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Diet and Foraging Behavior of Nesting Roadside Hawks in Petén, Guatemala

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ABSTRACT.—In 1993 and 1994, we collected data on the diet and foraging behavior of Roadside Hawks (*Buteo magnirostris*) in primary tropical forest with slash-and-burn farming landscape nearby. We identified 140 prey items brought to nests: 90 in the farming landscape and 50 in the forest. Reptiles (57.1%, mostly lizards) and amphibians (24.3%) were the main prey types delivered to nestlings in both habitats, but size and type of prey differed between nests in the two habitats. Relatively more amphibians and reptiles were delivered to slash-and-burn nests and more mammals and insects to forest nests. In 40 of 44 prey capture attempts, Roadside Hawks utilized the typical *Buteo* technique, searching for prey from a perch and attacking once prey was sighted. In addition, two aerial attacks were directed at a flying and at a perched bird, and hawks walking on the ground twice captured beetles. Of 44 capture attempts, 84% were successful. In the forest, half of 32 attacks were launched from perches protruding above vegetation along a road or in clearings; the other half were launched from perches beneath the forest canopy. These hawks often took advantage of special hunting opportunities: attending army-ant swarms, taking many frogs immediately after rain showers, and catching prey fleeing from fires. Received 14 Feb. 2000, accepted 20 June 2000.

The diet and hunting habits of most tropical raptors are not fully documented. The Roadside Hawk (*Buteo magnirostris*) is a dietary generalist and most published accounts relate a varied diet consisting of amphibians, reptiles, insects, and mammals. Early collectors reported that Roadside Hawk stomach contents contained a variety of organisms including lizards, salamanders, small snakes, caterpillars, spiders, grasshoppers, beetles, mice, and birds (Dickey and van Rossem 1938,

Lowery and Dalquest 1951, Tashian 1953, Haverschmidt 1962). The few quantitative studies of the diet and hunting behavior of the Roadside Hawk were based on small samples. As part of a broader study on the comparative ecology of Roadside Hawks in primary forest and in slash-and-burn farming habitats, we collected data on prey brought to eight nests in these two habitats and on foraging behavior.

METHODS

Our two study areas were 25 km apart and located in and adjacent to Tikal National Park (17° 11' N, 89° 48' W), Guatemala. The 576 km² park supports mid-height to tall sub-perennial tropical forest (Pennington and Sarukhan 1968) that is mostly unlogged, primary forest. Forest vegetation varies as a continuum along a topographic and soil-type gradient from well drained to poorly drained (Schulze and Whitacre 1999). Topography is gently rolling, mostly 200–350 m in elevation. Mean annual precipitation is 1350 mm with a pronounced dry season from February to May. There are no permanent streams in the area; during the dry season, surface water is found in scattered water holes. Slash-and-burn farming was 10 km south of the park within the buffer zone of the Maya Biosphere Reserve. This habitat mosaic contained disturbed fragments of primary forest, crop fields [mostly corn (*Zea mays*)], pastures, clear-cuts, bracken fern (*Pteridium aquilinum*) monocultures, and extensive areas in various stages of succession from low brush to 10 m second-growth. Less than 10% of the study area was covered by mature forest remnants.

During 1994, T.P. and three field assistants studied Roadside Hawk food habits at eight nests in the two study areas. We made observations from blinds on the ground and platforms in trees at least 30 m from nest trees using 10× binoculars and spotting scopes. Nests were observed from dawn to dusk (13 h) to monitor birds during all daylight hours, with a change of observers at mid-day. We recorded prey type and size at five slash-and-burn nest sites observed for 243 hours and at three forest nest sites observed for 151 hours, April–June 1994. We identified prey items as precisely as possible, often to genus, estimated their length, and placed them in the following size classes: tiny (≤ 5 cm: insects and the smallest lizards), small (6–25 cm: most lizards and frogs), and medium (> 25 cm: mostly

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mammals and snakes). We used G-tests to compare prey types and sizes in the diet in the two habitats.

In 1993 and 1994, we collected data on foraging behavior during nest observations, nest searches, and monitoring nesting pairs. We also observed foraging bouts whenever we observed a Roadside Hawk attacking prey. For each foraging attempt we recorded the date, time, habitat (edge, continuous forest, farming landscape), hunting technique, perch height, prey location, and success or failure of the attack. All statistical tests were performed using the SAS System version 6 (SAS Institute, Inc. 1989). Mean values are presented with standard deviations.

