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ELEVATIONAL MOVEMENTS OF LARGE FRUGIVOROUS BIRDS AND TEMPORAL VARIATION IN ABUNDANCE OF FRUITS ALONG AN ELEVATIONAL GRADIENT

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Resumen. – **Movimientos altitudinales de aves frugívoras grandes y variación temporal de frutos a lo largo de un gradiente altitudinal en Costa Rica.** – Datos sobre la abundancia de aves migratorias altitudinales frugívoras grandes y los frutos que éstas consumen fueron sistemáticamente colectados durante 1998 en cuatro diferentes elevaciones en la vertiente Caribe de Costa Rica. Las aves fueron abundantes en elevaciones altas durante su época reproductiva y en elevaciones más bajas durante su época no reproductiva. La presencia y abundancia de las aves en tierras altas y bajas se traslapó parcialmente con periodos de alta abundancia de frutos a esas elevaciones. Los datos sugieren que la abundancia de frutos podría ser un factor próximo dirigiendo las migraciones altitudinales de aves frugívoras grandes, pero no sería el único. Cambios temporales en las precipitaciones tampoco parecen ser la clave que las aves utilizan para determinar cuando migrar. Sin embargo, en casi todas las especies, algunos individuos permanecieron en las tierras altas mientras que otros migraron hacia tierras mas bajas después de la época reproductiva, impidiendo la detección de posibles correlaciones entre estos factores. El entendimiento de las causas de este patrón diferencial de migración dentro de las especies podría ser la clave para entender las causas de migración altitudinal en el Neotrópico.

Abstract. – Data on the abundance of large elevational migrant fruit-eating birds along with the abundance of the fruits they eat were systematically collected during 1998 at four different elevations on the Caribbean slope of the Tilarán mountain range in Costa Rica. The birds were abundant at high elevations during their breeding season and abundant at lower elevations during their non-breeding season. Presence and abundance of birds in the highlands and lowlands partially overlapped with periods of high fruit abundance at those elevations. The data suggest that fruit abundance might be a proximate factor driving elevational movements of large frugivorous birds, but would not be the only one. Changes in precipitation do not seem to be the cue used to determine the initiation of migration either. However, in almost all species, some individuals stayed in the highlands, while others migrated to the lowlands after the breeding season, precluding the detection of potential correlations between these factors. Understanding the causes of this

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differential migration within species might be the key to understand the causes of elevational migration in the Neotropics. *Accepted 31 March 2004.*

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INTRODUCTION

Elevational migration is the most conspicuous short-distance movement of birds in the Neotropics (Stiles 1983). It consists of annual movements between elevations over a range of 500 m or more (Stiles 1983, 1988), passing through several forest types (i.e., life zones *sensu* Holdridge 1967; Loiselle & Blake 1991, Powell & Bjork 1995, Young *et al.* 1998, Blake & Loiselle 2000).

It has been proposed that temporal and spatial variation in food abundance could drive elevational migration (Stiles 1988, Levey & Stiles 1994). In Costa Rica, the Neotropical area where elevational migration has been studied in more detail, most elevational migrant species are frugivorous or nectarivorous (Stiles 1985, 1988). In this country, small fruit-eating birds (e.g., thrushes, tanagers) breed in highlands or middle elevations during periods of fruit scarcity (Loiselle & Blake 1991, Rosselli 1994) but spend the non-breeding season at lower elevations when fruits are abundant (Levey 1988, Loiselle & Blake 1991). Therefore, it seems that small frugivorous birds track fruit abundance only during the non-breeding season. Protein abundance (e.g., insects) might be more important for the timing of the breeding season in the highlands (Loiselle & Blake 1991).

Protein-rich fruit abundance could be an important factor determining timing of migration. Fruits rich in proteins and lipids (e.g., Lauraceae, Myristicaceae) provide enough protein without excess of calories (Foster 1978) but are generally inaccessible to most birds due to their large size (Howe &

Smallwood 1982, Herrera 1985, Moermond & Denslow 1985, Wheelwright 1985). However, these fruits are commonly eaten by large fruit-eating birds (e.g., quetzals, bellbirds; Wheelwright *et al.* 1984, Wheelwright 1985), and there is some evidence suggesting that their phenology might dictate the elevational movements of these species (Wheelwright 1983, D. DeRosier pers. com.). Hence, fruit abundance could be driving elevational movements of large frugivorous birds to a greater extent than in small frugivorous birds.

