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Nestling food of the congeneric and sympatric Rusty-margined and Social flycatchers

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ABSTRACT. We studied the food of nestling Rusty-margined (*Myozetetes cayanensis*) and Social flycatchers (*M. similis*) in 1998 and 1999 at Barro Colorado Island, Panama. Food samples were taken from nestlings by fecal analysis and the neck-collar method. In both species most food items were beetles, winged ants, dragonflies, spiders, and seeds of *Miconia* spp. Water animals (mainly backswimmers, freshwater snails, and dragonfly larvae) constituted 7.8%–13.5% of animal prey. The nestlings of the Social Flycatcher received significantly more flying insects, while the proportion of fruits and seeds was significantly higher in the diet of Rusty-margined Flycatcher nestlings. Length of animal prey varied from 4–25 mm in the Rusty-margined Flycatcher and 2–50 mm in the Social Flycatcher, and the length of fruits and seeds were 4–11 mm and 2–19 mm, respectively. The average length of animal food was larger in the Rusty-margined Flycatcher despite its slightly smaller size. The number of broods with nestlings or fledglings present in the study area was positively correlated with the abundance of fruits in the Social Flycatcher.

SINOPSIS. **Alimento de las crías de congéneres y simpatricas *Myozetetes cayanensis* y *M. similis***
Estudiamos el alimento ofrecido a las crías de *Myozetetes cayanensis* y de *M. similis* en 1998 y 1999 a lo largo de las playas de la isla de Barro Colorado en Panamá. Las muestras de alimento se obtuvieron por análisis de heces fecales y por el método del collar-cuello. La mayor porción de la comida de ambas especies fueron Coleópteros, Hymenopteros, Odonatos, Arácnidos y semillas de *Miconia* sp. Animales acuáticos (primcipalmente Notonectidae, Gasterópodos y larvas de Odonata) constituyeron del 7.8% al 13% de presa animal. Los pichones de *M. similis* recibieron significativamente más insectos voladores, mientras que la proporción de frutas y semillas fué significativamente mayor en la dieta de *Myozetetes cayanensis.* El largo de las presas animales varió entre 4 y 25 mm en *Myozetetes cayanensis* y entre 2 y 50 mm en *M. similis*, mientras que el largo de frutas y semillas varió entre 4 y 11 mm y entre 2 y 190 mm respectivamente. El promedio de largo del alimento animal fué mayor en *Myozetetes cayanensis* aunque entre ambas especies tiene un tamano corporal menor. El número de camadas cop pichanes a volantones de *Myozetetes similis* presentes en el área de estidio fué correlacionado positivamente con la abundancia de frutos.

Key words: food, *Myozetetes cayanensis*, *Myozetetes similis*, nestling, sympatry

There are several hypotheses to explain the high avian species diversity in the tropics. One hypothesis suggests that increased resource diversity or structural complexity of habitat may maintain diversity (MacArthur and MacArthur 1961; MacArthur 1969; Orians 1969). Another hypothesis suggests that increased specialization maintains diversity (Klopfer and MacArthur 1961; May and MacArthur 1972). Conversely, an additional hypothesis proposes that increased ecological overlap allows more species to live in a given area. Ecological overlap is usually measured in terms of items in the diet, period of activity, microhabitat used for foraging, feeding method, or combinations of these. The particular dimensions of the niche included in any study depend partly on what is easy to measure and partly on inituitive notions about important niche dimensions (Ricklefs 1979).

The aim of our study was to determine food composition and differences in diets of two closely related species of tropical birds co-existing in the same habitat. All nests of both species were found in the same habitat along the shores of Barro Colorado Island. Nests of the Rusty-margined Flycatcher were frequently near nests of Social Flycatchers (Dyrcz 2002), and both species bred at the same time of the year. Our research focused on food of nestlings, which in passerines, as a rule, does not markedly differ in composition from that of adults (Morehouse and Brewer 1968; Royama 1970; Bryant 1973; Dyrcz and Flinks 1995). General information on Social Flycatcher diet is available in Skutch (1960).

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Table 1. Number of analysed items (no. of nests in parentheses).

