

## Short-distance partial migration of Neotropical birds: a community-level test of the foraging limitation hypothesis

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Partial migration of tropical birds was long believed to be driven by variation in food abundance. Recent evidence from a partially-migratory species suggests that in contrast, limited foraging opportunities at high elevations during severe wet season storms drives the most metabolically-challenged individuals down to elevations where rainfall is lighter. Here, I test community-level predictions of this hypothesis by examining the relationship between high-elevation rainfall in the second half of the year and counts of migrant birds in lowland forest during late December each year from 1990–2009. I contrast results derived from analysis of all migrant species with both analyses of only the frugivorous migrants, and analyses of resident species. Counts of migrant species were on average positively associated with montane rainfall with differences of up to 72% in the numbers of birds counted in drier or wetter years. Frugivores and smaller birds responded more strongly to variation in rainfall compared to the broader migrant species pool. Interestingly, counts of resident species were also higher following wetter montane wet seasons. Results of analyses exploring the cause of resident responses were not consistent with climatic effects on breeding productivity or short-term weather effects on detectability. Results were, however, consistent with cryptic down-slope migration of individuals breeding at higher elevations augmenting lowland resident populations in wet years. These results suggest that changes in rainfall amount, storm intensity, and timing of severe weather events would lead to large increases in or losses of an important behaviour.

Thousands of animal species undergo annual migrations between breeding and non-breeding areas, and the majority of these are partially migratory (Berthold 2001). Facultative partial migrant species are those in which individuals make choices each year whether or not to migrate, with the outcome of those decisions changing over their lifetimes depending on exogenous (e.g. food availability, weather, density of competitors) and/or endogenous factors (e.g. reproductive value, condition, social status; Chapman et al. 2011). Facultative partial migrants are particularly amenable to testing hypotheses regarding the underlying costs and benefits of residency or migratory behaviour (Gillis et al. 2008, Ogonowski and Conway 2009, Jahn et al. 2010) as their migratory strategy appears not to be constrained genetically.

Many tropical animals migrate altitudinally (e.g. bats, Timm and LaVal 2000; insects, Haber and Stevenson 2004; birds, Johnson and Maclean 1994, Loiselle and Blake 1991, Ornelas and Arizmendi 1995), and probably most of these taxa are partial migrants. Among tropical altitudinal migrants, birds have received considerably more research attention than other taxa. For decades, annual bird movements up and down mountain slopes were thought to reflect spatial and temporal variation in food resources (Stiles 1988). This hypothesis was widely accepted, partly because most altitudinal migrant taxa are primarily frugivorous or nectarivorous. Additionally, both broad scale phylogenetic comparative analyses and

community-level comparative field studies have revealed associations between migratory tendency and the degree of frugivory in Neotropical birds (Levey and Stiles 1992, Boyle and Conway 2007, Boyle et al. 2011a). However, several species-specific studies of food resources have failed to reveal the temporal patterns of fruit abundance that would be expected if food abundance alone explains altitudinal migration patterns (Rosselli 1994, Solórzano et al. 2000, Chaves-Campos et al. 2003, Boyle 2010). Furthermore, hypotheses relying on simple variation in food abundance cannot explain why some individuals choose to remain resident each year while conspecifics migrate to lower elevations after breeding.

A series of studies of the partial altitudinal migrant, the white-ruffed manakin *Corapipo altera*, proposed and tested an alternative hypothesis to explain tropical altitudinal migration. The limited foraging opportunities (LFO) hypothesis postulates that not food abundance per se, but weather-related reductions in foraging opportunities results in taxa with the highest foraging needs migrating down-slope to avoid starvation during heavy wet-season storms. Small birds with high metabolic rates, those that depend on foods with low nutritional concentrations (e.g. frugivores and nectarivores), and individuals whose condition is compromised due to pathogens, moult, or reproductive stressors are predicted to be those most likely to abandon breeding areas for lower elevations where weather conditions are more

benign. All evidence from white-ruffed manakins is thus far consistent with the LFO hypothesis. Central American Caribbean slope populations of white-ruffed manakins breed in areas receiving over double the annual rainfall of adjacent lowland forests. Much of that rain falls during multi-day storms in the latter half of the year following the breeding season (Gómez and Herrera 1986, Walsh 1996). Migratory tendency is biased toward the smaller sex (males), adult-biased among males, and related to body condition (Boyle 2008). Arrival timing in the lowlands varies annually, and is synchronous with deterioration of weather conditions (Boyle et al. 2010). Isotopic evidence from two years varying in wet-season severity indicate that a greater proportion of individuals migrated (and/or remained in lowland areas for longer) during the wetter year (Boyle et al. 2011b). Individuals respond to storms on physiological levels by elevating hormones associated with stress (i.e. corticosterone), increasing fat stores (consistent with preparation for foraging uncertainty), and burning fat as fuel with these effects greater in residents than migrants (Boyle et al. 2010). Thus, the ultimate cost of residency is likely a reduction in non-breeding survival, which is countered in males by increases in social rank and attractiveness to females for mating when they remain resident (Boyle et al. 2011b).

The consistency of multiple lines of evidence strongly suggests that climatic variables and their interaction with diet and size shape migratory tendencies in white-ruffed manakins. However, many species of diverse body sizes and diets migrate altitudinally. Can the LFO hypothesis explain community-wide movement patterns? The objective of this study was to test community-level predictions of the LFO hypothesis in the Costa Rican Caribbean slope avifauna. If storms drive birds downhill due to limited foraging opportunities, then in years with more severe storms and wetter wet-seasons, a greater number of individuals should migrate, arriving in lowland forest toward the end of the wet season. The LFO also predicts that variation in species-level responses should be related to both diet and body size. Using Christmas Bird Count data from lowland forest, I examined relationships between montane rainfall and abundance of altitudinal migrants over a twenty year period, contrasting these relationships with similar analyses conducted using lowland resident species. Additionally, using rainfall data from the lowlands, I evaluated hypotheses based on detectability, productivity, and cryptic migration for relationships between climatic factors and counts of resident species.

## Methods

### Study area and datasets

Braulio Carrillo National Park and surrounding reserves in NE Costa Rica are comprised of nearly 50 000 ha of protected wet forest extending from the lowlands at La Selva Biological station up to ~3000 m at the top of Barva Volcano. The avifauna in the region has been the subject of many ecological studies dating back 50 years (Slud 1960), and a few studies dating from the 1980s documented and explored the causes of altitudinal bird movements (Stiles 1980, Levey 1988, Loiselle and

Blake 1991). Consequently, the movements of birds along this gradient are better understood than in most other regions in the Neotropics. Most altitudinal migrants breed in montane forests (roughly 400–2500 m) in March–June, and migrate downhill after breeding. Many of the altitudinal migrants in the region are partial migrants, with a portion of the population remaining on their breeding grounds year-round. Some migrants do not migrate all the way to lowland forest each year, so the data analysed here represents a subset of the whole altitudinal migrant community.

Annual Christmas Bird Counts began in N. America in 1900 (Butcher 1990) and in recent decades have become popular in other regions of the Americas. Biologists, naturalists and bird watchers started the La Selva Christmas Bird Count in 1985. In the early years, observer effort and geographic coverage was variable, but in the past 20 years this world-renown biological station has consistently attracted a skilled group of ~30–60 observers to participate in the annual day-long count. Because the 24.13 km diameter count circle includes areas of montane forest, large rivers and towns, I restricted my analyses to the terrestrial routes within the boundaries of the La Selva property that were surveyed in most of the past 20 years.

I eliminated species from the analyses that were 1) primarily aerial, not relying on the old-growth forest, secondary forest, or recovering pastureland of La Selva, 2) nocturnal and thus inconsistently observed, 3) aquatic as these species may respond quite differently to rainfall and flooding than terrestrial species, 4) species seen in fewer than three years, as these are likely not regularly-occurring in the region (perhaps best considered vagrants rather than part of the community), and 5) long-distance migrants. I categorized species as altitudinal migrants if Stiles and Skutch (1989) or Loiselle and Blake (1991) noted any kind of seasonal movement of individuals to lower elevations. This is likely a conservative estimate of the species that engage in altitudinal migrations as the movement patterns of many tropical species is poorly known. An independent assistant assigned birds to broad dietary groupings (i.e. frugivore, nectarivore, omnivore, carnivore, insectivore) based on the primary types of prey mentioned in Stiles and Skutch (1989). I grouped granivores and species such as parrots, doves and guans that primarily consume fruit, but digest the seeds in addition to pulp (resulting in a higher-protein and -fat diet) with the omnivores. I used body mass data from Stiles and Skutch (1989) taking the mean of male and female masses in dimorphic species and used ln-transformed values in all analyses.

The number of birds counted in any such survey depends upon the number of observers and the amount of time spent searching (Link and Sauer 1999). However, the relationship between observer effort and number of birds counted is curvilinear, with the relationship between effort and number of birds detected eventually reaching an asymptote. For this reason, including raw numbers of observers, observer-hours or party-hours as a covariate is not appropriate. Thus, I adjusted effort in each year by dividing the number of party-hours in that year by the mean effort in all years, raising that value to the power of  $-1.5$ , subtracting from 1, and then dividing by  $-1.5$  following methods recommended in (Link and Sauer 1999, Link et al. 2006). I used this measure of observer effort as a covariate in all analyses.

The number of birds counted also depends upon how suitable the weather conditions are for foraging, and how weather affects the observers' ability to detect birds. Heavy rain reduces both foraging activity and reduces the audibility and visibility of birds to observers; in preliminary analyses count day rainfall was very strongly related to the number of birds counted. Therefore, I included the amount of rain falling at La Selva on the day of the count as an additional covariate.

