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Seasonal differences in rainfall, food availability, and the foraging behavior of Tropical Kingbirds in the southern Amazon Basin

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ABSTRACT. Little is known about the relationship between seasonal food availability and the foraging strategies of insectivorous Neotropical birds. We studied a population of Tropical Kingbirds (*Tyrannus melancholicus*), a primarily insectivorous species, in eastern Bolivia to examine relationships between rainfall, food availability, and foraging strategies throughout the year. Our study site in the southern Amazon Basin was characterized by strong seasonal variation in the abundance of the kingbird's main insect prey (coleopterans and hymenopterans), with reduced abundance during the nonbreeding season which largely overlaps the dry season. Overall, mean search times for insect prey by Tropical Kingbirds during the breeding (96.9 ± 85.6 [SD] sec) and nonbreeding (83.7 ± 91.2 sec) seasons did not differ ($P = 0.23$). However, during the nonbreeding season, kingbird search times were negatively, but nonsignificantly, correlated with coleopteran abundance ($r^2 = 0.43$, $P = 0.16$) and significantly and negatively correlated with hymenopteran abundance ($r^2 = 0.72$, $P = 0.03$). Although insect abundance differed seasonally, kingbird search times did not, perhaps because kingbirds forage on a greater variety of insects during the nonbreeding season or, during the breeding season, kingbird search times may be influenced by the need to monitor and defend nests as well as constraints on the types of prey that can be fed to nestlings. However, the reduced abundance of their primary insect prey and negative relationships between the abundance of those prey and search times during the dry, nonbreeding season suggest that Tropical Kingbirds in southern Amazonia may be food limited, potentially explaining why some migrate and spend that season elsewhere.

RESUMEN. **Diferencias entre temporadas en la lluvia, disponibilidad de comida y el comportamiento de forrajeo de *Tyrannus melancholicus* en el sur de la Cuenca Amazónica**

Existe poca información sobre la relación entre la disponibilidad de comida por temporada y las estrategias de forrajeo de aves insectívoras Neotropicales. Estudiamos una población de *Tyrannus melancholicus*, una especie principalmente insectívora, en el este de Bolivia para examinar la relación entre lluvia, disponibilidad de comida y las estrategias de forrajeo a través del año. Nuestro sitio de estudio en el sur de la Cuenca Amazónica fue caracterizado por una fuerte variación entre temporadas en la abundancia de la comida principal de *T. melancholicus* (coleópteros e himenópteros), con una abundancia mucho menor durante la temporada no-reproductiva, cual generalmente corresponde a la temporada seca. En general, el promedio del tiempo durante la cual los *T. melancholicus* buscaron insectos durante la temporada reproductiva (96.9 ± 85.6 seg) y no-reproductiva (83.7 ± 91.2 seg) no varió significativamente ($P = 0.23$). Sin embargo, durante la temporada no-reproductiva, el tiempo de búsqueda de *T. melancholicus* para comida fue negativamente pero no significativamente correlacionado con la abundancia de coleópteros ($r^2 = 0.43$, $P = 0.16$) y fue significativamente negativamente correlacionado con la abundancia de himenópteros ($r^2 = 0.72$, $P = 0.03$). Aunque la abundancia de insectos varió significativamente entre temporadas, el tiempo de búsqueda de *T. melancholicus* para comida no varió, posiblemente porque forrajean sobre una variedad de insectos mas alta durante la temporada no-reproductiva, o porque durante la temporada reproductiva el tiempo de búsqueda para insectos podría ser influenciada por la necesidad de monitorear y defender al nido. También podría ser que hay limitaciones sobre los tipos de insectos que puede dar a los pichones. Sin embargo, la reducción en la abundancia de los insectos que come y la negativa relación entre la abundancia de esos insectos y el tiempo de búsqueda para comida durante la temporada seca y no-reproductiva sugiere que los *T. melancholicus* en el sur

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de la Amazonía podrían ser limitados por la disponibilidad de comida, posiblemente explicando porque algunos *T. melancholicus* migran para pasar esa temporada en otro lugar.

