are based on 6–16 mist nets open in the same locations for 5–7 days per month at each elevation. The increase in captures at 750 m during Mar. probably reflects both the arrival of birds that breed at this elevation and the passage of migrants moving through the study area to breed at higher elevations. The increase in captures at 750 m during July corresponds to fledging of hatch-year birds. No White-ruffed Manakins were captured at either of the lower two elevations between Apr. and June. Values in B represent daily fruit production rates per hectare for 18 species of plants whose fruits are common in the diet of White-ruffed Manakins. I monitored 173 marked plants, and used per-plant values combined with density estimates (number of reproductive individuals/ha) for each species to calculate the daily number of fruits produced per hectare. Values in C represent the mean (SE) number of individuals of potential prey for White-ruffed Manakins captured during sweep samples within 5 m × 5 m plots from monthly mean of 8.1 samples/elevation.

of two species in the Melastomataceae (*Conostegia micrantha* Standl., and to a lesser extent *Ossaea robusta* (Triana) Cogn.). All 15 fecal samples of hatch-year birds captured in July contained *C. micrantha*, and only 2 samples contained seeds from additional species. Both *C. micrantha* and *Ossaea* spp. were common in the diets of birds of all ages during July–Aug., and newly fledged birds tended to consume these fruits in slightly greater proportions than older birds (63% of 27 seed records vs. 54% of 41 seed records).

Protein-limitation hypothesis

Arthropod abundance was not higher at 750 m than at lower elevations during the breeding season. Despite considerable variation (Fig. 1C), the mean number of arthropods in sweep samples was not related to elevation (one-way ANOVA, $F_{[2,274]} = 0.1$, $P = 0.903$). There was also no interaction between elevation and season ($F_{[6,265]} = 0.9$, $P = 0.470$). Results were similar using mass rather than n arthropods in samples. Because most arthropod remains in fecal samples were spiders, I separately examined patterns of spider abundance. Relative spider abundance reflected the patterns of relative abundance of all arthropods; spider abundance was not higher during breeding or postbreeding seasons at 750 m relative to other seasons or elevations. Spiders were most abundant in sweep samples collected during the nonbreeding season (Oct.–Jan,). Mean spider abundance differed among seasons (two-way ANOVA, $F_{[3,241]} = 2.5$, $P = 0.061$) but not among elevations ($F_{[2,241]} = 0.9$, $P = 0.426$), and I found no evidence of an interaction between elevation and season.

Arthropod abundance was strongly related to the weather at the time of collection; samples collected on sunny days

contained more arthropods (23.3 ± 1.3) than those collected during overcast (16.0 ± 1.2) or damp (14.8 ± 1.3) days ($F_{[2,240]} = 10.6$, $P < 0.001$). This effect was greater during the breeding season than in other seasons (weather × season interaction, $F_{[6,240]} = 2.8$, $P = 0.012$). To control for the effects of weather, I tested for an interaction between elevation and season in an ANOVA model using residual variation in arthropod abundance as the response variable. Although the relationship between season and residual arthropod abundance depended upon elevation ($F_{[6,240]} = 2.2$, $P = 0.040$), arthropods were not more abundant at 750 m during the breeding season relative to the two lower elevations after controlling for weather.

On average, more fecal samples from adult females (62%) contained any arthropod remains than did those from adult males (36%; one-tailed Fisher's exact test, $P < 0.001$). The percentage of fecal matter consisting of arthropods was also

higher in samples from adult females (6.2% ± 0.7%) than adult males (2.4% ± 0.6%; one-tailed Student's t test, $t_{[189]}$ = 3.9, P <0.0001). Among females, the proportion of fecal samples containing arthropod remains was higher during the breeding season (74%) than during other seasons (46%; one-tailed Fisher's exact test, P = 0.012).