Rainfall in the region is high throughout the year, but on average, the months of Feb–Apr (and to a lesser extent, Sep–Oct) are drier than at other times of the year. Total annual rainfall varies with elevation; forests between ~700–1000 mm receive twice the rainfall of lowland forests (8000 mm vs 4000 mm) and are likely the wettest regions of the whole gradient (weather data from Rara Avis and La Selva biological stations and the Instituto Costarricense de Electricidad). Much of the rain (including major wet-season storms) originates from southwestern trade winds off the Caribbean ocean that drop moisture as air rises over the mountainous spine of Central America (Holdridge 1967). Thus, seasonal patterns of rainfall are relatively uniform along the gradient. The montane rainfall data used in this paper come from the private Rara Avis reserve, adjacent to Braulio Carrillo National Park. Daily rainfall totals have been collected in the Rara Avis clearing at 720 m since June of 1990. Table 1 presents summaries of each year's count data and observer effort for the routes included in these analyses as well as the rainfall data included in statistical models.

### Analyses: migrant species coefficients

I used a multi-tiered approach to analysing the relationship between high-elevation rainfall during the post-breeding season (Jul–Dec) and counts of migrant birds in lowland forest. First, I ran a series of general linear models (using a Poisson distribution and a log link function) with counts of each altitudinal migrant species being the response variable. I included observer effort and centred year (year  $y$  – mean year; to account for long-term population trends), and count-day rain as covariates, with each one of the following main rainfall variables as predictor variables in sequence; 1) total rainfall at Rara Avis between Jul–Dec of the count year, 2) Rara Avis rainfall between Oct–Dec, 3) Rara Avis rainfall in Dec only, or 4) the proportion of days of severe rainfall (> 50 mm) at Rara Avis between Jul–Dec (arcsine square-root transformed). I then used the partial regression coefficients for these rainfall responses to determine if community level variation in the abundances of altitudinal migrants was related to rainfall, and which of the four rainfall variables was most strongly associated with variation in the abundances of migrant species. This analytical approach avoids the risk that high counts of a few species could skew results because the response variable is one step removed from raw count data, instead representing the direction and strength of the relationships between abundance and rainfall. I used one-tailed  $t$ -tests to compare the means of these rainfall coefficients against a null expectation of no difference or a negative relationship between bird counts and high elevation rain. The LFO hypothesis also predicts that the smaller-bodied species and the frugivores and nectarivores would respond most strongly to variation in rainfall. I evaluated that prediction by assessing the relationship between the nature and

magnitude of the rainfall response in migrant species models with species-level attributes of diet and body mass.

### Analyses: pooled migrants

I evaluated the impact of the aggregate number of individuals on the lowland avifauna by pooling counts of all altitudinal migrant individuals (species combined) and analysing their relationship with high-elevation rainfall variables, again including centred year, adjusted effort, and count-day rainfall as covariates. Analysing the data in this way obscures the variation among species, and unlike the previous approach, significant relationships could be driven by strong associations between rainfall and the abundance of one or a few species. However, these analyses are provided to complement the results based on individual species model coefficients as they permit a more intuitive evaluation of the aggregate effect of migrants on the lowland bird community.

### Analyses: resident species coefficients

I constructed species-level models similar to those used in analyses of migrants but using instead the counts of lowland resident species as the response variables, expecting little or no relationship with montane rainfall variables. Because results of these models indicated that counts of resident species were also positively associated with montane rainfall, I tested three alternative hypotheses to explain this pattern. The first possibility is that during wetter wet seasons with greater reductions in foraging time, birds may be less predator-averse and therefore more detectable during the times when they are able to forage. This hypothesis would predict that resident counts should be even more strongly positively associated with increases in lowland rainfall in the weeks and days prior to the count than they were in the months prior to the count. Second, wetter wet seasons may occur in years that are wetter overall, and wetter breeding seasons could result in more successful breeding and a population-level response among residents. If so, the amount of rain falling in the lowlands during the previous Mar–Jun (when many species breed; Loiselle and Blake 1991) should be correlated with Jul–Dec montane rainfall, and counts of lowland species should be positively related to breeding season rainfall amounts. A third hypothesis is that counts of lowland residents are augmented by migrant conspecifics breeding at higher elevations, but that these migrations have gone unnoticed due to the year-round presence of residents. If this were the case, then the other predictions of the LFO should apply to 'resident' species; counts of frugivores and smaller birds should increase the most when montane rainfall is high. Additionally, species whose elevational range extends higher into montane areas should be the species most likely to make these cryptic migrations.

## Results

### Migrant species coefficients

Table 2 lists the 31 migrant species included in analyses, their diet classification, body mass, model coefficients for

Table 1. Summary of the La Selva Christmas Bird Count data and rainfall data for all years included in this study. Numbers of individual birds, species and effort (party hours) are calculated based on only the terrestrial routes within the La Selva boundaries. Montane rainfall values are calculated based on daily rainfall values (mm) from Rara Avis reserve, and lowland rainfall values (mm) come from daily rainfall values at La Selva Biological Station.

Year	Count date	Party hours	n res individuals	n res species	n mig individuals	n mig species	Montane rainfall					Lowland rainfall				
							Jul-Dec	Oct-Dec	Dec	Days > 50 mm	Count day	3 d prior	Week prior	Mar-Jun	Jul-Dec	Oct-Dec
1990	31 Dec	35.5	1364	139	118	13	4232	2868	1459	30	0	0	4.2	1494		
1991	31 Dec	97.8	1845	154	180	19	4897	2224	531	27	0.6	58.9	81.3	992		
1992	31 Dec	34.5	908	127	80	14	4380	1981	703	29	23.5	57.3	177.2	939		
1993	31 Dec	112.8	2304	159	170	18	4039	1514	583	25	0.8	5.7	20.4	933		
1994	31 Dec	66.5	2463	152	220	19	4796	2588	996	31	0.8	2.4	5.2	866		
1995	29 Dec	98.8	3103	158	200	19	3107	1235	360	18	0	83.4	137.7	849		
1996	29 Dec	97.5	2894	159	232	24	4432	2355	872	30	0	49.5	89.1	1291		
1997	28 Dec	137.8	3511	169	333	20	5904	2691	864	45	0	0	2.5	1219		
1998	26 Dec	125.8	3048	155	366	22	4719	2580	1240	30	3.5	78.1	354.6	982		
1999	19 Dec	101.5	1794	152	148	16	4532	2538	1300	34	44.3	76.6	124.6	1260		
2000	30 Dec	123.3	2759	151	210	17	4197	2024	628	27	5.7	10.1	103.3	1101		
2001	29 Dec	122.5	2644	160	233	20	4571	2930	1035	30	0.7	41.9	70.0	1307		
2002	29 Dec	129.5	4564	162	452	22	4907	2095	498	30	10.8	29.4	34.2	1790		
2003	28 Dec	128.3	3098	162	268	24	4870	2820	1201	32	0	72.9	118.1	1369		
2004	26 Dec	147.5	3380	166	355	20	4780	2538	979	36	1.2	4.5	124.6	2119		
2005	30 Dec	117.3	2552	145	240	19	3702	2187	650	21	4.4	45.2	55.0	799		
2006	30 Dec	128.0	3908	156	362	18	3630	1644	592	15	0.4	47.5	58.5	1502		
2007	15 Dec	132.5	3960	156	197	14	4458	2462	914	27	0	20.0	189.0	886		
2008	20 Dec	144.0	3147	157	326	20	3593	2070	724	17	2.8	45.4	112.0	1047		
2009	19 Dec	141.5	4534	160	339	19	4161	2122	661	20	0	11.2	105.4	1235		

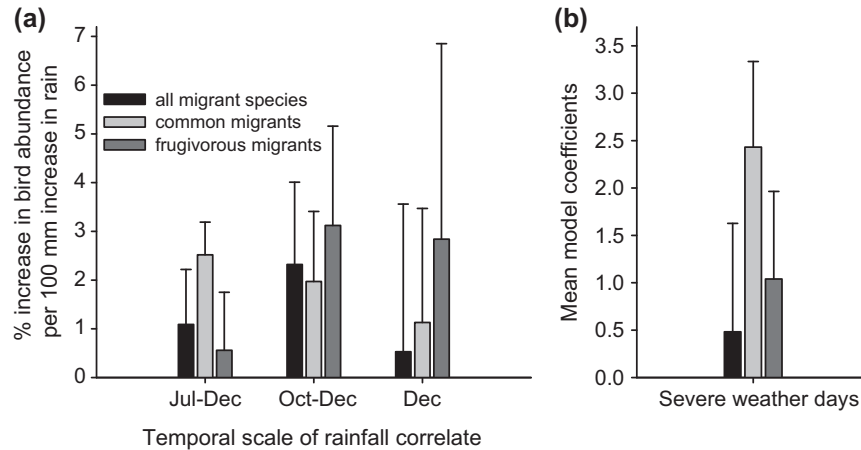


Figure 1. Variation in the nature of the relationship between counts of all migrant species (black bars), the migrant species counted in at least half the years of this study (pale grey bars), and the frugivorous migrant species (dark grey bars) relative to the amount of rain falling in montane forest during the months prior to the Christmas Bird Count. In (a), bars represent the mean effect size of the species-level rain relationships expressed as % increase in birds counted per 100 m increase in rain (after accounting for population trend, observer effort, and count day rain). Bars in (b) represent mean model coefficients for the (arcsine square-root transformed) proportion of days during Jul–Dec during which > 50 mm rain fell at the montane site. Error bars represent one SEM.

the four rainfall variables, and summaries of their frequency and abundance in counts over the twenty year period. Among all migrant species, the mean coefficients for each of the four montane rainfall variables was positive (Fig. 1). On average, increases of 100 mm of montane rainfall were associated with a 1.1% (Jul–Dec rain), 2.3% (Oct–Dec), or 0.5% (Dec) increase in the number of birds counted. These coefficients provide a very conservative estimate of the effect of rainfall as several species were counted in only a few years or in low numbers each year. Accordingly, these means did not differ statistically from zero. However, analyses of the 19 more commonly-detected species (counted in at least half of the years of this study) revealed that the mean response was indeed dependent on the amount of montane rainfall, and the consistency of the response depended upon when the rain fell. Counts of these more commonly-detected species were positively associated with the amount of rain falling at higher elevations over the Jul–Dec period ( $t = 3.8$ ,  $p = 0.001$ ) and the number of days during which rainfall exceeded 50 mm ( $t = 2.7$ ,  $p = 0.008$ ) with similar trends in associations with rainfall during Oct–Dec ( $t = 1.4$ ,  $p = 0.092$ ). The amount of rain falling only during Dec at high elevations was not associated with increases in counts of these species ( $t = 0.5$ ,  $p = 0.297$ ). Increases of 100 mm rain during Jul–Dec and Oct–Dec were associated with mean increases of 2.5% and 2.0% ( $\pm 0.7\%$  and  $1.4\%$  SEM) respectively more individuals of the 19 common migrant species being counted in the lowlands (Fig. 1a). Given that total montane rainfall during Jul–Dec between 1990 and 2009 ranged from 3107 mm to 5904 mm (Table 1), these effect sizes translate to a 72.5% and a 33.4% difference (for Jul–Dec and Oct–Dec respectively) in counts of common migrant species between the driest and wettest years of this study.