Key words: Caparú Biological Station, cerrado, diet, insect abundance, *Tyrannus melancholicus*

Food is commonly regarded as a limiting resource for birds, particularly during the winter (Alerstam and Hogstedt 1982, Lovette and Holmes 1995, Brown and Sherry 2006). However, most of what is known about food limitation during the nonbreeding season comes from work in the temperate zone, where the scarcity of food resources, especially insects, during the nonbreeding season is relatively obvious. In the Neotropics, most research on food limitation has focused on overwintering Nearctic-Neotropical migrants (Strong and Sherry 2000, Brown and Sherry 2006, Studds and Marra 2007, Smith and Robertson 2008).

Although arthropod taxa vary in their response to rainfall (Frith and Frith 1985, Wolda 1988, Poulin et al. 1992, Strong and Sherry 2000), the abundance of arthropods that are a major food resource for many tropical birds is often positively linked to rainfall (Pinheiro et al. 2002, Amorim et al. 2009). It is therefore not surprising that the breeding cycles (Gibbs 2007), survival (Dugger et al. 2004), abundance (Faaborg et al. 1984, Tarroux et al. 2003, Herremans 2004, Williams and Middleton 2008), and community diversity (Rompré et al. 2007) of many tropical birds are positively associated with rainfall (but see Karr 1976, Schaefer et al. 2006).

The cerrado of eastern Bolivia, located at the southern edge of the Amazon Basin, is characterized by distinct dry and wet seasons, resulting in strong seasonality of flowering and fruiting (Batalha and Martins 2004) and the abundance of insects (Pinheiro et al. 2002, Amorim et al. 2009). The breeding season of Tropical Kingbirds (*Tyrannus melancholicus*; hereafter "kingbirds") in eastern Bolivia largely overlaps with the wet season, after which some kingbirds migrate and spend the dry, nonbreeding season elsewhere (i.e., kingbirds are partial migrants; Jahn et al. 2010). Kingbirds that do not migrate may experience strong seasonal changes in food supply throughout the year that might influence their foraging behavior. Thus, our objectives were to: (1) describe kingbird diet and seasonal shifts in the abundance of their primary prey (flying arthropods), (2) determine if kingbird foraging rates differed between the breeding and nonbreeding seasons, and (3) determine if search times for food during the nonbreeding season were negatively correlated with prey abundance, which would be evidence of food limitation. Because kingbirds are primarily insectivorous (Fitzpatrick 1980) and insect abundance is likely lower during the drier nonbreeding season, we predicted that search times for insect prey would be longer during the nonbreeding season than the breeding season or that kingbirds would switch to a different foraging strategy (e.g., frugivory).

METHODS

Our study site was the Caparú Biological Station (CBS) located in the Department of Santa Cruz in eastern Bolivia (14°49′S, 61°11′W; 170 m asl). From 2004 to 2007, we studied kingbirds in an area of approximately 700 ha, comprised mostly of cerrado grassland, with a low tree layer 4–6 m in height and dominated by *Curatella americana* (Dilleniaceae). This grassland was bordered to the north, east, and west by humid forest. On the west side was a 50-ha patch of cattle pasture with scattered trees. Kingbirds treated the pasture much like cerrado, foraging from and nesting in isolated trees. We obtained rainfall data from the El Refugio Biological Station located about 9 km north of CBS. Those data match closely the more limited data on rainfall collected at CBS (A. E. Jahn, unpubl. data).

To document the breeding cycle, we searched for nests on study plots the same way we searched for kingbirds (see further). To collect fecal samples, determine breeding condition, and individually mark our study population, we captured kingbirds prior to and throughout the collection of behavioral data, capturing and banding birds from October 2004 to July 2007 using mist nets (12 m and 18 m × 2.6 m, 36-mm and 38-mm mesh). We banded each bird with one numbered aluminum band and up to three celluloid color bands in unique color combinations.

Arthropod sampling. Kingbirds typically forage by aerial sallies (*sensu* Remsen and Robinson 1990), flying out from an exposed perch to catch flying insects in mid-air (Fitzpatrick 1980, Cintra 1997, Gabriel and Pizo 2005). We assessed the availability of aerial prey by sampling flying insects using malaise traps. Malaise traps were made of fine green mesh and were open on four sides (108 × 106 cm per side). At the top and bottom of each trap were collection bottles with 70% alcohol. Ten traps were placed along a 900-m transect at 100-m intervals in cerrado grassland and five traps were similarly placed along a 400-m transect in the cattle pasture, along the border with humid forest. The cerrado transect was surrounded by at least 100 m of cerrado vegetation on all sides. The transect in the cattle pasture was located about 20 m from the edge of the humid forest. Traps were suspended 2–4 m above ground from tree branches or poles and positioned as far as possible from vegetation, thereby sampling arthropods in the open airspace where kingbirds typically forage.