RESULTS AND DISCUSSION

Hunting behavior.—Roadside Hawks used still-hunting (hunting from a perch and dropping down to capture a prey item) 40 of 44 foraging attempts (91%) and ground-hunting (walking on the ground and seizing prey in the talons) twice (4.5%). The hawks made two aerial attacks on birds (4.5%). Thirty-seven of the 44 foraging attempts (84%) were successful. Both ground-hunting attempts were successful, yielding beetles (Coleoptera), and one of the two aerial attempts was successful, yielding a Black-cowled Oriole (*Icterus pros-themelas*). Of the 40 still-hunting attempts, 34 were successful (85%). We could not compare success in the two habitats because only eight foraging attempts were observed in the farming landscape.

The mean height of the perch from which still-hunting attacks were launched was 6.4 ± 4.5 m (range = 1–17 m). The mean perch height of the eight still-hunting attempts in the slash-and-burn landscape was 8.9 ± 4.3 m and all attacks originated from perches taller than the surrounding vegetation. In the primary forest, half of the observed attacks (16 of 32) were launched from perches (trees) protruding above areas of lower forest canopy, either along a dirt road ($n = 11$) or an artificial clearing ($n = 5$). Four Roadside Hawks launched hunts from perches about 5 m high along forest edges and successfully captured adult cicadas on tree trunks or other vegetation 1–2.5 m above the ground. We watched one banded male descend from a 2.5 m high perch along a clearing edge, capture a tarantula at the opening of its burrow, remove the spider's legs, and consume it there.

Sixteen of the 32 still-hunting hawks hunted from perches beneath the forest canopy. On

TABLE 1. Prey delivered to nests by Roadside Hawks in the two study areas in Petén, Guatemala in 1994.

Prey type	Primary forest	Slash-and-burn
Reptiles	23	57
<i>Sceloporus</i> spp.	0	4
<i>Anolis</i> spp.	9	0
<i>Corythophanes</i> spp.	0	1
Unidentified lizards	11	51
Skinks	2	0
Snakes	1	1
Amphibians	9	25
Frog	9	24
Toad	0	1
Mammals	9	2
<i>Heteromys</i> spp.	4	0
<i>Ototylomys</i> spp.	0	2
Unidentified rats	2	0
<i>Sciurus deppei</i>	1	0
Bats	2	0
Birds	0	2
Insects	9	4
Cicadas	7	1
Grasshoppers	2	2
Caterpillars	0	1
Total	50	90

13 occasions these hawks hunted from perches 1–15 m from the ground where they hunted insects ($n = 7$) fleeing from army ant swarms (including *Eciton* spp.) and lizards ($n = 6$) on the ground or in vegetation requiring a shallow angle of descent. In the other three, Roadside Hawks dropped steeply from tree limbs averaging 14.8 ± 2.3 m above ground and seized lizards or cicadas from the perch tree bole ($n = 2$) or neighboring tree bole ($n = 1$) about 5 m below their perch.

Dickey and van Rossem (1938) observed a Roadside Hawk snatch a Blue Honeycreeper (*Cyanerpes cyaneus*) from a feeding flock. We observed an unsuccessful aerial pursuit of a Squirrel Cuckoo (*Piaya cayana*) through low secondary vegetation about 1–2 m in height (Panasci 1995). The other aerial attack by a Roadside Hawk was the successful capture of a Black-cowled Oriole (Panasci 1995).

Diet.—We identified 140 prey items, 90 at slash-and-burn nests and 50 at forest nests (Table 1). Reptiles comprised 57.1% of the nestling diet overall and 46% of prey at forest nests and 63.3% of the prey at the slash-and-burn nests. Amphibians were the second most

frequent prey, making up 24.3% of nestling diets overall. Insects (especially cicadas and grasshoppers) comprised 9.3% of prey items, mammals 7.9% (with 1 squirrel, 8 other rodents, and 2 bats), and birds 1.4%. Reptiles and amphibians comprised 81.4% of the prey delivered to all nests. Lizards, frogs, and insects typically were delivered to nests intact, but most mammals were decapitated or partially eaten before delivery. Birds were plucked before they were brought to the prey exchange site. Prey types delivered to nests differed significantly with habitat (G-test: $G = 15.11$, 3 df, $P = 0.002$), as did prey size (G-test: $G = 19.10$, 2 df, $P = 0.001$). Relatively more mammals and insects were delivered to forest nests, and more amphibians and reptiles to slash-and-burn nests (Table 1).