	Rusty-margined Flycatcher	Social Flycatcher
Nestling droppings	107 (11)	268 (32)
Animals and plants in droppings	808	2304
Samples taken by the neck-collar method	45 (7)	159 (30)
Animals and plants in neck-collar samples	164	423

STUDY AREA AND METHODS

The study was done in March–April 1998 and March–May 1999 on Barro Colorado Island, Panama. It is an island of 1642 ha with the status of nature reserve in the artificial Lake Gatun, created during the building of the Panama Canal. It is mainly covered with tropical moist forest, both old growth and secondary. Nearly all pairs of flycatchers nest along the shore (about 50.7 km), avoiding the forest interior (Dyrcz 2002). We used a small motorboat to find nests and take samples. Food samples were taken from nestlings by fecal analysis and the neck-collar method (Kluijver 1933). After collection, fresh droppings were conserved in the field with a small amount of salt and later refrigerated. For examination, the feces were prepared by soaking in water for two hours and analysed under a binocular microscope at 20× magnification. Based on the animal, fruit, and seed remains, the number of prey individuals was calculated (Flinks and Pfeifer 1987). Feces analysis has been validated by Davies (1976, 1977a,b), Ralph et al. (1985), and Jenni et al. (1989). The neck-collar method does not harm the nestling if applied properly (Bogucki 1964).

The length (or diameter in the case of round fruits) of prey items, as an indicator of their size, was determined based on samples obtained through the neck-collar method, in which animals, fruits, and seeds usually remained whole. Fragmented items were omitted. While measuring the body length of invertebrates, legs and antennae were not taken into account (Table 1). Both methods have some weaknesses and could be considered complementary. In fecal samples, the prey with hard chitinous parts are better preserved than other taxa. In throat samples, small items can be swallowed in spite of the neck-collar and large items can be spat out.

Resemblance between different samples was assessed using the Renkonen (1938) index. In the case of bird assemblages, the value 50–70% of the Renkonen index shows clear similarity, while more than 70% may indicate belonging to the same community (Tomiałojć 1970). Taxonomy of insects followed Richards and Davies (1977) and plants that of Crosby (1980).

Weekly censuses of seed-trap data were acquired from J. Wright. From these data, we calculated the abundance of fruits and seeds available to the birds. Because the two flycatchers suffered high nest losses (amounting to 80%; Dyrcz 2002), correlations used only the potential number of nestlings and fledglings (up to the 7^{th} day after fledging), i.e., the number if all the broods commenced were successful. We assumed that eggs are laid at 1-d intervals, the period of incubation lasts 15 d, and the nestling period is 20 d.

In χ^2 tests, Yates' correction was used in 2 × 2 contingency tables.

RESULTS

Food composition. *Rusty-margined Flycatcher.* Nestling diet consisted of both animals (mainly insects) and plants (fruits and seeds of woody plants; Tables 2, 3). The most common food items were beetles, spiders, winged ants, dragonflies, and seeds of *Miconia* spp. Aquatic animals (mainly backswimmers, freshwater snails, and dragonfly larvae) constituted 9.6% (droppings) and 7.8% (neck-collars) of the animal prey. Flying insects (mainly dragonflies, true flies, butterflies, winged ants, and bees) caught mostly in the air were an important part of the prey (30.9% in feces and 29.7% in neck-collars). The remaining prey was mostly plants. Fruit and seeds made up 34.3% (feces) and 61.0% (neck collars) of items.

The length of animal prey ranged between 4–25 mm and, that of fruits and seeds 4–11 mm (neck-collars). Animals 8–12 mm and fruits and seeds 4–7 mm in length composed

Table 2. Animal food in the diet of Rusty-margined Flycatcher nestlings.