We operated traps from February 2006 to January 2007, except during April and June. Traps were opened at dawn and closed at dusk on five consecutive days per month, although traps were opened for fewer days in March (2 days) and May (4 days). All arthropods were collected from traps each day at closing. Arthropods were identified to order and counted using a dissecting microscope.

To determine possible differences in prey quality between seasons, we measured body length (anterior end of head to distal end of abdomen) of most arthropods captured on the first day of arthropod sampling for each month. All arthropods collected were deposited in the entomological collection of the Museo de Historia Natural Noel Kempff Mercado in Santa Cruz de la Sierra, Bolivia.

Kingbird diet. To determine the diet of kingbirds, we collected fecal samples by holding recently captured individuals in a clean cotton bag for approximately 30 min before banding them. Each fecal sample was stored in 70% alcohol and later examined under a dissecting microscope to identify arthropod remains to order. Because arthropods were in small pieces, determining the number of individuals consumed per taxonomic group was not possible. We were primarily interested in determining presence/absence of prey taxa in each season. Thus, we used the presence or absence of each taxonomic category to calculate the proportion of samples containing each taxon. To obtain an adequate sample size, we analyzed samples collected from the entire banding period (2004–2007).

The use of fecal samples to document bird diets has important limitations that have been reviewed elsewhere (Jenni et al. 1990, Rosenberg and Cooper 1990, Kleintjes and Dahlsten 1992). However, fecal sample analysis is useful for describing basic diet when detailed knowledge of prey hard parts can be used to identify arthropod taxa (Davies 1976, Ralph et al. 1985, Poulin and Lefebvre 1997). We rejected an alternative technique, stomach flushing, because it entails a greater risk of mortality than collecting fecal samples (Moody 1970, Durães and Marini 2003, Carlisle and Holberton 2006).

Kingbird behavior. To ensure an even sampling of kingbirds across our study site, we divided the site into 23 sampling plots ranging in size from 5 to 20 ha and collected data on kingbird behavior in each plot one or two times per month from February 2006 to January 2007, except for June 2006. To find kingbirds, we walked slowly (approximately 4 km/h) across each plot in a zigzag pattern. Data on foraging behavior were collected by following individual kingbirds and speaking into digital voice recorders (Sony ICD-B16), until the focal individual disappeared from sight. We usually made observations during the morning and late afternoon (i.e., after 16:00). Observers regularly worked together to minimize observer error.

We defined search time as the period between consecutive aerial sallies for arthropods. Time was measured using the digital clock on voice recorders. Although binoculars were used, the speed of aerial sallies and the distance between observers and birds usually prevented identification of the type of arthropods taken by kingbirds and whether a particular sally was successful.

We observed approximately three kingbirds, typically including at least one banded individual, per plot visit. From the ratio of banded to unbanded individuals observed on a daily basis, we estimate that our study population consisted of approximately 50 kingbirds.

Kingbirds bred at the site from September to February (earliest date of nesting activity was 14 September 2006, and latest date was

9 February 2007). Because most nests (>85%) were active from October to January, with few active nests in either September or February, we defined the breeding season as being from October to January and the nonbreeding season as all other months.

Statistical analyses. We calculated mean monthly number of captures of the most common arthropods captured per trap-hr and assessed seasonal arthropod availability using a Wilcoxon test. We compared body size of the two orders most commonly consumed by kingbirds (i.e., coleopterans and hymenopterans; see further) between seasons using a Mann-Whitney *U*-test.

We compared kingbird search times for food between seasons using a Mann-Whitney *U*-test. To ensure that we compared foraging behavior, diet, arthropod abundance and arthropod size typical of each season, and because the nonbreeding season is twice as long as the breeding season (i.e., 8 months vs. 4 months), we used data from 3 months that represent the middle of the nonbreeding season (i.e., May–August, excluding June because we did not sample behavior during that month) to 3 months that represent the middle of the breeding season (i.e., October–December) for all comparisons between seasons.