Among altitudinal migrant species, three of the four (all except Jul–Dec rain) mean rainfall coefficients for species in primarily frugivorous lineages were more strongly positive than means for the entire assemblage of migrant species.

For instance, Oct–Dec rainfall responses for frugivores were 35% higher than those of all migrant species (3.1% increase per 100 mm vs 2.3%; Fig. 1a) and coefficients for the proportion of severe rain days Jul–Dec were nearly three times higher for frugivores than for other species (Fig. 1b). However, diet and body size appeared to be interrelated in their effect on species' responses to variation in montane rainfall. In univariate models, neither dietary group nor body mass explained a significant portion of the variation in model coefficients for any of the four rainfall variables. Yet in models including both variables, both diet and body mass were related to rainfall coefficients (e.g. proportion severe weather days Jul–Dec; full model  $F_{4,26} = 4.5$ ,  $p = 0.007$ ; body mass effect test,  $F_{1,26} = 8.2$ ,  $p = 0.008$ ; diet effect test  $F_{1,26} = 5.3$ ,  $p = 0.005$ ). Body size effects were all consistent in that counts of smaller birds were more positively related to increases in rainfall than were counts of larger birds. Furthermore, in some models, diet and body mass interacted in their effect on species responses to variation in rainfall. In models comparing frugivore and nectarivore Jul–Dec rainfall coefficients compared to coefficients of all other dietary groups, the slope of the relationship between body mass and rainfall coefficients was nearly flat in frugivores and nectarivores, and strongly negative in other dietary groups (full model  $F_{3,27} = 3.6$ ,  $p = 0.026$ ; body mass  $\times$  diet effect test,  $F_{1,27} = 6.4$ ,  $p = 0.018$ ; Fig. 2).

Individual species did vary in their associations with rainfall (Table 2). For instance, counts of olive-striped flycatcher, pale-vented thrush and thick-billed seed-finch were significantly positively associated with all four rainfall variables analysed in these models, while counts of green hermit and chestnut-headed oropendola were significantly negatively associated with all four variables. The coefficients for amount of rain falling during Jul–Dec were the most consistently associated with migrant species count data; in 22 species these coefficients were positive (eight of them significantly so) compared to negative coefficients in nine species (three significant).

Table 2. All species counted in three or more Christmas Bird Counts in forested areas of La Selva Biological Station for which seasonal altitudinal movements are mentioned in Stiles and Skutch (1989) or Loisele and Blake (1991). Species are listed in taxonomic order following American Ornithologists' Union (1998) and Chesser et al. (2010). Body masses and broad dietary groups are based upon information in Stiles and Skutch (1989). Dietary groups are based upon the primary foods consumed, and classifications were corroborated for many species based on fecal sample data (Boyle et al. 2011). Diet classes are as follows; carn = carnivore, omn = omnivore including species that eat fruit but digest the seeds as well as fruit pulp, nect = nectarivore, frug = frugivore, insect = insectivore. Model coefficient data show the nature and strength of the relationship between counts of bird numbers and four montane rainfall variables in statistical models that account for variation in observer effort, count-day weather, and population trends (Methods). Italicized values indicate statistically significant models, and an asterisk indicates statistically significant partial effect tests for the rainfall variable (at  $p < 0.05$ ). Count summaries provide information on the number of years each species was counted, the total number of individuals counted summed over all 20 counts, the mean number of individuals counted per year, and the max and min numbers of individuals counted in different years.

Common name	Scientific name	Body mass (g)	Diet	Severe days	Model rainfall coefficients					Count summaries			
					Jul-Dec	Oct-Dec	Dec	n years	Total	Mean	Max	Min	
Barred hawk	<i>Leucopternis princeps</i>	1000	carn	-13.2017	-0.0944	-0.1234	-0.1806	4	5	0.2	2	0	
Great green macaw	<i>Ara ambiguus</i>	1300	omn	0.7989	0.0034	-0.0030	0.0648*	12	259	12.3	94	0	
Brown-hooded parrot	<i>Pyrrhula haematotis</i>	165	omn	1.8862*	0.0267*	0.0128	0.0009	20	1056	50.3	99	18	
Green hermit	<i>Phaethornis guy</i>	6	nect	-18.7032*	-0.1597*	-0.1794*	-0.3585*	5	9	0.4	5	0	
White-necked jacobin	<i>Florisuga mellivora</i>	7	nect	5.3533	0.0240	0.0199	-0.0004	13	43	2.1	6	0	
Violet-crowned woodnymph	<i>Thalurania colombica</i>	4.5	nect	2.6442	0.0446*	0.0131	-0.0238	20	188	9.0	20	2	
Lattice-tailed trogon	<i>Trogon clathratus</i>	130	frug	-0.5569	0.01749	-0.0393	-0.1409*	14	40	1.9	7	0	
Collared trogon	<i>Trogon collaris</i>	70	omn	10.0526	0.0988	0.1622	0.2096	3	7	0.3	3	0	
Pied puffbird	<i>Notharctus tectus</i>	27	insect	1.6468	0.0444	0.0580	0.0932	10	23	1.1	5	0	
Yellow-eared toucanet	<i>Selenidera spectabilis</i>	220	frug	-6.4223	-0.0769*	-0.0075	0.0664	6	19	0.9	6	0	
Plain antvireo	<i>Dysithamnus mentalis</i>	14.5	insect	-4.1498	0.0640	0.0367	-0.0629	4	7	0.3	3	0	
Olive-striped flycatcher	<i>Mionectes olivaceus</i>	14.5	frug	8.6885*	0.0305	0.1109*	0.2079*	16	62	3.0	17	0	
Ochre-bellied flycatcher	<i>Mionectes oleagineus</i>	13	frug	0.7209	0.0097	0.0058	0.0076	20	304	14.45	27	2	
Paltry tyrannulet	<i>Zimmerius villosus</i>	8.5	frug	3.1894*	0.0471*	0.0329*	0.0272	20	369	17.6	42	6	
Royal flycatcher	<i>Onychorhynchus coronatus</i>	21	insect	-3.3530	0.0894	-0.0082	-0.1417	4	4	0.2	1	0	
Bare-necked umbrellabird	<i>Cephalopterus glabricollis</i>	385	frug	-0.6246	0.0031	-0.0214	-0.0602	20	80	3.8	9	1	
Three-wattled bellbird	<i>Procnias tricarunculatus</i>	220	frug	-3.4971	0.0582	0.0538	-0.3048	4	9	0.4	5	0	
Snowy cotinga	<i>Carpodectes nitidus</i>	105	frug	2.4478	0.0593*	0.0088	-0.0409	19	107	5.1	17	0	
White-ruffed manakin	<i>Corapipo altera</i>	12.5	frug	0.3832	0.0108	-0.0082	-0.0130	19	139	6.6	17	0	
White-crowned manakin	<i>Pipra pipra</i>	14	frug	0.6511	-0.0034	0.0892	0.0152	8	11	0.5	3	0	
Red-capped manakin	<i>Pipra mentalis</i>	16	frug	1.0394	0.0252*	-0.0051	-0.0500*	20	436	20.8	47	3	
Black-faced solitaire	<i>Myadestes melanops</i>	33	frug	8.0630	0.0274	0.2259	0.5024*	4	6	0.3	3	0	
Pale-vented thrush	<i>Turdus obsoletus</i>	80	frug	5.2323*	0.0467*	0.1116*	0.1925*	19	469	22.3	92	0	
White-throated thrush	<i>Turdus assimilis</i>	72	frug	4.2623	0.0173	0.2289*	0.2463	5	9	0.5	3	0	
Bay-headed tanager	<i>Tangara gyrola</i>	23	frug	3.0610	-0.0071	0.0028	0.0377	10	45	2.1	13	0	
Emerald tanager	<i>Tangara florida</i>	19	frug	1.4017	-0.1387	-0.1024	-0.0207	4	9	0.4	4	0	
Silver-throated tanager	<i>Tangara icterocephala</i>	21	frug	-1.5258	-0.0132	-0.0119	0.0388	19	288	13.7	39	0	
Scarlet-thighed dacnis	<i>Dacnis venusta</i>	16	frug	0.4269	0.0152	-0.0525*	-0.1337*	19	248	11.8	36	0	
Thick-billed seed-finch	<i>Oryzoborus funereus</i>	13.5	omn	14.5085*	0.1068*	0.1962*	0.1615*	10	43	2.1	13	0	
Black-thighed grosbeak	<i>Phœnicurus tibialis</i>	70	frug	-6.3244	-0.0233	-0.0389	-0.0452	7	15	0.7	4	0	
Chestnut-headed oropendola	<i>Psarocolius wagleri</i>	225	omn	-2.2818*	-0.0156*	-0.0573*	-0.1308*	19	824	39.2	151	0	

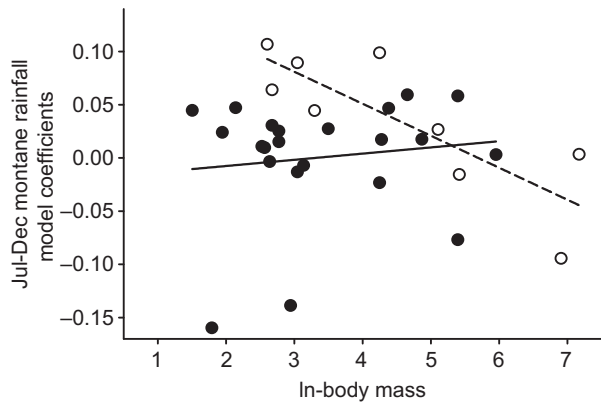


Figure 2. Visualization of the relationship between body mass (ln-transformed) and diet in the nature of the response to variation in Jul–Dec montane rainfall. Frugivorous and nectarivorous species (filled circles, solid line) are contrasted with species primarily relying on other types of food (open circles, dashed line). Y-axis values represent the rainfall coefficient in models accounting for population trend, variation in observer effort, and count day rain.