In the slash-and-burn habitat, 4 of 90 prey items were classified as tiny, 81 as small, and five as medium. In the forest plot, prey items did not fall predominantly in one size category and were distributed as follows: 11 tiny, 29 small, and 10 medium. Most prey items were in the small size category because it included most of the lizards. Lizards ($n = 78$), made up 55% of the prey items delivered to nests in both habitats (Table 1). *Anolis* lizards, which are mainly arboreal and occur in the forest interior, were identified only at nests in the primary forest, whereas *Sceloporus* lizards (mainly terrestrial and found in open habitats) were identified only at nests in the farming landscape. We did not estimate prey biomass, but doing so would probably reduce the importance of insects and increase the importance of mammals.

Various authors have characterized Roadside Hawks as opportunistic hunters (Dickey and Van Rossem 1938, Robinson 1994). We observed these hawks to opportunistically exploit prey types during brief periods of high availability or vulnerability. For example, after a night of heavy rain, we watched a male Roadside Hawk catch eight frogs at a newly refilled waterhole, and other Roadside Hawks hunted insects fleeing ant swarms. In two cases, Roadside Hawks caught a small rodent (from an 8 m perch) and a grasshopper (from a 3 m perch) that were fleeing fires in the slash-and-burn farming landscape.

Comments in the literature usually characterize Roadside Hawks as dietary generalists

(Robinson 1994). In Argentina, based on 45 prey items, Beltzer (1990) documented a diet of insects and spiders (78%), frogs and toads (11%), fishes (7%), and rodents (4%), with one species of grasshopper comprising 51% of the diet. In one Argentinean study (Massoia 1988, data provided by A. G. Di Giacomo, pers. comm.) prey remains (guinea pig, *Cavia aperea*; thick-tailed opossum, *Lutreolina crassicaudata*; European hare, *Lepus capensis*; large opossum, *Didelphis albiventris*) were erroneously attributed to Roadside Hawks and probably were left by a larger raptor. At six nests studied at artificial forest openings in Guatemala, Vásquez and Reyes (1992) identified 52 prey items as 37% reptiles, 29% rodents, 15% birds, 17% insects, and 2% frogs; 1 item was unidentified.

The hunting behavior of Roadside Hawks from perches or occasional ground-walking and aerial attacks was typically buteonine. Johnson and Peeters (1963) characterized the Roadside Hawk as *Accipiter* like and raised the question of whether this *Buteo* might participate in an unfilled *Accipiter* niche. We found no evidence of this, and records of birds in the diet are few.

This species is able to exploit a wide range of prey items and to successfully use many human-modified habitats. The dietary difference in the two habitats may reflect differences in the available prey base, but we have no data on the relative abundance of these prey types in the forest and farming habitats.

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Nutrient Preferences of Brazilian Hummingbirds

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ABSTRACT.—The Stripe-tailed Hummingbird (*Eupherusa eximia*) prefers nectar that is highly supplemented in both vitamins and minerals, when offered the choice of no, low, or high supplemented nectar. We tested the responses of hummingbirds in southern Brazil to four solutions: nectar, nectar supplemented with vitamins, nectar supplemented with minerals, and water with both vitamins and minerals added. Hummingbirds spent less time at and made fewer visits to the supplemented water than to the different nectar solutions, suggesting that nutrients alone are not enough to attract birds. One of eight species, the Violet-capped Woodnymph (*Thalurania glaucopis*), visited the mineral supplemented nectar more often than both nectars and one unidentified hermit species (*Phaethornis* sp.) visited the mineral treatment more than straight nectar. The Black-throated Mango (*Anthracothorax nigricollis*) made more visits to the vitamin supplemented nectar than to mineral-rich nectar whereas the Glittering-bellied Emerald (*Chlorostilbon aureoventris*) avoided the vitamin treatment, preferring straight nectar. A gen-

eral pattern of preference was not found among species. *Received 11 Feb. 2000, accepted 23 Oct. 2000.*

The foraging strategies and energetic requirements of hummingbirds are well documented and it is generally accepted that they are energy limited (Montgomerie et al. 1984, Brice and Grau 1991). Foraging decisions of hummingbirds may be influenced by numerous factors, such as the energetic qualities of nectar (Montgomerie et al. 1984, Houston and Krakauer 1993), digestibility (Diamond et al. 1986), competition (Pimm et al. 1985, Tiebout 1993), predation risk (Lima 1991), and sexual dimorphism in bill morphology (Temeles and Roberts 1993). Abiotic factors might play important roles. For instance, ambient temperature affects thermoregulation and in turn, diuresis and the need to replace lost electrolytes (Calder 1979). Because the amount of energy in nectar is easily manipulated and quantified, most researchers working on the foraging ecology of hummingbirds have focused on the

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energetic benefits of different foraging strategies.