To compare food availability to search time during the nonbreeding season (i.e., February–September 2006), we regressed the mean monthly search time for food by kingbirds against mean monthly captures of arthropods, omitting the months of April and June due to lack of data on arthropod abundance. For comparison of search times between seasons as well as the regression of search time and captures of arthropods during the nonbreeding season, we used data only from kingbirds that were actively foraging by excluding those with search times >8 min and avoiding those primarily engaged in other activities (e.g., preening). To avoid pseudoreplication, we used only the interval between the first two aerial sallies in each observation of a given kingbird. Values are presented as means ± 1 SD.

RESULTS

The wettest months were December and January; rainfall steadily decreased thereafter, with the least precipitation in June and July (Fig. 1). This pattern is typical of the annual rainfall cycle in the region (L. Emmons, unpubl. data). Temperatures varied less than rainfall; mean daily temperature from mid-September to

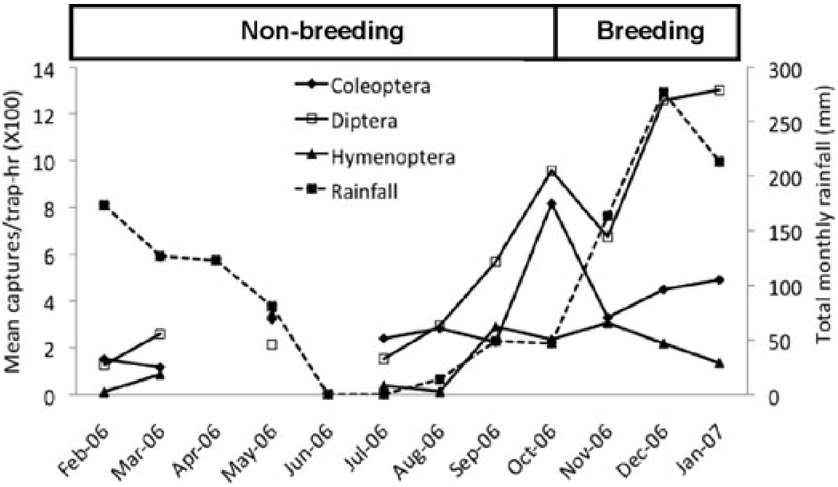

Fig. 1. Abundance of the three most abundant orders of arthropods captured in malaise traps at Caparú Biological Station, Bolivia, from February 2006 to January 2007. Arthropods were not sampled in April and June. Total monthly rainfall in the study area for that period is also shown (L. Emmons, unpub. data). The breeding/nonbreeding seasons of Tropical Kingbirds are indicated by the horizontal bar at the top of the figure.

Table 1. Abundance of the three most common orders of insects in traps at CBS during the breeding and nonbreeding seasons. Numbers represent mean (SD) monthly number of captures trap-hr^{-1}.

Order	Breeding	Nonbreeding	z^a	P
Coleoptera	5.3 (4.1)	2.7 (2.2)	2.3	0.021
Diptera	9.6 (6.3)	2.2 (2.4)	5.2	<0.0001
Hymenoptera	2.5 (2.8)	1.0 (3.0)	3.6	<0.0001

[a] Wilcoxon test.

Table 2. Abundance of arthropod taxa in fecal samples of Tropical Kingbirds during the breeding ($N =$ 24 samples) and nonbreeding ($N = 18$) seasons. Numbers represent mean (SD) monthly number of fecal samples containing each arthropod order.

Order	Breeding	Nonbreeding
Coleoptera	6.0 (1.7)	3.3 (2.5)
Homoptera	0.7 (1.2)	0
Hymenoptera	1.3 (1.2)	0.7 (0.6)
Lepidoptera	0	0.7 (1.2)
Odonata	0	1.0 (1.0)
Orthoptera	0	0.3 (0.6)

mid-February (27.5 ± 13.8° C) was only slightly warmer than during the rest of the year (26.4 ± 9.2° C).

Arthropod sampling. For the cerrado and cattle pasture combined, arthropods in the orders Coleoptera (30% of mean monthly captures of all arthropods), Diptera (44%), and Hymenoptera (14%) were most commonly captured. Other orders captured (Dictyoptera, Hemiptera, Homoptera, Isoptera, and Orthoptera) made up 12% of all captures and were less abundant in both seasons than the three most common orders (A.E. Jahn, unpubl. data).

Coleopterans, dipterans and hymenopterans were all significantly more abundant during the breeding season than the nonbreeding season (Table 1, Fig. 1). The number of coleopterans almost doubled, hymenopterans more than doubled, and dipterans more than quadrupled from the nonbreeding to the breeding season (Table 1).