### Pooled counts of migrants

In analyses of the summed counts of all altitudinal migrant birds (accounting for long-term trends, observer effort, and count day rain), total rainfall during the six months prior to the count was the rainfall variable most strongly associated with the number of individuals counted in lowland forest (whole model likelihood ratio  $\chi^2 = 440.7$ ,  $p < 0.0001$ ; rainfall partial effect test  $\chi^2 = 54.825$ ,  $p < 0.0001$ ). Increases of 100 mm rain during this period were associated with increases of on average 1.8% ( $\pm 0.2\%$ ) in the number of all altitudinal migrants counted (Fig. 3) and 2.1% ( $\pm 0.3\%$ ) of frugivores counted. These effect sizes equate to differences of 50.3% and 60.0% respectively over the observed range of rainfall during the twenty year period.

### Resident species coefficients

Table 3 lists the 170 lowland resident species included these analyses, their diet classification, body mass, upper elevational range, model coefficients for two montane and three lowland rainfall variables, and summaries of their frequency and abundance in counts. In models relating counts of lowland resident species to montane rainfall during both Jul–Dec and Oct–Dec, the means of rainfall coefficients among species were greater than zero. Increases of 100 mm rain during Oct–Dec were associated with an increase of 1.0% ( $\pm 0.3\%$ ;  $t = 3.4$ ,  $p < 0.001$ ) and during Jul–Dec, an increase of 2.0% ( $\pm 0.2\%$ ;  $t = 8.3$ ,  $p < 0.0001$ ) in counts of resident species. Given the observed range of rainfall values over the period of the study, these effect sizes are equivalent to 57.1% and 19.2% differences in counts of residents between the driest and wettest years respectively. Species whose counts were most consistently positively and strongly associated with increases montane rainfall included brown-capped tyrannulet, grayish saltator, barred antshrike, lesser greenlet, bay wren, golden-hooded tanager and five species of flycatcher.

Mean Jul–Dec rainfall coefficients among resident species was similar to that of the migrant species and the resident

Oct–Dec rainfall response averaged roughly half of the comparable value among migrants, but was still significantly positive, contrary to expectation. These result indicate that one of at least three possible rainfall-related factors influences the number of resident birds counted in lowland forest: 1) rainy wet seasons may influence the detectability of birds by increasing their foraging activity or making them less predator-averse, 2) rainier wet seasons may be correlated with rainier dry seasons and increased productivity of breeding birds, and 3) populations of lowland species whose breeding ranges include higher elevation forests are being augmented by cryptic migration of higher-elevation breeding individuals.

To test the first of these alternatives, I analyzed the relationship between resident species counts and the amount of rain falling immediately prior to the count. If weather-related differences in detectability accounts for apparent increases in the number of birds in wet years, then high rain falling in the week prior to the count should most strongly affect those responses. Counts of resident species were, however, negatively associated with the amount of rain falling locally immediately prior to the count, with increases of 100 mm rain during the three days and week prior associated with decreases of 33.1% and 8.7% in counts of birds, respectively.

To test the second alternative, I analyzed resident species counts in relation to breeding season rainfall at La Selva (Mar–Jun), predicting both a positive association between these variables, and a positive association between local breeding season rainfall and montane wet-season rainfall. Increases of 100 mm rain falling in the lowlands during Mar–Jun were associated with an average of 1.7% ( $\pm 0.4$  SEM) more birds of resident species being counted late Dec. However, breeding productivity cannot explain the relationship between montane rainfall and lowland resident species counts; breeding season lowland rainfall was not related to either montane rainfall in Jul–Dec or Oct–Dec (Jul–Dec,  $R^2 = 8.5$ ,  $p = 0.211$ ; Oct–Dec,  $R^2 = 7.9$ ,  $p = 0.229$ ).

To test the third alternative that lowland populations of residents are being augmented during the wet season by higher-elevation-breeding individuals moving down hill, I examined the relationships between counts and diet, body mass and elevational range. Body mass was consistently related to

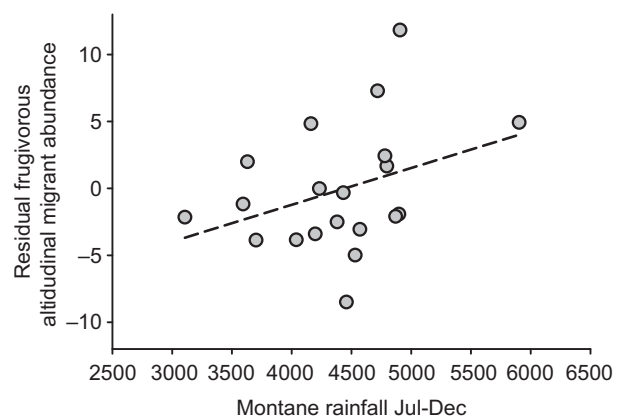


Figure 3. Residual abundance (controlling for population trend, observer effort, and count day rain) of pooled altitudinal migrant species counted in lowland forest in relation to rainfall in montane forests during the six months prior to the count. Each point represents one of 20 years count and rainfall data (1990–2009).

Table 3. All resident species counted in three or more Christmas Bird Counts in forested areas of La Selva Biological Station. Species are listed in taxonomic order following American Ornithologists' Union (1998) and Chesser et al. (2010). Body masses, broad dietary groups and highest elevation that each species is commonly found on the Caribbean slope are based upon information in Stiles and Skutch (1989). Dietary groups are based upon the primary foods consumed. Diet classes are as follows: carn = carnivore, omn = omnivore including species that eat fruit but digest the seeds as well as fruit pulp, nect = nectarivore, frug = frugivore, insect = insectivore. Model coefficient data show the nature and strength of the relationship between counts of bird numbers and a series of rainfall variables in statistical models that account for variation in observer effort and population trends (Methods): montane rainfall during Jul-Dec and Oct-Dec, lowland rainfall the week prior and three days prior to the count day, and lowland rainfall during the preceding Mar-Jun. Coefficients for rainfall variables for Jul-Dec, Oct-Dec and Mar-Jun are expressed in terms of change in bird abundance per 100 mm rain. Models of the Jul-Dec and Oct-Dec rainfall effects include the additional covariate of count day rain at La Selva Biological Station. Italicized values indicate statistically significant models, and an asterix indicates statistically a significant partial effect tests for the rainfall variable (at  $p < 0.05$ ). Count summaries provide information on the number of years each species was counted, the total number of individuals counted summed over all 20 counts, the mean number of individuals counted per year, and the max and min numbers of individuals counted in different years.

