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BREEDING ECOLOGY OF THE SOCIAL (*MYIOZETETES SIMILIS*) AND RUSTY-MARGINED (*M. CAYANENSIS*) FLYCATCHERS AT BARRO COLORADO ISLAND, REPUBLIC OF PANAMA

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Resumen. – Ecología de la reproducción del Pitirre Copete Rojo (*Myiozetetes similis*) y del Atrapamoscas Pecho Amarillo (*M. cayanensis*) en la isla Barro Colorado en la República de Panamá. – En los años 1998 y 1999, a lo largo de las costas de la Isla Barro Colorado, Panamá, se encontraron nidos de Pitirré Copete Rojo (*Myioxetetes similis*) 36 y 53 pares, y 8 y 14 nidos de Atrapamoscas Pecho Amarillo (*M. cayanensis*), respectivamente. Soló el Pitirré Copete Rojo construyó los nidos en los troncos que estaban por encima del nivel del agua. Ambas especies pusieron huevos al final de la estación seca. El primer huevo puesto por los Pitirrés Copete Rojo en 1998 fue casi un mes más temprano que en el 1999, tal vez esto se produjo a consecuencia de una extremadamente severa estación seca después del fenómeno El Niño. La puesta media de huevos fue de 3.36 (SD = 2.34, n = 84) para el Pitirré Copete Rojo y de 2.80 (SD = 0.41, n = 20) para el Atrapamoscas Pecho Amarillo. Las puestas tempranas del Pitirré Copete Rojo fueron significativamente más grandes que las puestas tardías. La pérdida de nidos (método de Mayfield) del Pitirré Copeto Rojo y del Atrapamoscas Pecho Amarillo, osciló entre 72.0%–79.8% y 79.6%–62.7% respectivamente. En ambas especies la mayoría de las pérdidas se debió a predación. Las nidadas tardías en el Pitirré Copeto Rojo, sufrieron significativamente mayor pérdida que las tempranas. La producción de pichones por nido del Pitirré Copeto Rojo fue de 0.87 en 1998 y 0.67 en 1999; en el Atrapamoscas Pecho Amarillo para ambos años fue, en suma 0.82.

Abstract. – Nests of 36 and 53 pairs of the Social Flycatcher (*Myiozetetes similis*) and 8 and 14 nests of the Rusty-margined Flycatcher (*Myiozetetes cayanensis*), respectively, were found in 1998 and 1999 along the shores of Barro Colorado Island, Panama. Only the Social Flycatcher built nests on stumps emerging from water. Both species laid eggs in the late dry season. The first eggs of Social Flycatchers in 1998 were almost a month earlier than in 1999, perhaps due to an extremely severe dry season in 1998 after an El Niño event. Mean clutch size was 3.36 (SD = 2.34, n = 84) for the Social Flycatcher and 2.80 (SD = 0.41, n = 20) for the Rusty-margined Flycatcher. Early clutches were significantly larger than late clutches in the Social Flycatcher. Nest losses (Mayfield method) ranged from 72% to 79.8% and 62.7% to 79.6%, respectively, for the Social and Rusty-margined flycatchers. In both species, most losses were due to predation. Late broods of the Social Flycatcher suffered significantly higher losses than early broods. In the Social Flycatcher, fledglings per nest were 0.87 in 1998 and 0.67 in 1999. In the Rusty-margined Flycatcher, the figure for both years together was 0.82. *Accepted 17 August 2001.*

Key words: *Myiozetetes similis, Myiozetetes cayanensis,* Social Flycatcher, Rusty-margined Flycatcher, breeding ecology, nest losses, comparison.