The mean body length of coleopterans and hymenopterans (the kingbirds main prey, see further) captured in traps did not differ between the breeding (mean = 0.59 ± 0.67 cm, $N =$ 28) and nonbreeding (mean = 0.53 ± 0.51 cm, $N = 29$) seasons ($U = 328.5$, $P = 0.21$). We did not compare body lengths of dipterans between seasons because they were rarely consumed by kingbirds (see later).

Kingbird diet. We collected fecal samples from 18 kingbirds during the breeding season and from 10 kingbirds during the nonbreeding season. Overall, coleopterans were present in 100% of the samples, hymenopterans in 21%, odonatans in 11%, homopterans and lepidopterans in 7% of samples each, and orthopterans in 4%. The two most common orders found in fecal samples (coleopterans and hymenopterans) were also the only two taxa found in fecal samples in both seasons (Table 2).

Kingbird behavior. Although kingbirds at CBS gleaned insects from leaves and consumed fruit, 91% of all observed foraging attempts were aerial sallies for arthropods. Fruit consumption was highest in December, representing 3% of foraging attempts. The number of search time intervals per month ranged from 21 (February) to 96 (March).

Overall, search times of Tropical Kingbirds during the breeding (mean = 96.9 ± 85.6 sec, $N = 27$) and nonbreeding (mean = 83.7 ± 91.2 sec, $N = 117$) seasons did not differ ($U = 1343.0$, $P = 0.23$). However, during the nonbreeding season, we found a negative, but nonsignificant, correlation between search times and coleopteran abundance ($r^2 = 0.43$, $F_{1,4} =$ 3.0, $P = 0.16$; Fig. 2) and, in addition, search times and the abundance of hymenopterans exhibited a significant negative correlation ($r^2 =$ 0.72, $F_{1,4} = 10.1$, $P = 0.03$; Fig. 3).

DISCUSSION

Our results revealed a dramatic decline in rainfall and the availability of insect prey on our study site during the nonbreeding season, but with no corresponding shift to longer search times by foraging Tropical Kingbirds. During the nonbreeding season, we found negative relationships between the abundance of the kingbird's main prey (coleopterans and hymenopterans) and search times by kingbirds, although the pattern was significant only for hymenopterans. These results suggest that kingbirds may experience food limitation at times during the nonbreeding season, possibly explaining why some kingbirds spend the nonbreeding season elsewhere (Jahn et al. 2010).

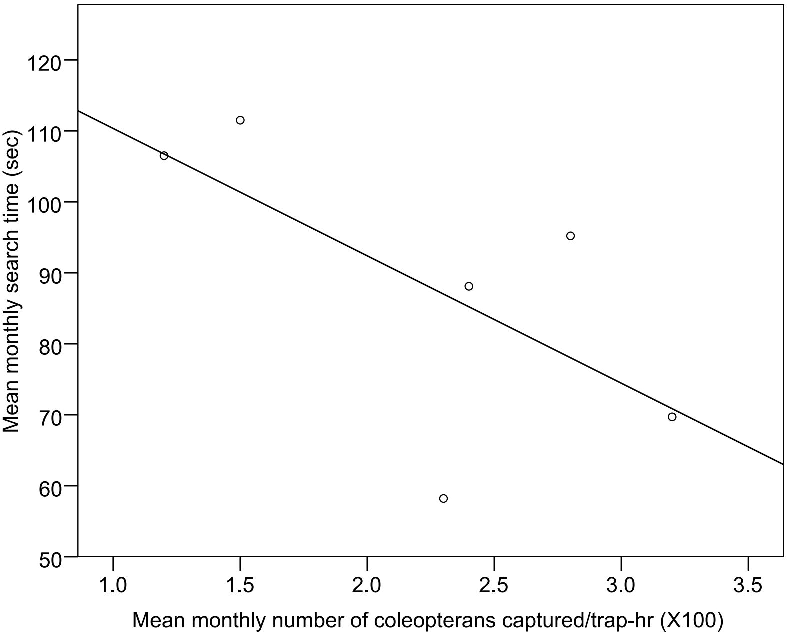

Fig. 2. Mean monthly search time between sallies by Tropical Kingbirds as a function of mean monthly coleopteran abundance during the nonbreeding season (February–September) of 2006. April and June are not included because insect abundance was not sampled during those months. Line represents the regression fit.