Common name	Scientific name	Diet	Body mass (g)	Upper elev	Model rainfall coefficients										Count summaries				
					Montane					Lowland					n yr	Sum	Mean	Max	Min
					Jul-Dec	Oct-Dec	Week prior	3 d prior	Mar-Jun	Jul-Dec	Week prior	3 d prior	Mar-Jun						
Great tinamou	<i>Tinamus major</i>	omn	1100	1500	-0.0022	-0.0248*	-0.0018*	-0.0059*	0.0083	0.0083	0.0083	0.0083	20	755	36.0	75	7		
Little tinamou	<i>Crypturellus soui</i>	omn	250	1500	-0.0042	-0.0273	-0.0003	-0.0031	0.0153	0.0153	0.0153	0.0153	20	200	9.5	20	1		
Slaty-breasted tinamou	<i>Crypturellus boucardi</i>	omn	500	700	0.0053	-0.0037	-0.0016*	-0.0050*	0.0324	0.0324	0.0324	0.0324	20	334	15.9	30	1		
Gray-headed chachalaca	<i>Ortalis cinereiceps</i>	omn	500	1100	-0.0117	-0.0117	-0.0005	-0.0065*	0.0260	0.0260	0.0260	0.0260	16	150	7.1	24	0		
Crested guan	<i>Penelope purpurascens</i>	omn	1700	1200	0.0023	-0.0102	0.0000	-0.0004	-0.0296*	-0.0296*	-0.0296*	-0.0296*	19	449	21.4	54	0		
Great curassow	<i>Crax rubra</i>	omn	4000	1200	-0.0148	-0.0272	-0.0008	0.0043	0.0050	0.0050	0.0050	0.0050	17	84	4.0	14	0		
Black vulture	<i>Coragyps atratus</i>	carn	1800	2000	-0.0094	-0.0193*	-0.0027*	-0.0011	0.0446*	0.0446*	0.0446*	0.0446*	20	995	47.4	133	7		
Turkey vulture	<i>Cathartes aura</i>	carn	1400	2000	0.0090	0.0013	0.0012*	0.0008	0.0192*	0.0192*	0.0192*	0.0192*	20	957	45.6	89	8		
King vulture	<i>Sarcophagus papa</i>	carn	3500	1200	0.0549*	0.0286	-0.0017	-0.0142*	0.1786*	0.1786*	0.1786*	0.1786*	13	55	2.2	14	0		
Gray-headed kite	<i>Leptodon cayanensis</i>	carn	440	750	-0.0367	-0.0576	-0.0037	-0.0038	-0.0501	-0.0501	-0.0501	-0.0501	16	42	2.0	6	0		
Double-toothed kite	<i>Harpagus bidentatus</i>	carn	180	1500	0.0220	0.0581	-0.0004	-0.0013	-0.0499	-0.0499	-0.0499	-0.0499	18	44	2.1	5	0		
Semiplumbeous hawk	<i>Leucopternis semiplumbeus</i>	carn	325	800	0.0178	-0.0134	0.0015	-0.0070	-0.0342	-0.0342	-0.0342	-0.0342	20	116	5.5	18	1		
Gray hawk	<i>Buteo nitidus</i>	carn	425	500	0.0876*	0.0303	-0.0018	-0.0030	-0.0059	-0.0059	-0.0059	-0.0059	11	22	1.1	5	0		
Short-tailed hawk	<i>Buteo brachyurus</i>	carn	480	600	-0.0030	0.0053	-0.0013	-0.0065	-0.0493	-0.0493	-0.0493	-0.0493	15	18	0.9	2	0		
Slaty-backed forest-falcon	<i>Micrastur mirandollei</i>	carn	485	300	0.0148	0.0732	-0.0010	-0.0020	-0.0668	-0.0668	-0.0668	-0.0668	12	32	1.5	7	0		
Collared forest-falcon	<i>Micrastur semitorquatus</i>	carn	642.5	1500	-0.0292	-0.0519	-0.0060*	-0.0037	0.0086*	0.0086*	0.0086*	0.0086*	13	36	1.7	5	0		
Laughing falcon	<i>Herpotheres cachinnans</i>	carn	600	300	0.0070	-0.0194	-0.0019	-0.0033	0.0030	0.0030	0.0030	0.0030	19	96	4.6	10	0		
Bat falcon	<i>Falco ruficularis</i>	carn	170	1675	0.0514	0.0638	-0.0016	-0.0103	0.1955*	0.1955*	0.1955*	0.1955*	11	19	0.9	4	0		
Gray-necked wood-rail	<i>Aramides cajanea</i>	omn	460	1400	-0.0357	-0.1041*	-0.0013	0.0046	-0.0199	-0.0199	-0.0199	-0.0199	15	49	2.3	7	0		
Pale-vented pigeon	<i>Patagioenas cayennensis</i>	omn	250	600	0.0734*	0.0220	0.0025	-0.0150*	0.1161*	0.1161*	0.1161*	0.1161*	16	88	4.2	18	0		
Red-billed pigeon	<i>Patagioenas flavirostris</i>	omn	230	2100	0.0226	0.0047	0.0014	-0.0022	0.0506*	0.0506*	0.0506*	0.0506*	19	135	6.4	19	0		
Short-billed pigeon	<i>Patagioenas nigrirostris</i>	omn	150	1100	-0.0225*	-0.0686*	-0.0015*	-0.0054*	0.0092	0.0092	0.0092	0.0092	20	991	47.2	117	5		
Ruddy ground-dove	<i>Columbina talpacoti</i>	omn	48	1400	0.0320	-0.0622	-0.0005	-0.0191*	0.0037	0.0037	0.0037	0.0037	11	48	2.3	7	0		
Blue ground-dove	<i>Claravis pretiosa</i>	omn	72	1200	0.0355	0.1466*	-0.0060*	-0.0121*	0.1329*	0.1329*	0.1329*	0.1329*	12	42	2.0	14	0		
White-tipped dove	<i>Leptotila verreauxi</i>	omn	165	800	0.0207	-0.0239	-0.0018	-0.0046	-0.0156	-0.0156	-0.0156	-0.0156	11	17	0.8	4	0		
Gray-chested dove	<i>Leptotila cassinii</i>	omn	165	750	0.0060	0.0063	-0.0008	-0.0026	0.0166	0.0166	0.0166	0.0166	20	250	11.9	28	3		
Olive-backed quail-dove	<i>Geotrygon veraguensis</i>	omn	165	450	0.0026	0.0000	-0.0003	-0.0029	-0.0381	-0.0381	-0.0381	-0.0381	20	115	5.5	12	2		
Ruddy quail-dove	<i>Geotrygon montana</i>	omn	135	1200	0.0172	0.0547	-0.0055	-0.0136	0.0686	0.0686	0.0686	0.0686	13	22	1.0	3	0		
Crimson-fronted parakeet	<i>Aratinga finschi</i>	omn	150	1000	0.0002	-0.0315*	-0.0018*	-0.0087*	-0.1186*	-0.1186*	-0.1186*	-0.1186*	16	215	10.2	40	0		
Olive-throated parakeet	<i>Aratinga nana</i>	omn	85	700	0.0259*	0.0020*	0.0024*	0.0024*	-0.0019	-0.0019	-0.0019	-0.0019	20	949	45.2	94	6		
Orange-chinned parakeet	<i>Prioniturus jugularis</i>	omn	65	1000	0.0141*	0.0033	0.0001	-0.0033*	-0.0078	-0.0078	-0.0078	-0.0078	20	917	43.7	118	8		
White-crowned parrot	<i>Pionus senilis</i>	omn	220	1200	0.0140*	0.0134*	0.0014*	0.0014*	0.0009	0.0009	0.0009	0.0009	20	1206	57.4	116	26		
Red-lore parrot	<i>Amazona autumnalis</i>	omn	420	800	-0.0108	-0.0269*	-0.0011*	-0.0020	0.0048	0.0048	0.0048	0.0048	20	1211	57.7	184	15		
Mealy parrot	<i>Amazona farina</i>	omn	600	500	0.0044	-0.0409*	0.0020*	0.0030*	0.0241*	0.0241*	0.0241*	0.0241*	20	2412	114.9	337	10		



Squirrel cuckoo	<i>Playa cayana</i>	105	2450	0.0042	-0.0006	-0.0001	-0.0006	-0.0028	20	608	29.0	52	10
Groove-billed ani	<i>Crotophaga sulcirostris</i>	75	2300	-0.0366*	-0.0774*	0.0019*	0.0005	0.0039	17	161	7.7	21	0
Bronzy hermit	<i>Glaucid aeneus</i>	5.3	300	0.0419*	0.0164	-0.0048*	-0.0032	0.0751*	19	86	4.1	15	0
Band-tailed barbthroat	<i>Threnetes ruckeri</i>	5.8	600	0.0035	0.0517	-0.0074*	-0.0042	-0.0447	17	56	2.7	13	0
Long-billed hermit	<i>Phaethornis longirostris</i>	6	1000	0.0181*	-0.0122	-0.0033*	-0.0080*	0.0143	20	847	40.3	78	2
Stripe-throated hermit	<i>Phaethornis strigularis</i>	2.6	1500	-0.0033	-0.0304*	-0.0027*	-0.0049*	-0.0047	20	544	25.9	62	6
Violet-headed hummingbird	<i>Klais guimeti</i>	2.8	1000	0.0614	0.0754*	-0.0079*	-0.0092*	0.0082	15	77	3.7	17	0
Blue-chested hummingbird	<i>Amazilia amabilis</i>	4.2	300	0.1059*	0.0395	-0.0058*	-0.0209*	0.0340	14	49	2.3	12	0
Rufous-tailed hummingbird	<i>Amazilia tzacatl</i>	5.2	1850	-0.0004	-0.0289*	-0.0011	-0.0023	0.0067	20	495	23.6	47	8
Brnze-tailed plumeleteer	<i>Chalchicomula urochrysa</i>	7	700	0.0002	0.0280	-0.0012	-0.0046	0.0041	19	131	6.2	15	0
Purple-crowned fairy	<i>Heliophryx barroti</i>	5.6	1300	-0.0304	-0.0126	-0.0004	-0.0049	0.0524	18	78	3.7	11	0
Slaty-tailed trogon	<i>Trogon massaena</i>	145	1200	0.0039	-0.0213*	-0.0023*	-0.0031	0.0107	20	526	25.1	45	5
Violaceous trogon	<i>Trogon violaceus</i>	56	830	0.0049	0.0164	0.0004	0.0010	0.0362	20	243	11.6	23	3
Black-throated trogon	<i>Trogon rufus</i>	57	1000	0.0007	-0.0231*	-0.0033*	-0.0004	0.0085	20	576	27.4	69	5
Rufous motmot	<i>Baryphthengus martii</i>	195	900	0.0209*	0.0061	-0.0051*	-0.0057*	0.0577*	20	371	17.7	48	3
Broad-billed motmot	<i>Electron platyrhynchum</i>	60	1000	0.0184*	0.0030	-0.0012*	-0.0026	0.0001	20	646	30.8	54	7
White-necked puffbird	<i>Notharchus hyperythynchus</i>	105	600	0.0149	0.0004	-0.0041	0.0000	-0.0224	16	65	3.1	13	0
White-whiskered puffbird	<i>Malacoptila panamensis</i>	42	900	-0.0333	-0.0267	0.0053*	0.0096	-0.0578	14	38	1.8	7	0
White-fronted nunbird	<i>Monasa morphoeus</i>	105	700	-0.0368*	-0.0994*	-0.0051*	-0.0099*	-0.0594	13	117	5.6	22	0
Rufous-tailed jacamar	<i>Galbula ruficauda</i>	27	750	0.0307*	0.0217	-0.0003	-0.0019	-0.0105	20	156	7.4	23	1
Collared aracari	<i>Pteroglossus torquatus</i>	230	1200	-0.0136*	-0.0184*	-0.0012	-0.0031	0.0070	20	1202	57.2	119	26
Keel-billed toucan	<i>Ramphastos sulfuratus</i>	500	1200	0.0106*	-0.0226*	-0.0005	-0.0028*	-0.0058	20	1124	53.5	136	15
Chestnut-mandibled toucan	<i>Ramphastos swainsonii</i>	665	1200	0.0128*	-0.0099	-0.0012*	-0.0053*	0.0067	20	1414	67.3	148	17
Black-cheeked woodpecker	<i>Melanerpes pucherani</i>	63	700	0.0128	-0.0053	0.0006	-0.0022	0.0104	20	617	29.4	73	7
Smoky-brown woodpecker	<i>Veniliornis fumigatus</i>	34	1850	0.1012*	0.1092	-0.0008	-0.0023	0.1007	10	18	0.9	4	0
Rufous-winged woodpecker	<i>Piculus simplex</i>	55	750	0.0357	0.0584*	0.0025	-0.0037	0.0302	19	102	4.9	13	0
Cinnamon woodpecker	<i>Celeus lorricatus</i>	83	750	-0.0024	-0.0044	-0.0021	-0.0014	-0.0129	19	58	2.8	9	0
Chestnut-colored woodpecker	<i>Celeus castaneus</i>	100	750	0.0071	0.0337	-0.0026	-0.0047	0.0000	19	74	3.5	6	0
Lineated woodpecker	<i>Dryocopus lineatus</i>	197	1100	-0.0124	-0.0205	-0.0023	-0.0029	0.0651*	20	102	4.9	12	1
Pale-billed woodpecker	<i>Campephilus guatemalensis</i>	225	1000	0.0143	0.0028	-0.0010	-0.0061*	-0.0132	20	509	24.2	51	4
Slaty spinetail	<i>Synallaxis brachyura</i>	18.5	1250	0.0719*	0.0678	-0.0035	-0.0110*	0.0340	15	42	2.0	11	0
Buff-throated foliage-gleaner	<i>Automolus ochrolaemus</i>	42	1200	0.0110	0.0233	-0.0012	-0.0053	0.0843	18	51	2.4	10	0
Plain xenops	<i>Xenops minutus</i>	12	1100	-0.0035	0.0174	0.0001	-0.0066	-0.0219	20	121	5.8	15	1
Plain-brown woodcreeper	<i>Dendrocincla fuliginosa</i>	42	750	0.0361*	0.0250	-0.0005	0.0016	0.0001	19	108	5.1	14	0
Wedge-billed woodcreeper	<i>Glyphorhynchus spirurus</i>	16.5	1100	0.0198*	0.0085	-0.0002	-0.0046*	-0.0029	20	963	45.9	73	3
Northern barred-woodcreeper	<i>Dendrocolaptes sanctithomae</i>	73	600	0.0109	0.0129	-0.0001	-0.0041	0.02442	20	344	16.4	29	3
Cocoa woodcreeper	<i>Xiphorhynchus susurrans</i>	21.5	650	0.0328*	0.0201	0.0010	-0.0083*	-0.0037	20	212	10.1	33	1
Black-striped woodcreeper	<i>Xiphorhynchus lachrymosus</i>	58	1000	0.0508*	-0.0065	-0.0054*	-0.0133*	-0.0582	17	84	4.0	12	0
Spotted woodcreeper	<i>Xiphorhynchus erythropygus</i>	50	1450	0.0420	0.0128	-0.0006	0.0061	0.1361*	13	22	1.1	4	0
Streak-headed woodcreeper	<i>Lepidocolaptes erythropygus</i>	28	1500	0.0193	0.0226	0.0016	-0.0011	0.0171	20	213	10.1	20	2
Fasciated antshrike	<i>Lepidocolaptes souleyetii</i>	41	600	0.0198	0.0253	-0.0018	-0.0044	0.0270	19	118	5.6	14	0
Great antshrike	<i>Cymbilaimus lineatus</i>	75	1000	0.0129	0.0170	-0.0038*	-0.0135*	-0.0326	19	71	3.4	12	0
Barred antshrike	<i>Taraba major</i>	28	1400	0.1102*	0.1007*	-0.0028	-0.0080	0.0941*	14	75	3.6	17	0
Western slaty-antshrike	<i>Thamnophilus doliatus</i>	24	700	0.0075	-0.0130	-0.0013	-0.0003	0.0067	19	404	19.2	59	0
Streak-crowned antvireo	<i>Thamnophilus atrinucha</i>	17	800	0.0127	-0.0177	-0.0020	0.0008	0.03400	16	74	3.5	11	0
Checker-throated antwren	<i>Dysithamnus striaticeps</i>	10.5	700	-0.0155	0.1100*	0.00149	-0.0058	0.1748*	12	52	2.5	20	0
White-flanked antwren	<i>Myrmotherula fulviventris</i>	8.5	700	0.0254	0.0237	0.0022	0.0090	-0.0013	15	67	3.2	9	0