Taxon	Fecal analysis		Neck collars	
	N (%)	Frequency	*N* (%)	Frequency
Mollusks (Gastropoda)	13 (2.4)	35.7	2 (3.1)	6.7
Ephemeroptera, larva	—	—	2 (3.1)	6.7
Spiders (Araneae)	99 (18.6)	85.7	11 (17.2)	40.0
Dragonflies (Odonata), larva	10 (1.9)	39.3	1 (1.6)	6.7
Dragonflies (Odonata), imago	26 (4.9)	64.3	7 (10.9)	20.0
Orthoptera	24 (4.5)	42.9	5 (7.8)	26.7
Cockroaches (Blattidae)	7 (1.3)	10.7	—	—
Mantids (Mantidae)	1 (0.2)	3.6	—	—
Termites (Isoptera)	5 (0.9)	3.6	—	—
Homoptera	10 (1.9)	32.1	—	—
Backswimmers (Notonectidae)	28 (5.3)	57.1	—	—
Other true bugs (Heteroptera)	25 (4.7)	42.9	3 (4.7)	13.3
Beetles (Coleoptera), larva	5 (0.9)	14.3	1 (1.6)	6.7
Beetles (Coleoptera), imago	121 (22.8)	89.3	16 (25.0)	53.3
True flies (Diptera)	16 (3.0)	42.9	—	—
Butterflies and moths (Lepidoptera), larva	13 (2.4)	32.1	4 (6.2)	13.3
Butterflies and moths (Lepidoptera), imago	10 (1.9)	35.7	3 (4.7)	13.3
Ants (Formicidae)	91 (17.1)	75.0	7 (10.9)	13.3
Bees (Apoidea)	11 (2.1)	35.7	1 (1.6)	6.7
Other Hymenoptera	5 (0.9)	10.7	1 (1.6)	6.7
Insecta, larva	4 (0.8)	14.3	—	—
Insecta, pupa	1 (0.2)	3.6	—	—
Insecta, imago	5 (0.9)	17.9	—	—
Reptiles (Reptilia)	1 (0.2)	3.6	—	—
Total	531 (~100)		64 (100)	

the highest share. The largest animals in the samples were dragonflies and a mantid.

Social Flycatcher. Winged ants, beetles, dragonflies, bees, spiders, and seeds of *Miconia* spp. were important (Tables 4, 5). Aquatic animals (mainly backswimmers, freshwater snails, and dragonfly larvae) composed 9.2% (feces) and 13.5% (neck-collars) of animal prey. Flying insects (mainly winged ants, dragonflies, bees, and true flies) caught mostly in the air constituted 49.8% (feces) and 54.1% (neck-collars) of the prey. Fruits and seeds made up 22.0% (feces) and 47.5% (neck-collars) of food items.

Length of animal prey ranged between 3–50 mm, and for fruits and seeds from 2 mm to 19 mm (neck-collars). Animals 5–11 mm, and fruits and seeds 4–6 mm long, made up the highest proportions. The largest animals eaten (50 mm) were dragonflies, fish, and a reptile.

Comparison between species. The share of animal prey (Tables 2, 4) in both species (Renkonen index) amounted to 79.0% (feces) and 57.7% (neck-collars). Differences in prey composition were statistically significant (respectively, $\chi^2_9 = 110.6$, $P < 0.0001$; $\chi^2_9 = 28.3$, $P = 0.0008$). The main differences lay in a higher percentage of spiders ($\chi^2_1 = 49.1$, $P < 0.0001$; fecal data) in Rusty-margined Flycatcher and winged ants ($\chi^2_1 = 13.9$, $P = 0.0002$; fecal data) and bees ($\chi^2_1 = 25.0$, $P < 0.0001$; fecal data) in the diet of the Social Flycatcher.

The proportion of plant food (Tables 2, 4) in both species (Renkonen index) equalled 84.0% (feces) and 70.8% (neck-collars). Differences in food composition were statistically significant (respectively, $\chi^2_7 = 27.0$, $P = 0.0003$; Fisher-Freeman-Halton test, Monte-Carlo estimate of $P < 0.0001$).

No differences were found between species in the proportion of aquatic animals in the nestling diet. However, nestlings of the Social Flycatcher received significantly more flying insects (feces, $\chi^2_1 = 58.4$, $P < 0.0001$; neck-collars, $\chi^2_1 = 10.9$, $P = 0.001$). The proportion of fruits and seeds was higher in the diet of the Rusty-margined Flycatcher nestlings (feces, $\chi^2_1 = 47.2$, $P < 0.0001$; neck-collars, $\chi^2_1 = 8.0$, $P = 0.005$).

Table 3. Vegetable food (fruits and seeds) in the diet of Rusty-margined Flycatcher nestlings.