The importance of products other than carbohydrates in nectar as possible constraints on hummingbird foraging strategies has received little attention. Hummingbirds are believed to require various proteins, minerals, and lipids in their diet (Brice and Grau 1989, 1991). Nectar of specific flowers may contain all or a mixture of amino acids, proteins, lipids, antioxidants (including vitamin C), organic acids, alkaloids, glycosides, allantoin and allantoic acid, sodium, potassium, chloride, and other substances (Ziegler et al. 1964, Baker and Baker 1982, Hiebert and Calder 1983, Galetto 1995). Amino acids are present only in trace amounts. Adding them to nectar does not increase its attractiveness to hummingbirds in laboratory experiments, leading most researchers to agree that the birds use insects to complete their diet and obtain their amino acids (Hainsworth and Wolf 1976, Brice and Grau 1991, Stiles 1995).

In one of the first studies to examine the influence of nutrients on the foraging behavior of hummingbirds, Carroll and Moore (1993) showed that Stripe-tailed Hummingbirds (*Eupherusa eximia*) were significantly more attracted to artificial feeders that contained nectar supplemented with high levels of vitamins and minerals than to feeders with low levels or no additional vitamins and minerals. However, because the vitamins and minerals were presented in combination, it was unclear whether the hummingbirds were attracted by the high concentration of only one of the components (vitamins or minerals), or by an additional flavor created by the supplements. Our objective was to test the attractiveness of vitamin and mineral supplements separately in high concentration in nectar and together in water.

METHODS

We conducted this study from 7–13 January 1997 in Intervalas Park (24° 16' S, 48° 24' W, elevation about 1000 m), São Paulo State, Brazil, in the Atlantic rain forest. We observed and monitored ten species of hummingbirds at our artificial feeders: female Amethyst Woodstar (*Calliphlox amethystina*), Black Jacobin (*Melanotrochilus fuscus*), female Black-throated Mango (*Anthracothorax nigricollis*), male Violet-capped Woodnymph (*Thalurania glaucopis*), Glittering-bellied Emerald (*Chlorostilbon aureoventris*),

TABLE 1. Vitamin and mineral concentration used in experiments on nutrient preferences by Brazilian hummingbirds.

Vitamins	Quantity (/l)	Minerals	Quantity (/l)
A	1760 I.U.	Calcium	130 mg
D3	264 I.U.	Sodium	60 mg
E	2.84 I.U.	Zinc	2.5 mg
C	88 mg	Manganese	1.5 mg
B1	0.88 mg	Copper	0.65 mg
B2	1.76 mg	Iodine	0.015 mg
B6	2 mg		
B12	0.0044 mg		
K	0.44 mg		
d-Pentonic acid	4.8 mg		
Niacinamide	17.6 mg		
Choline	4.4 mg		

Sombre Hummingbird (*Aphantochroa cirrhochloris*), Versicolored Emerald (*Amazilia versicolor*), White-throated Hummingbird (*Leucochloris albicollis*), White-vented Violetear (*Colibri serrirostris*), and one hermit species (*Phaethornis* sp.) that could not be positively identified.

We suspended four 300 ml hummingbird feeders 2 m apart on a horizontal string 1.6 m above the ground in an open area, making it difficult for the birds to defend territories around our feeders. To control the position of hummingbirds while drinking, we blocked two of the three feeding apertures. We used liquid avian vitamins (Avitron; Lambert Kay[®]) and a mineral supplement (Avimin; Lambert Kay[®]) to create the different treatments.

Feeders were washed daily with mild soap, repeatedly rinsed with filtered water, and filled with 150 ml of one of the solutions. We used filtered water and cane sugar (5:1 by volume) as a basic nectar solution (control) and added either 6 drops of the vitamin or 1.5 ml of the mineral supplement (Table 1). To determine if the supplements alone were enough to attract hummingbirds, we filled one of the feeders with filtered water and the same concentrations of both vitamin and mineral supplements as we used with the nectar.