(continued)

Table 3. (Continued)

Common name	Scientific name	Diet	Body mass (g)	Upper elev	Model rainfall coefficients						Count summaries				
					Montane			Lowland			n yr	Sum	Mean	Max	Min
					Jul-Dec	Oct-Dec	Week prior	3 d prior	Mar-Jun						
Dot-winged antwren	<i>Microhoppia quixensis</i>	insect	8.5	1000	-0.0175	-0.0040	-0.0032	0.0033	0.0482	0.0033	15	59	2.8	7	0
Dusky antbird	<i>Cercomacra tyrannina</i>	insect	18	1000	-0.0052	0.0351	0.0031*	0.0085*	-0.0580*	0.0085*	20	149	7.1	17	1
Chestnut-backed antbird	<i>Myrmeciza exsul</i>	insect	28	900	0.0177*	0.0104	0.0002	0.0005	0.0129	0.0005	20	785	37.4	74	3
Spotted antbird	<i>Hylophylax naevioides</i>	insect	18	800	0.0927*	0.0343	-0.0013	-0.0074	0.0382	-0.0074	15	49	2.3	10	0
Bicolored antbird	<i>Gymnophithys leucaspis</i>	insect	30	1500	-0.0011	-0.0025	0.0007	0.0089*	0.0153	0.0089*	17	79	3.8	11	0
Ocellated antbird	<i>Phaenostictus mcleannani</i>	insect	55	1200	0.0239	0.0664*	-0.0020	-0.0015	-0.0232	-0.0015	18	135	6.4	17	0
Black-faced antthrush	<i>Formicarius analis</i>	insect	60	500	0.0195*	0.0305*	-0.0013	-0.0023	0.0235	-0.0023	19	301	14.3	44	0
Thicket antpitta	<i>Hylopezus dives</i>	insect	44	900	0.0315	0.0578	-0.0058*	-0.0134*	-0.0326	-0.0134*	13	40	1.9	10	0
Brown-capped tyrannulet	<i>Ornithion brunneicapillus</i>	insect	7	900	0.1668*	0.0902*	0.0011	0.0055	-0.0423	0.0055	14	67	3.2	14	0
Yellow tyrannulet	<i>Capsiempis flaveola</i>	insect	8	600	0.0321*	0.0653*	0.0014	-0.0039	0.0173	-0.0039	19	131	6.2	17	0
Yellow-bellied elaenia	<i>Elaenia flavogaster</i>	frug	25	1850	0.0301	0.0331	0.0016	-0.0028	-0.0097	-0.0028	20	88	4.2	8	1
Black-capped pigmy-tyrant	<i>Myiornis atricapillus</i>	insect	5.2	600	0.0162*	-0.0132	-0.0017*	-0.0063*	-0.0202	-0.0063*	20	481	22.9	58	3
Northern bembill	<i>Oncostoma cinereigulare</i>	insect	7.3	750	0.0791*	0.0602*	-0.0103*	-0.0143*	0.0380	-0.0143*	18	93	4.4	14	0
Common tody-flycatcher	<i>Todirostrum cinereum</i>	insect	6.5	1150	0.0147	0.0167	0.0020*	-0.0017	0.0341	-0.0017	20	206	9.8	18	3
Black-headed tody-flycatcher	<i>Todirostrum nigriceps</i>	insect	6.3	700	0.0537*	0.1427*	0.0036*	0.0074	0.0676	0.0074	15	62	3.0	8	0
Eye-ringed flatbill	<i>Rhynchocyclus brevirostris</i>	insect	23	1700	0.0342	0.0111	-0.0003	-0.0065	0.0380	-0.0065	15	30	1.5	5	0
Yellow-olive flycatcher	<i>Tolmomyias sulphurescens</i>	insect	14.5	1400	0.0872*	0.0912*	0.0008	-0.0065	0.0762*	-0.0065	13	76	3.6	10	0
Yellow-margined flycatcher	<i>Tolmomyias assimilis</i>	insect	15	600	0.0223	0.0332	-0.0008	-0.0008	-0.0479	-0.0008	20	109	5.2	10	2
Golden-crowned spadebill	<i>Platyrinchus coronatus</i>	insect	9	700	0.0632	0.0637	0.0000	-0.0007	0.0621	-0.0007	12	28	1.3	4	0
Ruddy-tailed flycatcher	<i>Terenotriccus erythrurus</i>	insect	7	1000	0.0106	-0.0395	-0.0039	-0.0122*	0.0558	-0.0122*	14	51	2.4	8	0
Tropical pewee	<i>Contopus cinereus</i>	insect	12.5	700	0.0030	0.0427	0.0032*	0.0042	-0.0101	0.0042	19	57	2.7	6	0
Long-tailed tyrant	<i>Colonia colonus</i>	insect	13	600	0.0147	0.0074	-0.0007	0.0021	0.0269	-0.0007	19	128	6.1	13	0
Bright-rumped attila	<i>Attila spadiceus</i>	omn	40	1850	0.0098	-0.0151	-0.0034*	-0.0023	0.0402*	-0.0023	20	465	22.1	57	4
Rufous mourner	<i>Rhytipterna holerythra</i>	omn	40	1200	0.0178	0.0181	-0.0006	-0.0045*	-0.0293	-0.0045*	19	350	16.7	42	0
Dusky-capped flycatcher	<i>Pitangus sulphuratus</i>	insect	20	1200	0.0164	0.0072	0.0012	-0.0005	0.0313	-0.0005	20	246	11.7	27	1
Great kiskadee	<i>Megarhynchus pitangua</i>	omn	68	1500	0.0210*	-0.0128	0.0000	-0.0059*	0.0254*	-0.0059*	20	589	28.1	52	9
Boat-billed flycatcher	<i>Myiozetetes similis</i>	omn	70	1850	0.0260*	0.0129	-0.0012*	-0.0040*	0.0185	-0.0040*	20	713	34.0	90	6
Social flycatcher	<i>Myiozetetes similis</i>	omn	27	1700	0.0216*	0.0076	0.0001	-0.0041*	0.0328*	-0.0041*	20	868	41.3	81	13
Gray-capped flycatcher	<i>Myiozetetes granadensis</i>	omn	30	300	0.0244*	0.0180*	0.0011*	-0.0030*	0.0649*	-0.0030*	20	681	32.4	71	15
White-ringed flycatcher	<i>Conopias albivittatus</i>	insect	24	600	0.0177	0.0168	-0.0011	-0.0014	0.0492*	-0.0014	20	249	11.9	25	3
Tropical kingbird	<i>Tyrannus melancholicus</i>	insect	40	1850	0.0366*	0.0043	0.0004	-0.0051*	0.0178	-0.0051*	20	410	19.5	46	6
Rufous pitta	<i>Lipaugus unirufus</i>	omn	75	600	0.0031	-0.0103	0.0001	0.0019	0.0437*	0.0019	20	279	13.3	29	3
Cinnamon becard	<i>Pachyrhamphus cinnamomeus</i>	insect	22	750	0.0270*	0.0100	0.0012	0.0004	0.0465*	0.0012	20	291	13.9	30	2
White-winged becard	<i>Pachyrhamphus polychopterus</i>	insect	21	1000	0.0132	0.0290	0.0012	0.0045	-0.0263	0.0045	16	53	2.5	6	0
Masked titiya	<i>Tityra semifasciata</i>	omn	88	1500	0.0180*	0.0100	0.0003	-0.0019	-0.0034	-0.0019	20	627	29.9	73	5
Black-crowned titiya	<i>Tityra inquisitor</i>	omn	50	1220	0.0114	-0.0271	0.0029*	-0.0017	0.0039	-0.0017	18	130	6.2	15	0
Purple-throated fruitcrow	<i>Querula purpurata</i>	frug	115	450	0.0272*	-0.0071	-0.0041*	-0.0068*	0.0137	-0.0068*	20	271	12.9	33	3
White-collared manakin	<i>Manacus candei</i>	frug	18.5	700	0.0020	-0.0143*	-0.0022*	-0.0047*	0.0182*	-0.0047*	20	1091	52.0	96	15
Tawny-crowned greenlet	<i>Hylophilus ochraceiceps</i>	insect	11	1200	0.0541	0.1220*	-0.0056	-0.0015	0.0462	-0.0015	14	31	1.5	9	0
Lesser greenlet	<i>Hylophilus decurtatus</i>	insect	9	900	0.0351*	0.0170*	-0.0015*	-0.0056*	0.0079	-0.0056*	20	896	42.7	109	9
Green shrike-vireo	<i>Vireolanius pulchellus</i>	omn	30	1000	0.0464	0.0871*	-0.0028	-0.0090	0.0118	-0.0090	13	42	2	10	0