Taxon	Fecal analysis		Neck collars	
	N (%)	Frequency	*N* (%)	Frequency
Zanthoxylum panamense (Rutaceae)	—	—	10 (10.0)	13.3
Guarea grandifolia (Meliaceae)	5 (1.8)	14.3	—	—
Vitis tiliifolia (Vitaceae)	—	—	4 (4.0)	13.3
Davilla nitida (Dilleniaceae)	32 (11.6)	50.0	9 (9.0)	20.0
Doliocarpus major (Dilleniaceae)	1 (0.4)	3.6	—	—
Passiflora auriculata (Passifloraceae)	3 (1.1)	3.6	—	—
Eugenia oerstedeana (Myrtaceae)	—	—	5 (5.0)	20.0
Miconia argentea (Melastomataceae)	—	—	5 (5.0)	6.7
Miconia spp. (Melastomataceae)	163 (58.8)	96.4	57 (57.0)	33.3
Shefflera morototoni (Araliaceae)	1 (0.4)	3.6	—	—
Unidentified	72 (26.0)	78.6	10 (10.0)	26.7
Total	277 (~100)		100 (100)	

Table 4. Animal food in the diet of Social Flycatcher nestlings.

Taxon	Fecal analysis		Neck collars	
	N (%)	Frequency	*N* (%)	Frequency
Mollusks (Gastropoda)	51 (2.8)	51.7	14 (6.3)	16.1
Saw bugs (Isopoda)	2 (0.1)	1.7	1 (0.4)	1.8
Scorpions (Scorpionoidae)	1 (0.1)	1.7	—	—
Spiders (Araneae)	143 (8.0)	87.9	24 (10.8)	32.1
Dragonflies (Odonata), larva	38 (2.1)	41.4	5 (2.3)	7.1
Dragonflies (Odonata), imago	160 (8.9)	86.2	33 (14.9)	32.1
Orthoptera	52 (2.9)	46.6	8 (3.6)	12.5
Cockroaches (Blattidae)	5 (0.3)	6.9	3 (1.4)	5.4
Termites (Isoptera)	23 (1.3)	8.6	—	—
Homoptera	18 (1.0)	19.0	5 (2.3)	5.4
Backswimmers (Notonectidae)	76 (4.2)	50.0	7 (3.2)	3.6
Other true bugs (Heteroptera)	47 (2.6)	48.3	2 (0.9)	3.6
Neuroptera	1 (0.1)	1.7	1 (0.5)	1.8
Beetles (Coleoptera), larva	13 (0.7)	12.1	3 (1.4)	5.4
Beetles (Coleoptera), imago	399 (22.2)	96.6	20 (9.0)	25.0
Scorpion flies (Mecoptera)	3 (0.2)	3.4	—	—
True flies (Diptera), larva	—	—	1 (0.4)	1.8
True flies (Diptera)	50 (2.8)	51.7	2 (0.9)	3.6
Butterflies and moths (Lepidoptera), larva	30 (1.7)	32.8	5 (2.3)	5.4
Butterflies and moths (Lepidoptera), imago	18 (1.0)	29.3	—	—
Ants (Formicidae)	450 (25.0)	82.6	68 (30.6)	19.6
Bees (Apoidea)	153 (8.5)	67.2	10 (4.5)	5.4
Other Hymenoptera	37 (2.1)	32.8	6 (2.7)	8.9
Insecta, larva	6 (0.3)	10.3	—	—
Insecta, imago	17 (0.9)	22.4	—	—
Fishes (Pisces)	1 (0.1)	1.7	3 (1.4)	3.6
Amphibia	—	—	1 (0.4)	1.8
Reptiles (Reptilia)	3 (0.2)	5.2	—	—
Total	1797 (~100)		222 (~100)	

Table 5. Vegetable food (fruits and seeds) in the diet of Social Flycatcher nestlings.

Taxon	Fecal analysis		Neck collars	
	N (%)	Frequency	*N* (%)	Frequency
Anthurium clavigerum (Araceae)	—	—	1 (0.5)	1.8
Pleiostachya pruinosa (Marantaceae)	—	—	3 (1.5)	1.8
Phthirusa pyrifolia (Loranthaceae)	—	—	4 (2.0)	1.8
Heisteria concinna (Olacaceae)	—	—	2 (1.0)	3.6
Guatteria dumetorum (Annonaceae)	—	—	1 (0.5)	1.8
Ocotea cernua (Lauraceae)	—	—	1 (0.5)	1.8
Zanthoxylum panamense (Rutaceae)	6 (1.2)	3.4	5 (2.5)	3.6
Guarea grandifolia (Meliaceae)	16 (3.2)	1.2	—	—
G. guidonia (Meliaceae)	—	—	1 (0.5)	1.8
Vitis tiliifolia (Vitaceae)	—	—	2 (1.0)	3.6
Davilla nitida (Dilleniaceae)	36 (7.1)	2.8	18 (9.0)	10.7
Havetiopsis flexilis (Clusiaceae)	—	—	2 (1.0)	1.8
Passiflora auriculata (Passifloraceae)	6 (1.2)	3.4	—	—
Miconia argentea (Melastomataceae)	—	—	4 (2.0)	3.6
Miconia sp. (Melastomataceae)	362 (71.4)	93.1	93 (46.3)	50.0
Shefflera morototoni (Araliaceae)	6 (1.2)	0.8	11 (5.5)	5.4
Ardisia fendleri (Myrsinaceae)	—	—	9 (4.5)	5.4
Unidentified	75 (14.8)	41.1	44 (21.9)	23.2
Total	507 (~100)		201 (100)	