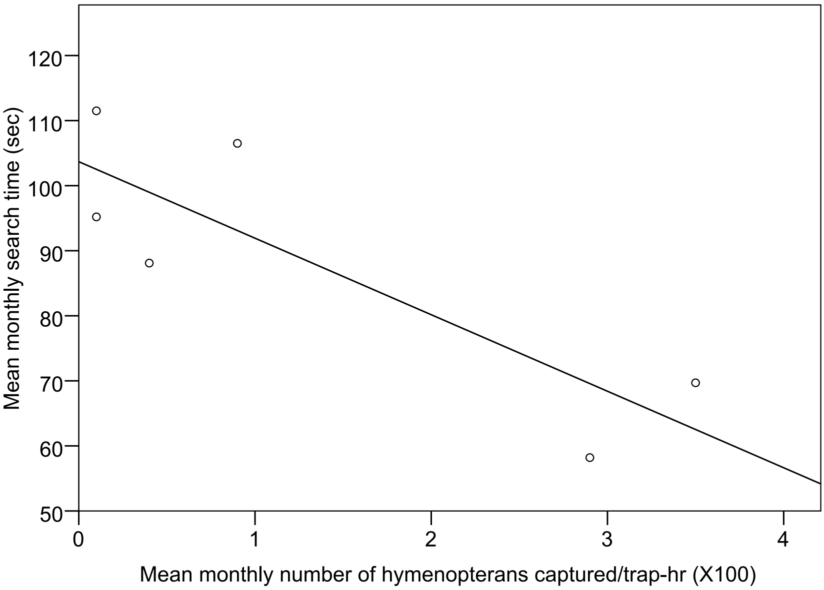

Fig. 3. Mean monthly search time between sallies by Tropical Kingbirds as a function of mean monthly hymenopteran abundance during the nonbreeding season (February–September) of 2006. April and June are not included because insect abundance was not sampled during those months. Line represents the regression fit.

Although search intervals are generally expected to decrease with greater food abundance (Hutto 1990, Lovette and Holmes 1995, Johnson 2000), we found that search times for insect prey by kingbirds did not differ between the breeding and nonbreeding seasons. There are several possible explanations for this.

First, although we found no significant differences in the size of the kingbird's main insect prey (i.e., coleopterans and hymenopterans) between seasons, other physical or nutritional aspects of insect prey, such as thickness of the exoskeleton and chemical composition, might have differed seasonally and affected foraging rates. Second, because avian foraging strategies can be remarkably flexible (e.g., Rotenberry 1980, Hutto 1981), kingbirds may have compensated for lower availability of preferred prey during the nonbreeding season by foraging on a greater variety of insect taxa. In support of this hypothesis, we found more arthropod orders in fecal samples during the nonbreeding season. Similarly, Red-capped Couas (*Coua ruficeps*) are known to forage at higher rates during the dry season than the wet season in Madagascar, even though the abundance of arthropods, their main source of food, is greater during the wet season (Choteau and Fenosoa 2008). In addition, couas appear to consume different types of prey between seasons to track seasonal variation in availability (Choteau and Fenosoa 2008).

Third, given the relatively high levels of nest predation at our study site (>70% of kingbird nesting attempts failed, probably due to predation; A.E. Jahn, unpubl. data), kingbirds may invest a disproportionate amount of time being vigilant for nest predators during the breeding season. Doing this in combination with searching for food could result in longer intervals between sallies for food than during the nonbreeding season. Finally, the seasonal pattern in search time we observed may be due to constraints on the types of prey (e.g., prey taxa or size) that can be fed to nestlings. Being more selective about the types of prey selected during the breeding season could result in longer search times to find those particular prey types.

Given that increasingly dry conditions have been predicted for at least some Neotropical regions (Neelin et al. 2006), understanding the relationships between rainfall, arthropod abundance, and the behavioral ecology of Neotropical insectivorous birds is important. However, as illustrated by our study and others (e.g., Johnston and Holberton 2009), relationships between food—both quantity and quality—and the foraging behavior of insectivorous tropical birds remain unclear. Further experimental, hypothesis-driven studies will be needed to help elucidate these ecological links (Stutchbury and Morton 2001, Vuilleumier 2004).

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