Discussion

Temporal and spatial variation in the abundance of food resources is undoubtedly a critical factor influencing the trade-offs associated with migrating. However, the seasonal patterns of bird captures, food abundance, and dietary data presented here are consistent with food limitation explaining only the uphill portion of the migratory cycle of a tropical frugivorous bird. These results extend results of comparative work (Boyle 2006; Boyle and Conway 2007) by providing direct evidence that food resource variability is associated with migratory movements from nonbreeding to breeding areas. Yet patterns of food abundance appear to be inadequate to explain the whole migratory cycle of White-ruffed Manakins. The results of this study suggest that further inquiry into the causes of bird migration (especially short-distance intratropical migrations) will benefit from empirical tests of alternative hypotheses based upon ecological processes other than food limitation. These data, in combination with results of related studies of altitudinal migrants (e.g., Boyle 2008a, 2008b) suggest that food availability likely explains the location and timing of breeding of many tropical montane birds, but alternate processes such as predators, parasites, or physiological tolerances to weather likely interact with the constraints of a frugivorous diet to influence the outcome of the decision whether or not to migrate to lower elevations following breeding.

Why do manakins migrate uphill?

The uphill migration patterns of White-ruffed Manakins and the patterns of fruit production by plants consumed by manakins are largely consistent with the fruit-limitation hypothesis. Fruit production rates peak at breeding elevations at the time when most young manakins fledge. This result is consistent with results from other tropical species that also appear to time fledging during periods of maximum food abundance (Young 1994). Although fruit production rates were not higher at breeding elevations at the time when White-ruffed Manakins leave lowland forest to migrate uphill, this result does not refute the fruit-limitation hypothesis; the time of maximum caloric requirements is not likely to be at the onset of breeding, but later in the nesting period and immediately postbreeding when females are feeding nestlings and young birds fledge. Dietary data are also consistent with the fruit-limitation hypothesis. The plant species producing most fruit during the postbreeding period dominated the diets of all White-ruffed Manakins sampled during this period, especially the diets of young birds. This result suggests that the distribution and phenology of relatively few plant species may have a disproportionate influence on the migrations of frugivorous birds, which is an important finding from an applied standpoint.

Although the nutritional demands of breeding do apparently influence protein intake by White-ruffed Manakins, the patterns of arthropod abundance currently available are not consistent with the protein-limitation hypothesis. Important caveats are that sweep samples are equivalent to sampling the standing crop (not the production rates) of arthropods, arthropod prey abundance may vary significantly among years, and that no perfect method of estimating arthropod abundance for active sallying understory birds exists (Cooper and Whitmore 1990). Additionally, without more detailed taxonomic and chemical data on both prey consumed and contents of sweep samples, we cannot know the extent to which reported patterns of arthropod abundance represent prey available to manakins (Wolda 1990). Yet regardless of sampling issues, dietary data reveal that adult White-ruffed Manakins manage to fill their nutrient requirements almost exclusively with fruit (overall only 3.3% of fecal remains consisted of arthropod pieces), again suggesting that the protein-limitation hypothesis is unlikely to explain manakin behaviour. Possibly even breeding females (like other frugivores; Pryor et al. 2001; Tsahar et al. 2005; Herrera et al. 2009) have low enough protein requirements and high enough digestive efficiencies that protein needs can be met regardless of fluctuations in arthropod abundance.

Why do manakins migrate downhill?

In contrast to uphill migration, patterns of fruit production are not consistent with the hypothesis that birds migrate downhill to exploit changes in the relative abundance of fruits among elevations and seasons. A possible explanation for the failure to find reciprocal shifts in fruit abundance is that production rates of the plant species I monitored differed from the production rates of the whole community of plants that White-ruffed Manakins consume during the non-breeding season, and downhill migration functions to exploit those other fruits. However, this possibility seems unlikely because seeds matching monitored plant species were better represented in diets of White-ruffed Manakins during the second half of the year when birds migrate downhill than in the first half of the year.