There are no quantitative data about temporal abundance of large frugivorous birds and fruits along large elevational gradients (> 500 m) for the Neotropics. For that reason, my objective is to document the temporal abundance of large fruit-eating elevational migrant species and the fruit plants they eat along an elevational gradient in Costa Rica, to explore how closely their elevational movements are related to fruit availability.

STUDY AREA

The study area was the Caribbean slope of Cordillera de Tilarán, Costa Rica (10°18'N, 84°45'W). Continuous protected forest extends from an elevation of 400 m to the top of the mountains (1850 m) in this area. The protected area encompasses approximately 40,000 ha and includes both national parks and private reserves (e.g., Monteverde Cloud Forest Preserve). The forest below 400 m has been removed and cleared for pastures and plantations during the last five decades. Dry season on this slope typically lasts from February to April (Coen 1983, Sanford *et al.* 1994,

Clark *et al.* 2000), and the seasonal pattern of rainfall is similar at all elevations (Blake & Loiselle 2000).

I conducted research at four elevations. The study sites included all the life zones (according to Holdridge 1967) in the forested area: lower montane rain forest (1400 m), premontane rain forest (1000 m and 800 m), and tropical wet forest cool transition (400 m; Haber 2000). I did not include higher sites (e.g., continental divide) because most species of large frugivorous birds are rare or absent above lower montane rain forest in the area (Stiles 1983, Fogden 2000). For a more detailed description of the study sites, see Chaves-Campos *et al.* (2003).

METHODS

Birds. I considered only species with a minimum gape width of 2 cm and a diet of at least 50% of fruits (Levey *et al.* 1994). All the species included feed mostly on fruits (Moermond & Denslow 1985, Stiles & Skutch 1989, Riley & Smith 1992, Remsen *et al.* 1993) and show high overlap in their diets (Wheelwright *et al.* 1984, Foster 1987, Wenny & Levey 1998).

I monitored bird abundance with transect counts. At each site, I established two transects of 2 km in mature forest. I sampled bird abundance at each site during seven sampling periods, 6–8 weeks apart, between January 1998 and January 1999. Every sampling period consisted of 2 days: on the first day I walked along one transect from 06:00 to 09:00 h, and on the second day I sampled the other transect using the same methodology. Bird abundance was registered along these transects by recording the number of birds seen or heard within a lateral distance of 50 m from each side of the trail. The median amount of time spent sampling birds per sampling period was 5.9 h. The transects were at least 2 km apart.

Fruits. I sampled fruit abundance during the same periods of bird abundance sampling. Following recommendations of Rosselli (1994) and Blake *et al.* (1990), I studied fruits as a resource for birds in area-based samples. I established three fruit transects (100 x 2 m each, 100 m apart) along each transect where birds were recorded (two transects per elevation) for a total of six transects per elevation. Each sampling period, I counted (from the ground with binoculars) the number of ripe fruits on trees whose trunks were inside or on the border of the transects. The crown area of the trees included in the transects was variable; for that reason the crown area of every tree was estimated in order to estimate the area sampled per elevation. The total sampled area at every elevation was close to 5000 m².

I considered only fruits displayed above 4 m, because most large fruit-eating birds feed above the upper levels of the understory (Stiles & Skutch 1989). For trees with thousands of fruits (e.g., figs), fruits were counted in a fraction using 10% of the crown, and the number of fruits in the fraction was extrapolated to the whole crown (Dinerstein 1986, Solórzano *et al.* 2000). For species with capsular fruits, I multiplied the total number of fruits per tree by the mean number of arillated seeds per capsule (Blake *et al.* 1990). I will refer to total fruit abundance (per transect or per elevation) as total number of fruits plus total number of arillated seeds. I restricted my analyses to those plants known to be visited by large fruit-eating birds, based on personal observations of foraging birds, and the data of McKey (1975), Snow (1981, 1982), Wheelwright *et al.* (1984), Moermond & Denslow (1985), Howe & Westley (1988), Stiles & Skutch (1989), Riley & Smith (1992) and Levey *et al.* (1994).