Brown jay	<i>Cyanocorax morio</i>	235	2500	-0.0845*	-0.1158*	0.0009	-0.0044	-0.1322*	13	89	4.2	21	0
Band-backed wren	<i>Campylorhynchus zonatus</i>	29	1700	0.0472*	0.0120	-0.0001	-0.0035	0.0300	20	207	9.9	27	1
Black-throated wren	<i>Thryothorus atrogularis</i>	24	1100	0.0201	0.0108	-0.0014	-0.0063*	-0.0342	19	174	8.3	21	0
Bay wren	<i>Thryothorus nigricapillus</i>	27	700	0.0294*	0.0350*	0.0014*	-0.0002	-0.0014	20	680	32.4	64	3
Stripe-breasted wren	<i>Thryothorus thoracicus</i>	17	1000	-0.0004	0.0125	-0.0001	0.0019	-0.0129	20	417	19.9	47	6
Plain wren	<i>Thryothorus modestus</i>	23	300	0.0320	0.0373	-0.0002	-0.0056	0.0662*	19	97	4.6	8	0
House wren	<i>Troglodytes aedon</i>	12	2750	0.0240	0.0081	0.0013	-0.0049	0.0020	19	108	5.1	11	0
White-breasted wood-wren	<i>Henicorhina leucosticta</i>	16	900	0.0231*	0.0250*	-0.0003	-0.0030*	-0.0045	20	1517	72.2	124	13
Nightingale wren	<i>Microcerculus philomela</i>	18	1200	0.0223	0.0368	0.0007	-0.0043	0.0374	15	58	2.8	8	0
Tawny-faced gnatwren	<i>Microbates cinereiventris</i>	11	900	0.0626	-0.0374	-0.0056	-0.0015	0.0462	8	24	1.1	8	0
Long-billed gnatwren	<i>Ramphocaenus melanurus</i>	10	1200	0.0328*	0.0406	0.0020	0.0011	-0.0651*	18	128	6.1	29	0
Tropical gnatcatcher	<i>Polioptila plumbea</i>	6.5	1500	0.0105	-0.0130	-0.0020*	-0.0061*	-0.0307*	20	403	19.2	50	1
Clay-colored thrush	<i>Turdus grayi</i>	76	2450	0.0399*	-0.0174*	-0.0010*	-0.0110*	0.0374*	20	850	40.5	125	10
Olive-crowned yellowthroat	<i>Geothlypis semiflava</i>	15.5	1000	0.0917*	0.0778	-0.0013	-0.0061	0.0800	14	33	1.6	7	0
Gray-crowned yellowthroat	<i>Geothlypis poliocephala</i>	15.5	1500	0.0508	-0.0350	0.00224	-0.0064	0.0003	9	15	0.7	2	0
Buff-rumped warbler	<i>Phaeothlypis fulvicauda</i>	14.5	1100	0.0042	-0.0116	0.0003	0.0023	0.0482*	20	345	16.4	42	2
Bananaquit	<i>Coereba flaveola</i>	9.5	1200	-0.0232	-0.0232	-0.0021*	-0.0035	0.0000	20	185	8.8	18	4
Dusky-faced tanager	<i>Mitrospingus cassinii</i>	42	600	-0.0263*	-0.0168	0.0012	0.0024	-0.0622*	19	359	17.1	43	0
White-shouled tanager	<i>Tachyphonus luctuosus</i>	16	750	0.0362*	0.0230	-0.0005	-0.0078*	-0.0044	20	280	13.3	32	1
White-lined tanager	<i>Tachyphonus rufus</i>	32	1400	-0.0123	0.0010	0.0029	0.0059	-0.0051	16	61	2.9	10	0
Crimson-collared tanager	<i>Ramphocelus sanguinolentus</i>	40	1100	0.0243	0.0344	0.0016	0.0051	0.0606	17	62	3.0	7	0
Passerini's tanager	<i>Ramphocelus passerinii</i>	31	1200	0.0005	0.0043	0.0001	0.0010	0.0336*	20	1481	70.5	119	35
Blue-gray tanager	<i>Thraupis episcopus</i>	32	2000	0.0326*	-0.0177	-0.0011	-0.0102*	0.0944*	20	487	23.2	67	2
Palm tanager	<i>Thraupis palmarum</i>	38	1500	0.0377*	0.0119	0.0004	-0.0157*	0.0920*	19	490	23.3	82	0
Golden-hooded tanager	<i>Tangara larvata</i>	19	1500	0.0223*	0.0168*	0.0002	-0.0045*	0.0292*	20	810	38.6	63	13
Plain-colored tanager	<i>Tangara inornata</i>	19	400	0.0106	-0.0284	-0.0012	-0.0103*	0.0328	20	149	7.1	19	1
Blue dacnis	<i>Dacnis cayana</i>	13.5	900	-0.0005	-0.0202	0.0002	0.0005	0.0198	20	261	12.4	28	2
Green honeycreeper	<i>Chlorophanes spiza</i>	19	1000	0.0069	-0.0426*	-0.0041*	-0.0046	0.0528*	20	240	11.4	36	1
Shining honeycreeper	<i>Cyanerpes lucidus</i>	11	1200	0.0387*	0.0052	0.0009	-0.0037	0.0593*	19	300	14.3	40	0
Red-legged honeycreeper	<i>Cyanerpes cyaneus</i>	13.5	1000	0.0666*	-0.0037	-0.0015	-0.0101*	0.1669*	14	134	6.4	36	0
Grayish saltator	<i>Saltator coerulescens</i>	54	1850	0.1275*	0.1542*	-0.0095*	-0.0152*	0.0721	12	32	1.5	11	0
Buff-throated saltator	<i>Saltator maximus</i>	50	1200	-0.0020	-0.0036	0.0016*	0.0003	0.0082	20	627	29.9	56	13
Black-headed saltator	<i>Saltator atriceps</i>	85	1330	0.0498*	0.0634*	0.0012	-0.0044	0.0139	20	203	9.7	30	3
Slate-colored grosbeak	<i>Saltator grossus</i>	50	1100	0.0078	-0.0196	-0.0001	-0.0001	-0.0149	17	97	4.6	11	0
Blue-black grassquit	<i>Volatina jacarina</i>	9.5	1700	0.0209	0.0089	0.0013	0.0097*	0.0034	16	164	7.8	50	0
Variable seedeater	<i>Sporophila americana</i>	11	1500	-0.0041	0.0032	0.0013*	0.0042*	0.0075	20	423	20.1	38	8
Orange-billed sparrow	<i>Arremon aurantiostris</i>	35	800	-0.0120	-0.0220*	0.0000	-0.0043*	-0.0059	20	590	28.1	47	3
Black-striped sparrow	<i>Arremonops conirostris</i>	37.5	1500	0.0330	0.0398	0.0015	-0.0004	0.0191	18	127	6.1	14	0
Red-throated ant-tanager	<i>Habia fuscicauda</i>	38	600	0.0068	0.0336*	0.0022*	0.0007	-0.0238	20	490	23.3	50	2
Black-faced grosbeak	<i>Caryothraustes pollogaster</i>	36	900	0.0011	0.0023	0.0017*1	-0.0013	0.0174	20	446	21.2	54	4
Blue-black grosbeak	<i>Cyanocompsa cyanoides</i>	32	1200	0.0165	0.0178	-0.0010	0.0022	0.0006	19	109	5.2	8	0
Black-cowled oriole	<i>Icterus prosthemelas</i>	32	700	0.0250	0.0058	-0.0037*	-0.0125*	0.0341	18	92	4.4	14	0
Yellow-billed caticue	<i>Amblycercus holosericeus</i>	65	3000	-0.0055	-0.0006	0.0014	0.0057	0.0589	18	75	3.6	8	0
Scarlet-rumped caticue	<i>Cacicus uropygialis</i>	60.5	300	0.0214*	0.0018	-0.0014*	-0.0029*	0.0010	20	1183	56.3	92	23
Montezuma oropendola	<i>Psarocolius montezuma</i>	375	800	-0.0255*	-0.0775*	-0.0012*	0.0019*	0.0533*	20	3403	162.1	511	48
Yellow-crowned euphonia	<i>Euphonia luteicapilla</i>	12.5	1200	0.0257*	-0.0085	-0.0013*	-0.0066*	0.0184	20	509	24.2	66	1
Olive-backed euphonia	<i>Euphonia gouldi</i>	12	750	0.0092*	-0.0015	-0.0014*	-0.0037*	-0.0045	20	1708	81.3	136	12
White-vented euphonia	<i>Euphonia minuta</i>	10	1100	0.0071	-0.0013	-0.0040*	-0.0083	0.0110	14	58	2.8	13	0