We randomly assigned feeder positions on the string and their contents each morning. The feeders were suspended at least one hour before the trials began to allow the hummingbirds to sample each feeder. We recorded the number and duration of visits of each species five times per day at 09:00, 11:00, 13:00, 15:00, and 17:00 CST. The four feeders were successively monitored during 5 min observation periods for a total of 700 min of observations. Although we observed ten species at our feeders, only eight made enough visits to allow statistical analysis. Therefore, we excluded Amethyst Woodstar and Black Jacobin from the analysis. We observed 580 min of feeding activity at the feeders.

We used analysis of variance (ANOVA) with duration of visit (log-transformed to satisfy the assumption

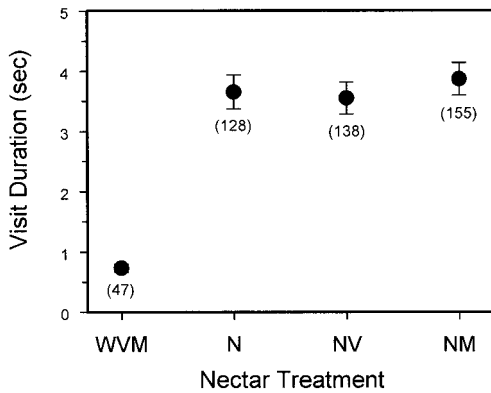


FIG. 1. Mean (solid circle) and standard error (vertical bars) of visit duration of Brazilian hummingbirds at four different nectar treatments; WVM: water supplemented with vitamins and minerals, N: nectar, NV: nectar supplemented with vitamins, and NM: nectar supplemented with minerals.

of normality) as the dependent variable and treatment, species, weather (no rain, light rain, heavy rain), and wind (none, mild, strong) as the independent variables to determine whether the duration of visits to feeders was influenced by supplementation with vitamins and minerals. Only independent variables that contributed to the variance were kept in the overall model; therefore, feeders ($F_{3,434} = 0.84$, $P > 0.05$) and their position ($F_{3,434} = 0.98$, $P > 0.05$) were discarded. We tested for preferences in the number of visits to the different nectar treatments for all species combined using χ^2 analysis. We used a contingency table to verify species effect. Because there was a species effect, additional χ^2 tests were performed on each species. We performed pairwise comparisons (using Tukey's method of correcting for multiple comparisons yielding confidence intervals) for each species that visited the nectar feeders unequally to find actual preferences. We set $P < 0.05$ for all tests, which were performed using S-Plus 4.5, Mathsoft© software on a PC.

RESULTS

We recorded 470 feeding bouts during the 580 min of feeding observations, only 5 of these bouts were interrupted by another bird at the feeder. The model for the duration of visits to the different solutions was highly significant ($F_{34,434} = 6.0$, $P < 0.001$) and duration varied significantly according to treatment ($F_{3,434} = 42.3$, $P < 0.001$) but this difference was attributed to the vitamin and mineral supplemented water treatment that the hummingbirds rejected (Fig. 1). Once we removed this treatment from the analysis, the model was still significant ($F_{26,395} = 2.3$, $P < 0.001$) but

there was no significant effect of nectar treatment on visit duration ($F_{2,395} = 0.6$, $P > 0.05$). Duration of visit did not differ among the different species both with and without the water treatment included in the model ($F_{21,434} = 1.2$, $P > 0.05$; $F_{14,395} = 1.4$, $P > 0.05$; respectively).

The hummingbirds did not visit the different treatments with the same frequency ($\chi^2_3 = 59.0$, $P < 0.001$) and made fewer visits to the vitamin and mineral supplemented water. Once we removed the water treatment, difference in the number of visits per nectar treatment remained significant ($\chi^2_2 = 17.1$, $P < 0.001$). The nectar treatments were visited differently by the eight species ($\chi^2_{14} = 51.3$, $P < 0.001$). Therefore, each was tested for preferences (Table 2). One species (the hermit) visited the mineral-supplemented nectar significantly more often than unsupplemented nectar; whereas male Violet-Capped Woodnymph preferred the mineral-rich nectar over both other nectar treatments. In addition, female Black-throated Mangos visited the vitamin supplemented nectar significantly more often than the mineral supplemented nectar. Glittering-bellied Emeralds made more visits to the unsupplemented nectar than to the vitamin supplemented nectar. Although Sombre Hummingbird visited the nectar treatments unequally, it showed no significant preference. No other species exhibited any preference for any of the nectar treatments (Table 2).