The median length of animal prey (neck-collars) of the Rusty-margined Flycatcher nestlings was 10 mm (interquartile range 8–13, $N = 64$) and in the Social Flycatcher, 8.5 mm (interquartile range 7–11, $N = 200$; median test, $\chi^2_1 = 10.47$, $P < 0.001$). The median length of fruits and seeds (neck-collars) was 5 (interquartile range 5–6, $N = 100$) and 5 (interquartile range 4–6, $N = 201$), respectively (median test, $\chi^2_1 = 1.16$, $P = 0.28$).

Feeding nestlings. We observed individually marked parents feeding their offspring in one nest of the Rusty-margined Flycatcher and in three Social Flycatcher nests. The observations at the Rusty-margined Flycatcher nest, containing two nestlings 13–15 d old, were carried out for 3 h on each of two days. Female made 67.9% of 112 feeding trips observed. This deviated significantly from a 50 : 50 ratio expected if both parents contributed equally (two-tailed $P = 0.0001$, calculated from the binominal distribution with $P = 0.5$). At the three nests (2–3 nestlings, 10–17 d old) of the Social Flycatcher, the observations lasted for 2–4 h a day during six days (16 h in total). Proportion of feedings by the female equalled 48.1 ($N = 54$, $P = 0.89$), 62.3% ($N = 154$, $P = 0.003$) and 46.3% ($N = 160$, $P = 0.38$). The last pair also was observed for 5 h when three nestlings were 4 d old, and it was the male who contributed significantly more in feeding in this phase of the breeding cycle (81.3% of 64 feeding trips, $P < 0.0001$).

Only one nest of each species was suitable for comparing the intensity of feeding the young. Both broods comprised two 13–14-d-old nestlings, and at both 6 h of observations (over two days) were carried out at the same time of day. The Rusty-margined Flycatcher nestlings were fed 113 times per 6 h (on average 18.8 times per h, SD = 5.9; 13 and 14 April 1998), and those of the Social Flycatcher, 156 times (26.0 times per h, SD = 5.66, 31 March and 1 April 1998).

The daily feeding intensity did not show significant irregularities, except for an increase in activity early in the morning. Periods of higher and lower intensity occurred alternately.

Timing of the breeding season and the availability of fruits and seeds. To compare the overall abundance of fruits and seeds with the number of potential broods with nestlings and fledglings in the same 7-d periods, we used data obtained in weekly censuses conducted on Barro Colorado Island. In the case of the Social Flycatcher, we found a correlation (Fig. 1) between the number of broods with nestlings and fledglings and the abundance of