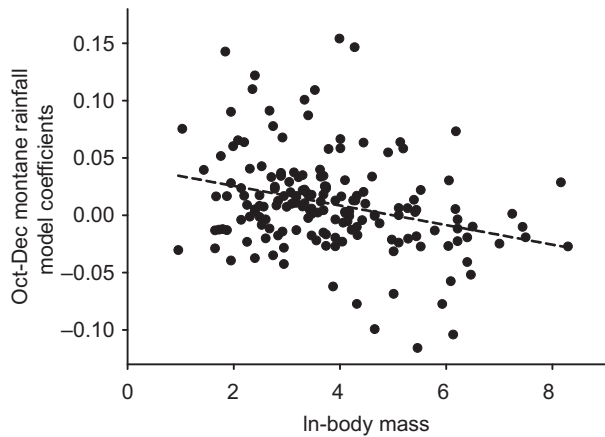


Figure 4. The relationship between body mass (ln-transformed) and the Oct–Dec montane rainfall coefficients (in models accounting for population trend, variation in observer effort, and count day rain) among lowland resident species.

rainfall coefficients with counts of smaller species increasing more strongly in response to heavy montane rainfall than counts of larger species (Jul–Dec,  $R^2 = 8.0$ ,  $F_{1,168} = 14.6$ ,  $p < 0.001$ ; Oct–Dec,  $R^2 = 8.8$ ,  $F_{1,168} = 16.1$ ,  $p < 0.0001$ ; Fig. 4). Diet was also related to rainfall coefficients (Jul–Dec,  $F_{4,165} = 3.0$ ,  $p = 0.020$ ; Oct–Dec,  $F_{4,165} = 4.6$ ,  $p = 0.002$ ) but not in the ways predicted; counts of insectivores increased the most strongly in response to heavy montane rainfall. In models including both diet and body mass together, these two variables did not interact in their association with rainfall responses, neither in models using all diet classes nor in models comparing frugivores and nectarivores to other dietary groups. The elevational range of a species did not explain variation in rainfall coefficients in either simple models (Jul–Dec,  $F_{1,168} = 0.7$ ,  $p = 0.410$ ; Oct–Dec,  $F_{1,168} = 2.4$ ,  $p = 0.127$ ) or in combination with diet and/or body mass.

## Discussion

The community-level patterns of partial altitudinal migration support the limited foraging opportunities hypothesis. As predicted, the counts of altitudinal migrants visiting lowland forest in late Dec were on average positively associated with montane rainfall variables from the previous three to six months. This finding was robust to different analytical approaches, being consistent between the pooled raw count data and the analysis of rainfall coefficients from species-level models. Furthermore, these responses were related to both diet and body size in the ways predicted by the LFO with counts of smaller-bodied birds and frugivores and nectarivores responding most strongly and positively to variation in rainfall amounts. Migrants exhibited variation in the nature of rainfall responses at different temporal scales, suggesting that species likely differ in the threshold of rainfall intensity that limits their foraging activities and ability to survive storms. Overall, the magnitude of migrant responses indicated a large community-level effect on the lowland avifauna. Severe weather during Jul–Dec is common; 24.5% of days during Jul–Dec at the montane site receive rainfall amounts greater than 50 mm, and as much as 292 mm of rain has

been recorded in a single day. This means that increases of 1.5–3% per 100 mm increase in rain over six months translate to differences of 42–84% among the wettest and driest years in this study.

While some species such as the paltry tyrannulet, olive-striped flycatcher, and pale-vented thrush seem to fit the predictions of the LFO perfectly (all frugivorous species that were significantly more abundant in counts in wetter years), results of counts of other species were surprising. For example, counts of the white-ruffed manakin, whose responses to rainfall inspired the LFO in the first place (Boyle 2008), were not significantly associated with any of the rainfall variables examined here. This result highlights the limitations of survey methods such as the CBC and also highlights the conservative nature of the results presented here. The relative abundance of small, fast-moving, or otherwise inconspicuous species may not be well reflected in observational data such as that obtained from the CBC (Kéry and Schmidt 2008). Thus, the migrations of many more species are likely influenced by rainfall intensity than detectable using count methods such as used here. Negative relationships between montane rainfall and counts of a few species also run contrary to the predictions of the LFO. Contrary to the typical altitudinal migrant pattern in this region, fewer individuals of such species are counted in lowland forests during wetter years than drier years. Possible explanations include larger-scale movements out of the study area of some of the more mobile, large species (e.g. yellow-eared toucanet, chestnut-headed oropendola) or possibly, mortality in years with particularly severe wet seasons, especially in small-bodied, open-cup nesting species such as green hermit.

Intriguingly, counts of resident species were also positively associated with montane rainfall amounts. Tests of alternate factors potentially driving this relationship suggest that a likely explanation is that lowland-breeding populations are being augmented by downhill migration of individuals of the same species that breed at higher elevations. Results were not consistent with the increased productivity hypothesis because, although breeding season rainfall was positively associated with counts of residents, breeding season rainfall was not correlated with the montane wet-season rainfall variables. Likewise, weather-induced changes in detectability also cannot explain these positive relationships because high rainfall in the days prior to the count was associated with strong reductions (not increases) in the numbers of birds counted.

Analyses of the relationship between body size and rainfall coefficients of resident species indicate that counts of smaller birds are more strongly and positively related to increases in montane rainfall than are counts of large birds, consistent with the LFO hypothesis. Interestingly, the relatively few frugivorous (17 of 170) and nectarivorous resident species did not consistently differ from other dietary groups in their responses to montane rain as predicted. Nor did a species' upper elevational range limit explain variation in rainfall responses. An important caveat here is that dietary groupings are necessarily coarse in a community-level study such as this, obscuring a great deal of variation in the nature and nutritional quality of the foods consumed by different species. It is this variation in nutritional quality that is hypothesized to influence fasting endurance and thence, the propensity to migrate. Likewise, upper elevational limit

does not reflect relative abundance and distribution of species along that gradient, which would influence the number of individuals affected by montane weather conditions. What these analyses do indicate is that climate-driven partial altitudinal migration is likely 1) more widespread than previously recognized in species whose elevational range includes lowland forest, and 2) small-bodied taxa of multiple foraging guilds (not only frugivores and nectarivores) likely engage in these movements.

With the exception of the recent literature focusing on white-ruffed manakins, few other studies of tropical altitudinal migrants have considered the role of weather in affecting migratory decisions. Furthermore, no other previous study has taken advantage of multi-year datasets, making comparisons between this study and results of other studies challenging. The classic work of Loiselle and Blake (1991) considered community-level patterns of bird abundance and fruit availability during 1985–1986 in the same region as this study. Although Loiselle and Blake (1991) didn't consider alternative hypotheses other than variation in food resources in driving altitudinal migration, several of their findings are interesting in the context of the LFO hypothesis. First, frugivore abundance and bird abundance were temporally correlated at their lower-elevation sites, but not their highest site. Frugivores depart montane areas during the latter months of the year, and food availability at their montane site was highest during this period, suggesting that factors other than food availability drive these downhill movements. Second, fat stores in all birds in their study peaked during the end of the wet season when storms are often the most severe, indicating that birds must prepare for foraging uncertainty during inclement weather. Third, Loiselle and Blake (1991) noted both that the years of their study were drier than average, and that they did not record a number of altitudinal migrant species in lowland forest that they and others had detected previously, consistent with variation in rainfall influencing the outcome of migratory decisions. The idea that heavy rainfall drives downhill altitudinal migration is not new. Skutch (1969) suggested that inter-annual variation in rainfall may account for year-to-year differences in the onset of altitudinal migration in the Three-wattled bellbird. In the more seasonal outer tropics of Mexico, both Nocedal (1994) and Ramos-Olmos (1983) noted that downhill movements of many species (including many insectivores) were associated with seasonal storms bringing heavy precipitation and cooler temperatures. This study is the first community-level study to test predictions of hypotheses based on climatic variation driving migration in tropical birds. Because annual counts and weather data likely exist for other tropical sites, replication of these results would be extremely valuable for determining the generality of the results presented here.

Weather may be far more important to tropical taxa than previously recognized. Climatic effects are rarely implicated in the evolutionary ecology of tropical birds (Stutchbury and Morton 2001) where mild mean annual temperatures vary less than the variation in diurnal temperatures. Seasonality of rainfall is widely acknowledged to govern many aspects of tropical dry forest phenology and behaviour (Stiles 1983), but not in year-round wet forests such as on the Caribbean slope of Central America. Results of this study suggest that rainfall during the whole wet

season and the severity storm events may have dramatic effects on the behaviour and community dynamics of wet forest bird communities. For instance, if the timing and intensity of storms affects migration to the degree it appears to, then likely timing of breeding, moult, and other key life-history traits may also be shaped by the rainfall as well, especially in extremely wet forests such as Caribbean slope mountains of Central America. Reduced foraging time would likely limit the suitability of the latter part of the year for breeding, independent of food availability. Likewise, variation in weather at much shorter time scales must be considered in short-term sampling efforts given that the amount of rain falling in the days prior to counts dramatically affected the detectability and perceived abundance of birds in this study.

These results imply that accurately predicting how anthropogenic alterations of global climatic regimes will influence the timing, duration, and severity of tropical storms is paramount for understanding how animal communities will respond to climate disruptions. If storm events become more severe (as some climate models predict; Albritton et al. 2001), then likely more species and more individuals of partially migrant species will descend to lowland forests post-breeding. Alternatively, if overall drying of tropical wet forests results (Karmalkar et al. 2008), we may see the reduction or loss of altitudinal migrations entirely.

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