Analyses. I classified species as elevational migrants in Costa Rica according to Stiles (1985) and Blake & Loiselle (2000). Two spe-

TABLE 1. Means (SD) of high and low-lipid-protein fruits potentially consumed by large fruit-eating birds (counted in six 100-m transects, see text) at four elevations in Cordillera de Tilarán, Costa Rica.

		Sampling periods						
1400 m	Date	31 Jan	20 March	25 April	14 June	1 Aug	5 Oct	20 Dec
	High-protein-lipids	8 (20)	0 (0)	0 (0)	8 (16)	113 (241)	22 (39)	3 (5)
	Low-protein-lipids	3728 (2555)	2687 (6043)	4359 (2793)	3943 (2434)	3143 (4104)	645 (219)	2577 (2489)
1000 m	Date	18 Feb	1 April	15 May	1 July	2 Sep	1 Nov	1 Jan
	High-protein-lipids	287 (519)	102 (128)	117 (183)	267 (484)	122 (160)	122 (144)	110 (176)
	Low-protein-lipids	792 (1837)	535 (809)	2266 (1595)	783 (1168)	406 (976)	3000 (6964)	930 (2159)
800 m	Date	21 Jan	6 March	14 April	22 May	25 July	22 Sep	29 Nov
	High-protein-lipids	450 (912)	500 (1033)	89 (157)	955 (2030)	550 (1204)	1233 (2828)	64 (81)
	Low-protein-lipids	373 (790)	655 (941)	1022 (990)	877 (599)	474 (553)	438 (448)	1182 (1976)
400 m	Date	21 Feb	6 April	18 May	16 July	7 Sep	9 Nov	13 Jan
	High-protein-lipids	50 (122)	93 (149)	127 (224)	37 (57)	0 (0)	0 (2)	8 (20)
	Low-protein-lipids	2797 (6203)	907 (2211)	105 (248)	55 (125)	6 (12)	423 (1008)	260 (469)

TABLE 2. Percentage of annual fruit production and (number of fruiting trees) of high and low-lipid-protein fruit species potentially consumed by large fruit-eating birds at four elevations in Cordillera de Tilarán, Costa Rica.

		Sampling periods						
1400 m	Date	31 Jan	20 March	25 April	14 June	1 Aug	5 Oct	20 Dec
	High-protein-lipids	5.4 (1)	0 (0)	0 (0)	5.4 (2)	73 (2)	14.2 (3)	2 (2)
	Low-protein-lipids	17.7 (16)	12.7 (10)	20.7 (10)	18.7 (9)	14.9 (8)	3.1 (14)	12.2 (11)
1000 m	Date	18 Feb	1 April	15 May	1 July	2 Sep	1 Nov	1 Jan
	High-protein-lipids	36.7 (1)	5.8 (1)	8.3 (1)	27.8 (1)	6.4 (3)	7.9 (2)	7.2 (2)
	Low-protein-lipids	9.1 (9)	6.1 (10)	26 (10)	9 (11)	4.7 (7)	34.4 (9)	10.7 (7)
800 m	Date	21 Jan	6 March	14 April	22 May	25 July	22 Sep	29 Nov
	High-protein-lipids	11.9 (2)	13.3 (2)	0.6 (1)	25.1 (2)	14.5 (2)	33.7 (2)	0.9 (3)
	Low-protein-lipids	7.4 (4)	13 (6)	20.3 (7)	17.5 (12)	9.4 (9)	8.7 (12)	23.5 (11)
400 m	Date	21 Feb	6 April	18 May	16 July	7 Sep	9 Nov	13 Jan
	High-protein-lipids	0.1 (1)	26.1 (4)	56.3 (4)	12.1 (2)	0 (0)	0.5 (1)	5 (1)
	Low-protein-lipids	61.4 (7)	19.9 (6)	2.3 (3)	1.2 (2)	0.1 (3)	9.3 (8)	5.7 (7)

cies of guans, not previously reported as elevational migrants, showed patterns of elevational migration during this study (see Chaves-Campos 2003). I classified plant species according to fruit lipid content: species with fruits composed of more than 10% dry weight lipid and 9% dry weight protein were classified as high-lipid-protein fruits; species with lower values were classified as low-lipid-protein fruits (E. W. Stiles 1993). To determine lipid and protein content, I used data from Snow (1981), Howe & Smallwood (1982), Wheelwright *et al.* (1984), Moermond & Denslow (1985), and E. W. Stiles (1993). If information was not available for a given species, I classified it according to a congener.