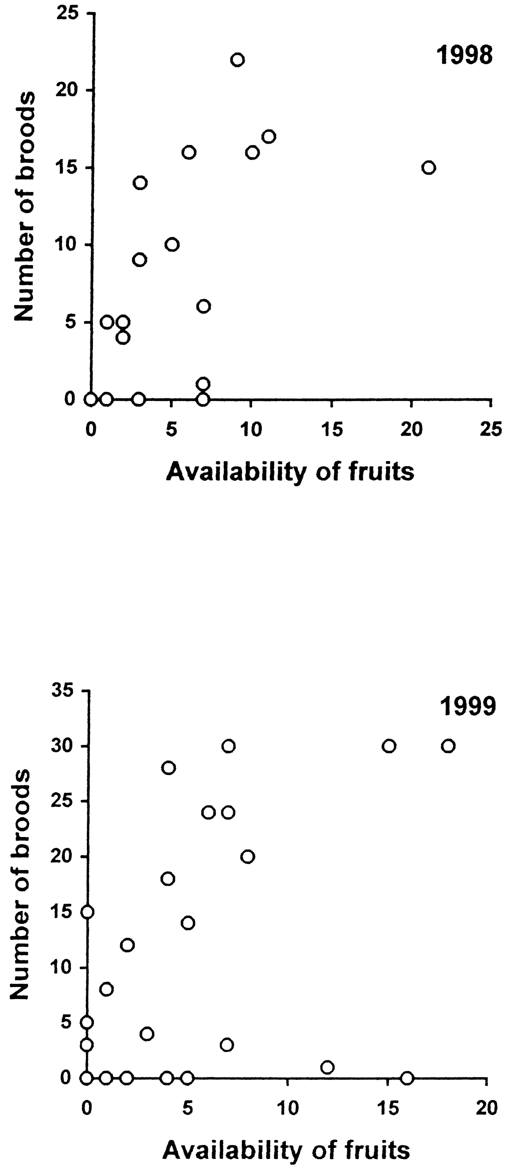

Fig. 1. Number of Social Flycatcher broods with nestlings plus fledglings in relation to the abundance of fruits in seven-day periods during 1998 and 1999.

fruits (1998, $r_s = 0.67$, $N = 22$, $P = 0.001$; 1999, $r_s = 0.43$, $N = 29$, $P = 0.019$). For seeds, a statistically significant correlation occurred only in 1999 ($r_s = 0.49$, $N = 29$, $P = 0.006$; Fig. 2). For the Rusty-margined Flycatcher, we also found a significant correlation (Fig. 3) between the number of broods and the abundance of fruits in 1999 ($r_s = 0.59$, $N = 26$, $P = 0.002$) and seeds ($r_s = 0.44$, $N = 26$, $P = 0.024$).

DISCUSSION

Although the tropics are characterized by exceptional species richness, there is much indirect evidence (Thiollay 1991) that food can be a limiting factor for birds, especially during the period of feeding the young. Food resources are more diverse in tropical than in temperate forest and productivity is spread over a longer period. Nevertheless, the overall annual production or the standing prey biomass may not be higher (Janzen 1973; Erwin 1983). Hails (1982) found that the aerial insect biomass during the breeding season in Scotland was ten times that of Malaysia. When studying a guild of small foliage gleaners, Thiollay (1988) found that in a rain forest in French Guiana the mean attack rate was four to six times lower than that in broad-leaf forest in France. In the Amazonian forest the prey biomass of foliage insectivores is not high, made up predominantly of small or inconspicuous arthropods (Owen 1983), and contributing to cases of slow growth or starvation of nestlings (Dyrcz 1983). We did not observe starvation of nestlings in these flycatchers (Dyrcz 2002), but high nest losses reduced the possibility of this.

On Barro Colorado Island, as in other tropical regions, wide seasonal fluctuation of both fruit and insect production has been demonstrated (Leigh et al. 1983). In our study, the nestling and fledgling periods fell during of increased abundance of insects (Wolda 1978, 1983) and fruits. This may suggest that at other times food resources might be insufficient for nesting. In the study area the peak of nesting was in March and April (Dyrcz 2002), shortly before the first heavy rains and the beginning of the rainy season. Timing of nesting probably reflects food abundance, as rains stimulate vegetation development and result in an increase in the number of insects (Wolda 1978, 1983; Turner 1983; Poulin et al. 1992).

Similar food composition of the two species and similar proportions of constituents of their diets suggest considerable overlap between the ecological niches of these two flycatchers. This supports the hypothesis that a high degree of diet overlap is frequent in the tropics, contributing to high tropical avian species diversity