INTRODUCTION

Breeding ecology studies of tropical bird species are relatively uncommon, perhaps due to difficulties in finding and checking a sufficient sample of nests. The Social Flycatcher (*Myiozetetes similis*) is a common species, whose breeding biology has been described (Skutch 1960). A closely related species, the Rusty-margined Flycatcher (*M. cayanens*is) is less common and finding large samples of nests poses difficulties. Hence, the species has been studied less intensively (Haverschmidt 1971, Ricklefs 1980, Dyrcz 1991). A comparison of the breeding biology and ecology of these two species on Barro Colorado Island, central Panama, could contribute to the discussion on whether nest losses are higher in tropical regions or at temperate latitudes (Skutch 1966, Oniki 1979, Gibbs 1991, Telleria & Diaz 1995, Robinson *et al.* 2000).

STUDY AREA AND METHODS

I studied nests of flycatchers along the coast of Barro Colorado Island on lake Gatun, Republic of Panama from March to April 1998 and March to May 1999. Barro Colorado Island, which is a forested nature reserve, has an area of 1642 ha, and a shoreline of 50.7 km. It is mainly covered with tropical moist forest, both primeval and secondary (for details, see Willis 1974). I evaluated productivity and phenology by locating and monitoring nests to determine the first-egg laying date, clutch size, hatching success and brood fate. From a small motorboat, I checked 89 active nests of the Social Flycatcher and 22 nests of the Rusty-margined Flycatcher, plus, respectively, 11 and 4 second broods in the same nests. I was not able to find any nests inland except a few high nests in the laboratory clearing which I did not include in my study. In 1998, I completed the study at the end of April, a month earlier than in 1999 because, despite thorough searching, I did not find any nest after 11 April. I classified the nest as destroyed by a predator when during the subsequent nest visit I found that eggs or nestlings (too young to leave the nests on their own) had disappeared. Some additional clues were deformed or destroyed nests, and remnants of eggs or nestlings. In four cases, the whole nest disappeared, which I also classified as predation. First-egg dates were estimated during laying period or by backdating from the hatching date or age of young, assuming one egg was laid per day.

Nests and eggs of the two species look similar and both species often gave alarm calls at the nest. Therefore, I classified the brood species according to the birds that incubated, brooded, fed the nestlings, or entered or left the nest.

Nest losses were estimated in two ways. The "traditional" way is to present the percent of nests destroyed irrespective of the stage at which they were found. This is useful for comparative purposes, since in most papers, nest losses are presented in this way. On the other hand, such an estimate is somewhat biased. If not all nests are found at an early stage (e.g., egg-laying period), it is possible that some of the destroyed nests early in the breeding cycle were not detected, which leads to an underestimate of nest losses. The Mayfield (1975) method based on the estimate of losses in relation to the known time of exposure of each nest to predation reduces such a bias. Therefore, nest predation rates were calculated also with the Mayfield's method. Comparisons of survival rates were done with the test proposed by Johnson (1979; referred as "Johnson test"). *P*-values marked with an asterisk were Bonferroni-corrected (Sokal & Rohlf 1995) to avoid bias due to multiple tests within the same data set.

Nests were checked every 2–5 days. Their contents were determined by touch. If necessary, eggs or nestlings were taken out for

TABLE 1. Number of nests (%) of the Social Flycatcher built on different substrates.

Nest location	1998	1999	1998 + 1999
Stump in water	24 (61.5)	6 (7.8)	30 (25.9)
Dead branch in water	5 (12.8)	19 (24.7)	24 (20.7)
Other (see text)	10 (25.6)	52 (67.5)	62 (53.4)

inspection. Standing on the deck of the boat (sometimes I put on additional box), I was able to check nests up to the height of c. 3.0 m. Only three nests had been built higher. In the case of inaccessible nests, only their height was taken into calculations.

RESULTS

Breeding pairs and nest distribution

Social Flycatcher. Assuming, on the ground of some direct observation, that a new nest built within 200 m from the destroyed one belonged to the same breeding pair, there were 36 breeding pairs in 1998 and 53 pairs in 1999. Nests were concentrated in different areas in the two study seasons. Nest sites were of three types (Table 1). The first type was represented by trunks emerging from water (remains of trees flooded about 90 years ago during the formation of the artificial lake). These were common in 1998 when the March–June water level was about 24–25 m, and rare in 1999 when the level was 26–27 m. Nests were located atop the trunk in hollows and cracks of the bark or among epiphytes, including five nests between tree trunk and lianas that have emerged from the water since the creation of the lake. The second type involved dead branches emerging from water (generally leafless branches of trees, which previously grew on the shore but later fell into the water) or dead bushes emerging from the water. The third type was that of nests built on leafy (living) bushes and small trees, generally located over water, but also three nests on lianas hanging over the water and two nests on a beam below the roof of a boat-house.