I tested for temporal variation in fruit abundance by comparing abundance over time (among sampling periods) at each elevation (using transects as replications) using Friedman tests. I also examined relationships between bird and fruit abundance using Spearman correlation tests. Sampling effort for birds (number of hours counting) varied

due to rain. Therefore, I used number of birds per sampling hour at each elevation as the measure of bird abundance.

RESULTS

Fruit abundance. I recorded 330 bird-dispersed fruiting plants. Only 123 individuals of 43 genera had fruits during the study period (Appendix 1). Spatial fruit abundance per transect varied widely at any given period at each elevation (Table 1). For that reason, the mean abundance over time did not show significant peaks at any elevation (Friedman test, $P > 0.25$ in all cases). The low number of fruits recorded in most transects suggest that the area covered by each transects is too small to measure fruit abundance. Therefore, the temporal variation at a larger scale (fruits in 5000 m², i.e., the sum of all fruits counted in the six transects per sampling period) was analyzed to look for patterns.

Total abundance of low-lipid-protein fruits above 400 m peaked between April–

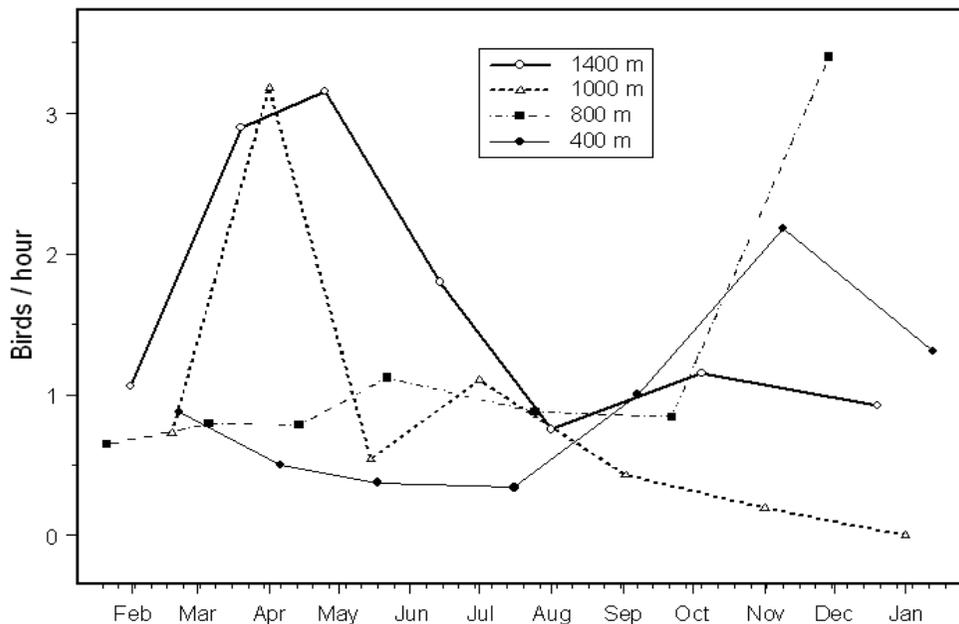


FIG. 1. Temporal abundance of elevational migrants at four different elevations in the Cordillera de Tilarán, Costa Rica (1998–1999).

June and again between October–November. At 400 m, these fruits were dramatically scarce between May–September (Table 2), which suggests an annual period of abundance starting around October and ending around April. High-lipid-protein fruit abundance peaked during January–March, and/or between July–September above 400 m. At 400 m, high-lipid-protein fruits were more abundant between April–July (Table 2). Periods of higher numbers of fruiting trees were not necessarily periods of high fruit abundance at any elevation (Table 2).