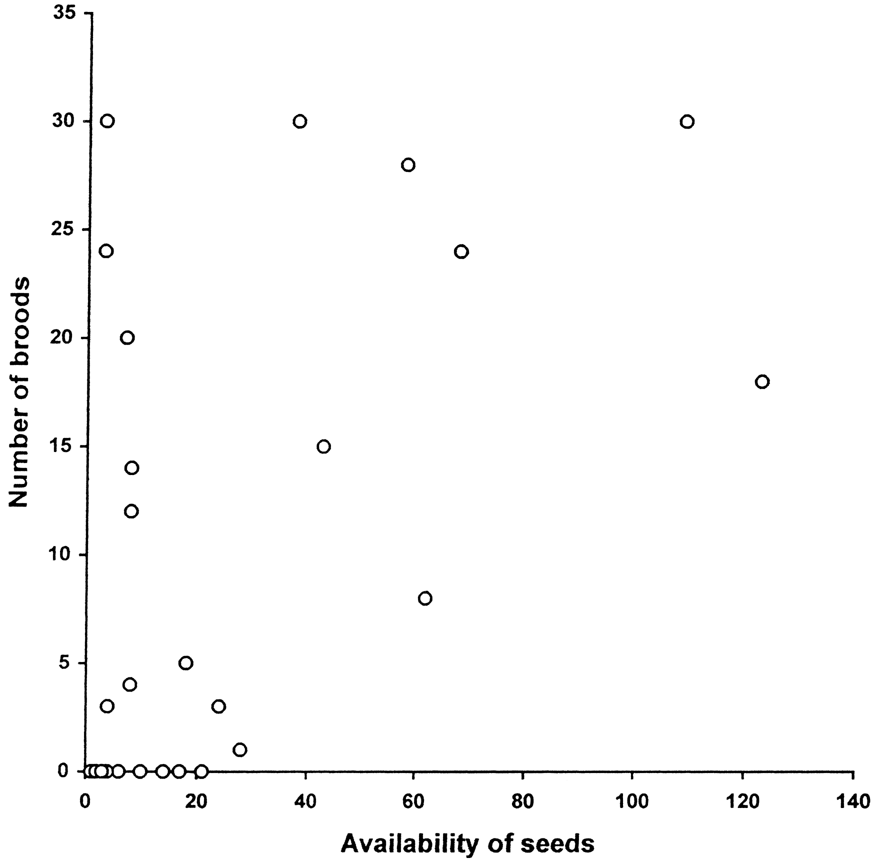

Fig. 2. Number of Social Flycatcher broods with nestlings plus fledglings in relation to the abundance of seeds in seven-day periods in 1999.

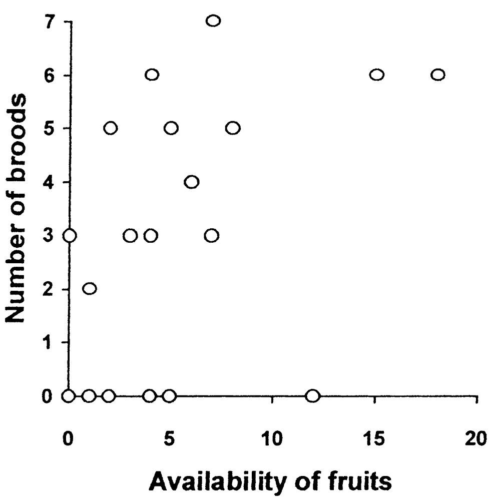

Fig. 3. Number of Rusty-margined Flycatcher broods with nestlings plus fledglings in relation to the abundance of fruits in seven-day periods in 1999.

(Croxall 1977). In a study in Costa Rica, Cracraft (1967) concluded that the foraging behavior of the Social Flycatcher and Gray-capped Flycatcher (*Myiozetetes granadensis*) was very similar but that the Social Flycatcher spent more time in the upper strata than the Gray-capped Flycatcher. Crowell (1968) studied two flycatcher species of the genus *Eleania* in the southern Lesser Antilles, including islands where the species occur in sympatry. A considerable overlap occurred in both method and height of feeding, but significant differences also existed. However, in three sympatric woodland species of different genera of tyrant flycatchers from the temperate zone (California), considerable differences in foraging tactics and perch sites were found (Verbeek 1975). Fitzpatrick (1980) presented an overview of the foraging characteristics of tyrant flycatchers with foraging-mode profiles of 44 species including the Social Flycatcher. He concluded that each of the three subfamilies contains behaviorally generalized genera as well as radiations into species with related, but more specialized, foraging modes. It seems that both species of flycatchers studied by us belong to the group of generalists.

Nevertheless, certain differences in the nesting diets of the two species did exist. There was a larger share of fruits and seeds, and a smaller percentage of flying insects, in the diet of the Rusty-margined Flycatcher. Furthermore, the fruits and seeds given to the nestlings of this species were slighty (but significantly) larger, although the Rusty-margined Flycatcher is somewhat smaller than the Social Flycatcher (Wetmore 1972; Dunning 1993). These findings support the conclusion reached by Hespenheide (1971) that size, rather than taxonomic differences, appear to be most important in the food of flycatchers.

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