The proportion of nests located on trunks was much higher in the dry year of 1998 (χ^2 with Yates' correction = 39.0, $P < 0.0001$) (Table 1), when trunks were common but branches of living and dead plants growing on the shore were situated over land and flycatchers did not build their nests there. In 1999, 19 nests (24.7%) were on bushes and small trees of *Annona glabra* (subfamily Annonaceae) emerging from water, and 7 nests (9.1%) on small branches of *Mimosa pigra*. In other cases, plants were not identified. All nests were situated from 35 to c. 400 cm above water. On average, nests were higher in low water levels of 1998 (mean = 167.7 cm, SD = 67.51) than in 1999 (mean = 139.1 cm, SD = 63.94) (Mann-Whitney *U*-test: $Z = 2.13$, $P = 0.034$).

One nest in 1998 and seven nests in 1999 were located next to an active wasp nest. In two cases the Social Flycatcher nest was built near active nest of ants. In 4 cases the Social Flycatcher nest was close to an active nest of the Tropical Kingbird (*Tyrannus melancholicus*).

Rusty-margined Flycatcher. I found 8 (1998) and 14 (1999) pairs with active nests. Nests were scattered: the two nearest, simultaneously active nests were about 200 m apart. In contrast, nests of Rusty-margined Flycatchers were frequently close to (minimum c. 10 m) nests of Social Flycatchers. Unlike the Social Flycatcher, no nests of Rusty-margined Flycatcher were found on trunks (χ^2 with Yates'

TABLE 2. Nest losses (%) in the Social Flycatcher calculated as by the "traditional" method.

Year	Percent succesful nests (n)	Percent lost nests (n)	
		Predation	Other
1998	39.4 (13)	51.5 (17)	9.1 (3)
1999	22.4 (15)	76.1 (51)	1.5 (1)
1998 + 1999	28.0 (28)	68.0 (68)	4.0 (4)

correction = 6.44, P = 0.01). The average height of nests above water level was 153.0 cm (SD = 71.36, n = 22, range 40–350 cm), and did not differ from that of the Social Flycatcher (148.0 cm, SD = 72.47, n = 106, range = 35–400 cm, $P > 0.05$). Three active nests of Rusty-margined Flycatchers were near an active wasp nest. All nests but one were built over water.

Breeding season

Social Flycatcher. Breeding started earlier in 1998 than in 1999. The median of first-egg laying date was 16 March (Quartile$_1$ = 8 March, Q_3 = 2 April, n = 30) in 1998 and 10 April (Q_1 = 26 March, Q_3 = 28 April, n = 56) in 1999 (Mann-Whitney U-test: Z = 4.35, $P <$ 0.0001).

Rusty-margined Flycatcher. The median of first-egg date in 1998 was 14 March (Q_1 = 24 February, Q_3 = 17 March, n = 5) and in 1999 was 6 April (Q_1 = 12 March, Q_3 = 16 April, n = 14; ns).

Clutch size and unhatched eggs

Social Flycatcher. Most clutches (71.4%) comprised 3 eggs; 2-egg (9.5%) and 4-egg (19%) clutches were less common. Mean clutch size was 3.36 (SD = 2.34, n = 84) with no difference between years. In 1998, clutches laid in February (mean = 3.50, SD = 0.55, n = 6, range 3–4) were larger than in April (mean = 2.86, SD = 0.38, n = 7, range 2–3) (U-test: Z = 2.11, P = 0.035). Likewise, in 1999, earlier clutches (laid up to 20 March) were on average larger (mean = 3.18, SD = 0.41, n = 11, range 3–4) than later ones (laid after 20 April) (mean = 2.88, SD = 0.33, n = 17, range 3–4) (U-test: Z = 2.01, P = 0.04).