Bird abundance. I registered 163 large frugivorous elevational migrants of eight species during 167.5 sampling hours (See Appendix 2 for species list). In general, all species were more abundant above 800 m during their breeding season (February–July), and then their abundance decreased at those elevations and

increased at 800 m and 400 m (Fig. 1). Species that are typically regarded as highland birds [species that inhabit the mountain tops, like Black Guan (*Chamaepetes unicolor*), Resplendent Quetzal (*Pharomachrus mocinno*), and Emerald Toucanet (*Aulacorhynchus prasinus*)] were seen at the 800 m site only between September–December. These highland species were not detected at the 400 m site.

Most species were recorded few times during the study or were recorded only once in either the highlands or lowlands. For this reason, they were not included in the correlation analysis. Only the two most abundant species, the Emerald Toucanet and Crested Guan (*Penelope purpurascens*), were included. Both species were partial elevational migrants (*sensu* Loiselle & Blake 1991); some individuals remained in montane forest all year, but other individuals moved to lower elevations after the breeding season (Figs 2 and 3). Both

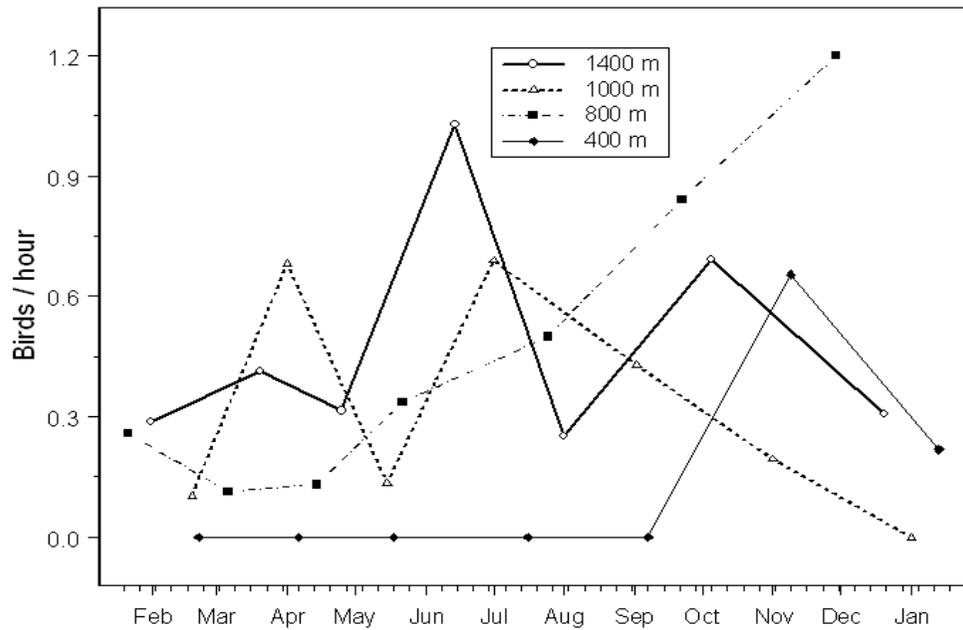


FIG. 2. Temporal abundance of Crested Guans at four different elevations on the Cordillera de Tilarán, Costa Rica (1998–1999).

species peaked in abundance at 1400 m and 1000 m during the breeding season (March–June for the Crested Guan, January–May for the Emerald Toucanet; Stiles & Skutch 1989). After the breeding season, their abundance decreased at those elevations but increased again between July and December. This was probably due to the downward movement of individuals that nested or fledged at higher elevations (Loiselle & Blake 1991, pers. observ.). Abundance of both species dramatically increased after July at 800 and 400 m.

The data did not seem to be significantly influenced by problems of detectability. Although the period of highest abundance at 1400 m and 1000 m occurred during the dry and early rainy seasons (February–June), when it is easier to detect birds because of nesting and displaying behavior as well as good visibility (less fog and rain), few birds were detected during this period at 800 and

400 m. Conversely, migrant abundance increased at 800 and 400 m during the rainy season, when it is more difficult to detect birds because of the rain, and because they are not breeding.