DISCUSSION

Carroll and Moore (1993) found that Stripe-tailed Hummingbirds preferred highly supplemented (in both vitamins and minerals) nectar over low supplements and unsupplemented nectar. They attributed the preference to the high concentration of vitamins, but they also discussed the possibility that minerals and/or their flavor were the attractant. We found that vitamin and mineral supplemented water was less attractive to the hummingbirds than any of the nectar treatments, suggesting that the intrinsic value of the added nutrients, or their flavor, is not enough by itself to attract the birds.

Our inability to identify the sex for species without morphological sexual dimorphism is a drawback because gender could be an important variable determining condition and

TABLE 2. Number of visits made by each of eight species of Brazilian hummingbirds to artificial feeders containing different nectar solutions^a. Differences among the treatments within each species were examined using χ^2 tests and when significant, pairwise comparisons using Tukey's correcting method for multiple comparisons, were performed to find preferences.

Species	N	NV	NM	<i>P</i>	<i>P</i> for the pairwise comparison
Versicolored Emerald	26	39	41	>0.05	
Black-throated Mango	21	35	19	<0.05	N-NV: >0.05 N-NM: >0.05 NV-NM: <0.05
Sombre Hummingbird	6	7	16	<0.05	N-NV: >0.05 N-NM: >0.05 NV-NM: >0.05
Glittering-bellied Emerald	21	5	13	<0.01	N-NV: <0.01 N-NM: >0.05 NV-NM: >0.05
White-vented Violetear	14	10	4	>0.05	
White-throated Hummingbird	16	13	5	>0.05	
Violet-capped Woodnymph	21	24	44	<0.01	N-NV: >0.05 N-NM: <0.01 NV-NM: <0.01
Hermit	3	5	13	<0.02	N-NV: >0.05 N-NM: <0.05 NV-NM: >0.05

^a N: nectar, NV: nectar supplemented with vitamins, and NM: nectar supplemented with minerals.

consequently the choice of supplements. Barclay (1994) suggested that calcium is a major constraint on reproduction in bats and birds, and that the small clutches of hummingbirds are explained by their low calcium diet. Because nectar is a poor source of minerals, breeding females might forage differently than males; indeed, breeding female hummingbirds spend more time hunting insects than conspecific males (Stiles 1995). Insects are a good source of proteins and electrolytes, especially potassium (Hiebert and Calder 1983); their consumption could help females meet the demands of raising young (Stiles 1995). But insects are generally low in calcium and there are observations of hummingbirds, mostly females, eating mineral-rich compounds such as soil, wood ashes, and sand (Des Lauriers 1994, Adam and Des Lauriers 1998).

All the species we observed during our experiments were potentially breeding (Grantsau 1989) and females could have been calcium/mineral stressed. If so, then we would predict a preference for the mineral supplemented nectar treatment. Indeed, potential female hermits visited the mineral treatment significantly more often than nectar. Coincidentally, we found a female hermit nesting less than 300

m from our feeders. However, we cannot confirm whether we observed that nesting female or not because neither the species nor the sex could be determined and none of the individuals was marked. Male Violet-capped Woodnymph preferred the mineral treatment and female Black-throated Mangos visited the vitamin supplemented nectar significantly more often than the mineral supplemented nectar, similar to the preference of Stripe-tailed Hummingbirds observed by Carroll and Moore (1993).

Although our results are consistent with the breeding female/mineral stress hypothesis or a general preference for supplemented nectar, our results were mixed. Glittering-bellied Emeralds made significantly fewer visits to the vitamin supplemented nectar, preferring the nectar without any supplements. Three species exhibited no preference among the three sources of nectars in terms of the number or duration of visits. Our findings are unlikely to result from competition; we recorded few competitive interactions and small species such as Glittering-bellied Emerald had access to all supplements. The simultaneous observation of three to four birds per species in the vicinity of our feeders as well as the number and rate of visits per day suggest that we did

not record only the preferences of a single bird of each species. However, because the birds were not marked we might have made multiple observations of some birds. This study highlights the need for further research on the requirements for products other than carbohydrates in the diet of hummingbirds. Such products might play a much larger role than is generally assumed in hummingbird foraging strategies. The ecological (e.g., temperature) and physiological (e.g., reproductive status) constraints affecting those requirements also need to be addressed.

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