Hatchability refers to the proportion of eggs that were not fertilized or of which the embryo died at the early stage of development. Clutches totally or partly damaged were not included into the analysis. The mean number of unhatched eggs per clutch was 0.45 (SD = 0.61) in 1998, and 0.14 in 1999 (SD = 0.35) (U-test; Z = 1.96, P = 0.050), averaging for both years 0.29 (SD = 0.292; n = 42).

Rusty-margined Flycatcher. Clutch size was determined for 20 nests: 4 comprised two eggs, and 16, three eggs. Mean (2.80, SD = 0.41) was lower than in the Social Flycatcher (3.36; U-test: Z = 1.92, P = 0.05). This difference resulted from a relatively large proportion of 4-egg clutches in the Social Flycatcher. The average number of unhatched eggs per nest (1998 + 1999) was 0.17 (SD = 0.39, n = 12).

Nest losses and production of fledglings

Social Flycatcher. Most nest losses were due to predation (Table 2 and 3). "Other" causes in Table 2 refer to nest desertion (3 cases) and nest destruction, probably by motorboats. An analysis of data in Table 3 revealed that Mayfield's estimators of nest predation rates were similar in both breeding season (71.9% vs. 79.7%; Johnson test: Z = 0.816, P^* = 1). Also survival rates of nests in egg and nestling

TABLE 3. Nest predation in the Social and Rusty-margined flycatchers in two breeding seasons. The table consists of daily survival rates (DSR), their standard errors (SE), and percentage of depredated nests. All statistics are expressed as percentages.

Species and year	Incubation stage			Nestling stage			Incubation and nestling stages		
	DSR	SE	% depredated*	DSR	SE	% depredated**	DSR	SE	% depredated***
Social Flycatcher									
1998	97.1	1.1	44.5	96.5	1.1	49.2	96.8	0.8	71.9
1999	96.5	0.8	51.0	95.2	1.1	60.7	96.0	0.6	79.9
1998 + 1999	96.7	0.6	48.9	95.8	0.8	55.7	96.3	0.5	77.3
Rusty-margined Flycatcher									
1998	97.2	1.4	43.3	97.8	1.3	34.5	97.5	0.9	62.9
1999	100.0	0.4	0.0	90.9	5.0	83.6	96.0	2.3	79.6
1998 + 1999	97.9	1.2	34.6	96.4	1.1	50.2	97.2	0.9	67.3

*For the total duration of 20 days, **19 days, ***39 days.

TABLE 4. Nest losses in the Social Flycatcher at different stages of the breeding season.

First egg dates	No. of successful nests	No. of destroyed nests	Chi square with Yates correction
9 Febr.-15 March 1998	10	4	8.11, $P = 0.004$
16 March-11 April 1998	1	11	
25 Febr.-24 March 1999	8	5	6.66, $P = 0.01$
25 March-23 May 1999	5	25	

stages did not differ significantly (48.9% vs. 55.7%; Johnson test: $Z = 0.920$, $P^* = 1$). Predation did not differ between low (< 110 cm) and high (> 200 cm) nests. In both years, late nests were less successful (Table 4).

In 1998 and 1999, the production of fledglings per nest was 0.87 and 0.67, respectively, and per successful nest was 2.33 and 2.87. There were no differences between seasons ($P > 0.05$).

Rusty-margined Flycatcher. All nest losses were due to predation. In 1998, 3 of 5 nests (60%), and in 1999, 9 of 16 (56.2%) were depredated. Results of both study years are combined for nest failure which averaged 63.2%, lower than in Social Flycatcher (72.0%; ns). Predation rates calculated with Mayfield (1975) method (Table 3) did not differ between years (62.9% vs. 79.6%; Johnson test: $Z = 0.609$, $P^* = 1$) and were similar in incubation and nestling stages of the breeding cycle (34.6% vs. 50.2%; Johnson test: $Z = 0.814$, $P^* = 1$).