Relationships between movements of birds and fruit abundance. In general, abundance of Crested Guans and Emerald Toucanets did not correlate (positively) with high or low-lipid-protein fruit abundance at any elevation (using total number of fruits, mean number of fruits, or total number of fruiting trees per sampling period as estimators of fruit abundance, and even taking into account possible time lags between fruit fluctuations and bird movements). Only 4 out of 48 correlations were positive and significant, but this could be expected just by chance. Negative significant correlations were found in four cases as well. Specific data about the diet of the Emerald

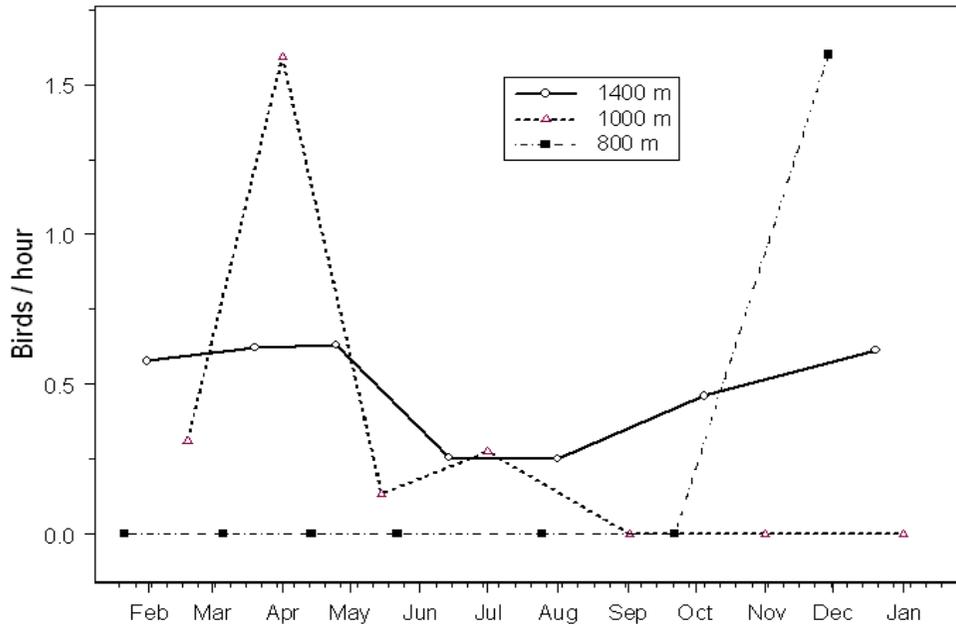


FIG. 3. Temporal abundance of Emerald Toucanet at three different elevations on the Cordillera de Tilarán, Costa Rica (1998–1999).

Toucanet in the Monteverde area is available (see Wheelwright *et al.* 1984, Riley & Smith 1992), and an analysis using only the fruits reported as consumed by Emerald Toucanets yielded a very similar result (i.e., similar number of negative and non-significant positive correlations).

In spite of lacking temporal correlation, some broader patterns could be seen in the data. Both the Crested Guan and Emerald Toucanet were more abundant at 800 m during September–November, overlapping the period of highest fruit production at that elevation (around September for high-lipid-protein fruits, and around November for low-lipid-protein fruits). Crested Guans were also more abundant at 400 m between November and January, coinciding with the period of high abundance of low-lipid-protein fruits. Although the sample size for other bird species is smaller, the movement to the lowlands

for all species coincided with the period of high fruit abundance at those elevations. At 1400 m and 1000 m, the pattern is less clear. Crested Guan and Emerald Toucanet were abundant during the breeding season but showed huge fluctuations. High-lipid-protein fruits were relatively scarce during that period, but low-lipid-protein fruits were very abundant during the second half of the breeding season (April–June).

DISCUSSION

Temporal bird abundance did not correlate with temporal fruit abundance at any elevation, but this might have been caused by problems in the experimental design. The area covered by each 100 m transects seems not to be an accurate representation of temporal patterns of fruit production due to the huge-between sample variance. The pooled

sampling unit of 5000 m² reflects better the number of trees in fruit and crop size observed in the forest during the study period (per. observ.) However, the lack of replication at this spatial resolution does not allow any statistical evaluation on this regard. On the other hand, the broad patterns detected in this study are very similar to the patterns that have been detected in small frugivorous birds (i.e., Loiselle & Blake 1991, Rosselli 1994), suggesting that the data generated are useful and should be discussed.