The use of fruit production rates rather than standing crop cannot account for discrepancies in results between this study and a previous study in the same region. In addition to calculating production rates, my methods permitted calculation of standing crop metrics from 2004 that are directly comparable with data reported previously. Loiselle and Blake (1991) found higher standing crops at their lowest elevation site (very close to the 100 m site used in this study) during much of 1985–1986. In contrast, fruits at 100 m during 2004 were more abundant (and only slightly so) than at higher elevations in only 2 of the 12 months (May and June; Fig. 1B). The spatial and temporal patterns I found in standing crop were similar to the patterns of fruit production rates, and thus also fail to support the hypothesis that fruit abundance explains downhill migration. One possible explanation for the differences in results between these two studies lies in the plant species used to estimate fruit abundance. Loiselle and Blake (1991) counted fleshy fruits produced by the whole plant community at their sites, whereas I restricted estimates of fruit abundance to plant species known to be important foods for the focal species. An alternative method of quantifying relative fruit abundance would be to calculate per-capita fruit abundance (fruits either pro-

duced or counted divided by capture rate). However, adopting this approach would not alter the results or conclusions presented here.

Despite the conclusions of this study being based on a single year's data, 2004 appeared to be typical with respect to both the timing and magnitude of bird movements, and the temporal and spatial patterns of fruiting phenology and weather. To date, no comparable data on arthropod abundance is available with which to compare the seasonal and spatial patterns presented here. However, seasonal and spatial patterns of capture rates of White-ruffed Manakins reported from the same region in four previous years closely match the patterns of abundance reported here (Loiselle and Blake 1991; Rosselli 1994). Field notes and botanical collections from these sites in 2001 (June–July), 2002 (May–Aug.), 2003 (Jan.–Feb.), 2007 (June–July), and 2008 (Feb.–May; Oct.–Dec.) reveal that the fruiting phenology of plant species consumed by manakins are remarkably consistent among years and match the year-long data collected in 2004 (W.A. Boyle, unpublished data). Likewise, Loiselle and Blake (1990) report little annual variability in phenological patterns over 3 years in the same region. Nevertheless, replication (ideally on other altitudinal gradients) will be required to rule out a role for fruit abundance in explaining downhill migration and arthropod abundance in explaining uphill migration.

It is likely that the inferences drawn from this species-specific study are applicable to a broader range of tropical migratory species. The spatial and temporal patterns of White-ruffed Manakin migration are typical of altitudinal migrants. Furthermore, in community-level comparative studies of diet and foraging choices, White-ruffed Manakins differed from other species of nonmigratory manakins in the same way that migrants from other families differed from their resident counterparts (Boyle 2006). In general, the concordance between fruiting and uphill migration patterns and discordance between fruiting and downhill migration patterns presented here echo the results of other species-specific studies of altitudinal migrants and their food resources (Rosselli 1994; Solórzano et al. 2000; Chaves-Campos et al. 2003). Together, these studies suggest that alternative factors may interact with food limitation to explain where and why some, but not all, birds migrate. In explaining downhill migration of altitudinal migrant frugivores, the abundance of certain micronutrients in fruits may potentially be more limiting to adult frugivorous birds than the overall quantity of carbohydrates (Levey and del Rio 2001; Pryor et al. 2001). The degree to which micronutrient limitation shapes foraging decisions and influences migratory behaviour of frugivores merits further study. In addition to examining how foraging choices and fruit nutrition could influence migratory decisions, future work should examine whether factors unrelated to food, such as tolerance to adverse weather conditions, could be more important than food abundance in causing birds to leave their breeding ranges during the nonbreeding season. Indeed, individual correlates of variation in migratory behaviour in White-ruffed Manakins suggests a role for heavy rains during the postbreeding and nonbreeding season interacting with the high food intake rates frugivores require to promote downhill movements in this and other altitudinal migrant species in the region (Boyle 2008a).

This study provides one of the few empirical tests of alternative hypotheses explaining the causes of migratory behaviour at the species level. These results suggest that food limitation is an important process influencing the evolution of migratory behaviour in birds. However, these results and a growing body of related work suggest that in the case of altitudinal migration, food limitation is unlikely to be the only important process responsible for such seasonal movements. The abundance of food probably interacts with a bird's nutritional needs, physiological traits, and local climatic factors to shape the diversity of bird migration patterns.

Acknowledgements

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