The comparison of Mayfield's statistics calculated for both species on data pooled across years and phases of the breeding cycle demonstrated no significant difference in predation rate (77.3% in Social Flycatcher vs. 67.3% in Rusty-margined Flycatcher; Johnson test: $Z = 0.903$, $P^* = 1$).

Production of fledglings per nest (1998 + 1999) was 0.82 (SD = 1.27), which is slightly higher compared to the Social Flycatcher (0.74, SD = 1.27; ns). The average production of fledglings per successful nest was 2.00 (SD = 0.71, n = 22), and was lower than in the Social Flycatcher (2.63, SD = 0.88, n = 96) (U-test: $Z = 173.5$, $P = 0.04$;), a result of smaller clutches.

Other observations

In 15 cases, after a brood loss or the departure of young from the nest a second clutch was laid in the same nest. In 10 cases, the two clutches belonged to the Social Flycatcher, in one case the first brood was from the Social Flycatcher and the second from the Rusty-margined Flycatcher, in another case the situation was opposite, and in three cases both broods belonged to the Rusty-margined Flycatcher. There was also one case of nesting of Mangrove Swallow (*Tachycineta albilinea*) in a nest of Rusty-margined Flycatcher and in a nest of the Social Flycatcher (Dyrcz 2000).

In four nests of the Social Flycatcher and one nest of the Rusty-margined Flycatcher, all nestlings were infected with 2–7 dipteran maggots (c. 10 mm) under skin on the head, on back and at the basis of wings. Some nestlings were very pale. Of five broods infected, three were destroyed by predators, and in the further two (including one of the Rusty-margined Flycatcher), I removed the maggots and the nestlings fledged.

In four nests of the Social Flycatcher and three nests of the Rusty-margined Flycatcher, I observed the young leaving the nest. They were 17–21 days old and might have left their nests prematurely due to my activity. Nevertheless, their first flight was successful. Young approximately 17-day old Rusty-margined Flycatchers flew up c. 7 m almost vertically to hide in the foliage. Another 21-day old nestling of this species flew c. 50 m, steadily increasing its height. One nest of the Social Flycatcher was placed c. 100 m from the land and three nestlings 19-day old, flushed off reached the shore flying low over water.

In 1998, 7 adult Social Flycatchers were individually color-banded, of which two were resighted in 1999. The first case was a female caught on the nest placed on a beam in dock on 10 April 1998. In the following year, it built the nest exactly in the same place. In the second case, I mist-netted a female at its nest on 1 April 1998 and saw it next year a few hundred meters away. In 1998, I color-banded 22 nestlings of the Social Flycatcher. One nestling banded in the nest on 10 April 1998 was observed again in 1999 as an adult alarming at the nest about 50 m away from its hatching place.

DISCUSSION

Nest location. The Social Flycatcher places its nest not only over water but also frequently above dry land (Skutch 1960). Nearly all found and searched nests in this study were located over water, making them less accessible to terrestrial predators. Only one nest of the Rusty-margined Flycatcher was placed above dry land but very close to the shore; it was well hidden among creepers at the trunk of a large tree. Skutch (1960) found in Costa Rica that nests above dry land are located higher compared to nests over water. In this study, nests were located on average much lower than in Skutch's (1960) study, which may have resulted among others from the type of shore vegetation.