The broader patterns described in this study suggest that temporal and spatial variation in food abundance partially explains elevational movements in large frugivorous birds. In general, large frugivorous birds seem to follow fruit abundance during the non-breeding season, which has also been observed in studies of small frugivorous birds (see Levey 1988, Loiselle & Blake 1991). Large frugivorous birds do not seem to track fruit abundance during the breeding season, showing the same pattern that as has been reported for small frugivorous birds on the Caribbean slope of Costa Rica (Loiselle & Blake 1991, Rosselli 1994).

Fruit abundance might not be the clue used by the birds to migrate after the breeding season. Temporal abundance of high-lipid-protein fruits is not predictable on an annual basis in the highlands where birds breed. In the Monteverde area, Lauraceae fruit production varies greatly between years and between species, with years of very high production separated by at least one year of very low production (Wheelwright 1986). During low production years, many trees fail to fruit (Wheelwright 1986). In 1998, for example, only 27% of sampled Lauraceae trees had fruits. The high temporal and spatial variance in Lauraceae fruit production suggests that high-lipid-protein fruit abundance is not a proximate cue used by birds to determine when to migrate. Birds decreased in abun-

dance in the highlands in July–August, a period of high abundance of high-lipid-protein fruits at those elevations, supporting this prediction. This pattern has been documented by at least another study (Rosselli 1994). The mechanism employed by elevational migrants to determine when to leave the highlands remains undiscovered. On the other hand, fruit abundance in the lowlands seems quite predictable. The clear peak of abundance by the end and beginning of the year has been reported in other low elevation forests on the Caribbean slope of Costa Rica (See Frankie *et al.* 1974, Opler *et al.* 1988, Levey 1988, Loiselle & Blake 1991), indicating that the pattern is not just local. The decrease in fruit abundance at those elevations after the peak (around January at 800 m, March at 400 m) could be the proximate factor that initiates migration to the highlands.

An alternative factor that birds may use to determine when to migrate is weather changes (Skutch 1967, Stiles 1983). On the Caribbean slope of Costa Rica, elevational migrants breed in the highlands during the period with the least rain, and spend the non-breeding season in the lowlands during the heavy rainy season (Stiles 1983). The data of the present study were collected during an El Niño year. During El Niño years, conditions are warmer, dryer, and sunnier than normal years in Central America; however, the timing of fructification of trees is not affected (Wright *et al.* 1999). If birds are programmed to migrate according to weather changes, it would be expected that they should stay in the highlands as long as the dry season persisted. Monthly precipitation data for 1998, provided by The Alberto M. Brenes Biological Reserve (1000 m site), showed that rains drastically increased in frequency and intensity at that elevation in early June. Both Crested Guans and Emerald Toucanets decreased their abundance at that elevation in early May, about one month before the rains started, suggesting

that heavy rains are not a proximate factor used to determine the initiation of migration.

One factor that could obscure patterns between bird abundance and fruit-abundance at high elevations is partial migration. Data from species with complete elevational migration (species in which most individuals of a population migrate; Loiselle & Blake 1991) showed correlation between bird abundance and fruit abundance in the highlands and lowlands of the Monteverde area (Chaves-Campos *et al.* 2003). In partial elevational migrant species, some individuals are elevational migrants and others are residents at a site (Rabenold and Rabenold 1985, Loiselle & Blake 1991). Crested Guans and Emerald Toucanets showed partial migrations during the study; some individuals stayed in the highlands during 1998, while others did migrate downslope after the breeding season (Figs 2 and 3), masking any possible relationships between fruit abundance and migrant abundance (because the individuals were not tagged). An alternative explanation is that elevational migration is a facultative character expressed only in some individuals according to their energetic demands or their ecological and social requirements, instead of a fix behavior expressed in entire populations (Rabenold and Rabenold 1985). I did not notice any differences in age between migrant and resident individuals (pers. observ.), but I did not measure size or determined sex in these nearly monomorphic species. Therefore, this possibility could not be ruled out.

Future research should focus on both proximate and ultimate factors causing elevational migration in partial elevational migrants. Dimorphic highly-frugivorous species (to avoid practical problems involved in the estimation of arthropod availability) with short elevational range, where some populations migrate and others do not (e.g., manakins; Rosselli 1994, Blake & Loiselle 2002) stand out as potential model species. A

critical factor in the selection of a model species is the amount of information available about its diet. The reason is that different species are adapted to assimilate and metabolize certain nutrients better than others (Levey & Martinez del Rio 2001), and therefore the abundance of particular fruits might be important only for particular species of birds. Potentially informative studies could be those focusing on estimating food abundance, energetic and nutritional demands, physical condition (including parasite infection; Young 1993), and survival to determine the effects of food availability and climate on migrant populations versus populations that do not migrate.

Elevational migration has been notoriously difficult to study and studies on the causes of this phenomenon are few. The new physiological techniques developed to estimate the cost of migration of free-flying birds (Wikelski *et al.* 2003), and the new generation of radio-transmitters designed to estimate energetics in the field (Wikelski *et al.* 2002) are new potential solutions to some of the practical limitations that have discouraged the study of ecological factors promoting elevational migration in the last decade.

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APPENDIX 1. Fruiting trees recorded in Cordillera de Tilarán during 1998–1999. Species marked with an asterisk (*) are reported as consumed by Emerald Toucanets (see text).

ANNONACEAE *Guatteria* sp. A, APOCYNACEAE *Stemmadenia alfari*, ARECACEAE *Enterpe* spp., *Iriartea deltoidea*, *Prestoea* spp, BURSERACEAE *Protium costaricense*, *Protium* spp., CECROPIACEAE *Conssapoa contorta*, *Pouroma bicolor*, CELASTRACEAE *Quetzalia occidentalis*, CHRYSOBALANACEAE *Licania* spp, CLUSIACEAE *Callophyllum brasiliense*, *Chrysocblamys allenii*, *C. glauca*, *Clusia* spp, *Symphonia globulifera*, EUPHORBIACEAE *Croton* spp, *Margaritaria nobilis*, *Sapium pachistachis**, *S.* spp, FLACOURTIACEAE *Lunania mexicana*, *Nectandra* spp, *Ocotea* spp, MALVACEAE *Hampea appendiculata**, MARCGRAVIACEAE *Margravia affinis**, MELASTOMATAACEAE *Conostegia oersterdiana**, *Henriettea tuberculosa*, MELIACEAE *Guarea glabra**, *G. rophalocarpa**, *Trichilia martiana*, MORACEAE *Ficus* spp., *Helicostylis towarensis*, *Pseudolmedia mollis*, *Sorocea* sp., MYRISTICACEAE *Otoba novogranatensis*, *Virola kosbyi*, MYRSINACEAE *Ardisia palmana**, PAPILIONACEAE *Swartzia simplex*, *Swartzia* sp., RHAMNACEAE *Colubrina spinosa**, RUBIACEAE *Elaeagia auriculata*, *E. uspanapensis*, *Guettarda chrysojiflora**, *Guettarda* sp, *Psychotria panamensis**, *Psychotria* sp.*, SABIACEAE *Meliosma glabrata**, SAPINDACEAE *Paullinia* sp.*, SAPOTACEAE *Chrysophyllum hirsutum*, *Pouteria* spp.*, SOLANACEAE *Cestrum megalophyllum**.

APPENDIX 2. Total observations of large fruit-eating elevational migrants in Cordillera de Tilarán, Costa Rica during 1998–1999. Nomenclature follows AOU (1998). Number of recorded individuals in parentheses.

CRACIDAE: Crested Guan *Penelope purpurascens* (53), Black Guan *Chamaepetes unicolor* (9); TROGONIDAE: Lattice-tailed Trogon *Trogon clathratus* (22), Resplendent Quetzal *Pharomachrus mocinno* (2); RAMPHASTIDAE: Emerald Toucanet *Aulacorhynchus prasinus* (38), Yellow-eared Toucanet *Selenidera spectabilis* (4); COTINGIDAE: Bare-necked Umbrellabird *Cephalopterus glabricollis* (21), Three-wattled Bellbird *Procnias tricarunculata* (14).