Breeding season. The peak of the nesting season for Central American birds falls between the vernal equinox and the summer solstice, with April the principal month for laying (Skutch 1960). The peak of the breeding season for the Social Flycatcher is in April and May, and the latest broods leave their nests in June or, exceptionally, in July (Skutch 1960). In my study, the peak of nesting was in March and April, shortly before the first heavy rains and the beginning of the rainy season. This may be an adaptation to food abundance as rains stimulate vegetation development, and the correlated increase in the number of insects (Wolda 1978, Leigh *et al.*1982). In 1998, insects constituted c. 51% of items brought by Social Flycatchers to their nestlings, compared to c. 47% for small fruits and berries (A. Dyrcz & H. Flinks, in prep.). Fruit production also peaked during peak nesting of Social Flycatchers. Monthly fruit dry mass production summed over all plant species was highest in February, March and April on Barro Colorado Island in 1987–1996 (Wrigth *et al.* 1999). Wright *et al.* (1999) found also that El Niño conditions enhance fruit production. As the dry season in 1998 was unusually severe after El Niño, fruit production was probably much higher in 1998 than in 1999. This may have resulted in an earlier start of the Social Flycatcher breeding season in 1998. The initiation of breeding in 1998 was also unusually early in comparison to Skutch's (1950, 1960) data from Central America.

Clutch-size. In the Social Flycatcher, there was a tendency to decreasing clutch size with the progress of the breeding season, which is typical of numerous temperate zone species (e.g., Perrins 1985). This has been explained by the fact that food supply for the young may be less abundant later in the season and/or the birds that breed later may be less efficient, or may be younger birds, and lay smaller clutches accordingly. In tropical bird species, this phenomenon has been recorded less frequently e.g., in the Clay-colored Robin (*Turdus* *grayi*) (Dyrcz 1983).

Nest losses. Nesting failures in the Social Flycatcher were caused primarily by predation (72%–77.3%). Both study years compiled, they amounted to 72% following the "traditional" method, and 77.3% following the Mayfield method (Tables 2 and 3). Nest losses in altricial temperate species with open nests (24 studies) ranged from 23–62% (mean = 51%) (Nice 1957). Martin & Clobert (1996) estimated nest losses at 29.6% in Europe (39 species) and at 40.7% in North America (88 species). In Central America lowlands, Skutch (1966) calculated losses of 23 species with open and domed nests in clearings and second-growth at 63–65%, whereas in the neighboring forests losses were as high as 76.5%. According to new data from central Panama (Robinson *et al.* 2000), the losses among 696 nests of understory forest birds ranged from 43% to 92%. When compared with success of nests in large, contiguous forest tracts of North America, tropical avian nesting success was approximately 23% lower. Nest losses (Mayfield) of two flycatchers: the Southern Bentbill (*Oncostoma olivaceum*) and Ochre-bellied Flycatcher (*Mionectes oleaginea*), which build enclosed nests, were 28.4% and 51.1%, respectively (Robinson *et al.* 2000). Nests losses of the Social Flycatcher in this study were high, even in comparison with the data from tropics, considering that the species builds domed nests (not easily accessible by predators) and actively defends them. Losses of domed nests have been found to be somewhat lower (Lack 1968, Oniki 1979, Loiselle & Hoppes 1983) or substantially lower (Robinson *et al.* 2000) than those of open nests. However, data from the tropics concerning several species studied on islands (including Barro Colorado Island) or small habitat patches showed that predation levels may be higher than in mainland forests (Willis 1974, Robinson *et al.* 2000).

Direct observations of intruders robbing the nests were few. Keel-billed Toucan (*Ramphastos sulfuratus*) depredated one Social Flycatcher nest and Snail Kites (*Rostrhamus sociabilis*) were observed pecking the top of another nest. Similarly as Robinson & Robinson (2001), I observed that a Keel-billed Toucan took only one from three nestlings, and within the next two days the remaining two, which were too young to fledge, disappeared from the nest. Other potential predators include the Gray Hawk (*Buteo nitidus*) and basilisk lizard (*Basiliscus basiliscus*). In 21% and 47% of lost nests, respectively in 1998 and 1999, eggs or nestlings vanished though the nest were undamaged and no remains of eggshells or nestlings had been left. This indirectly indicates that the important nest predators were snakes, which may eat eggs or nestlings without damaging the nest. In 1998, the proportion of this type of loss was lower as many nests were placed on thick stumps, probably not as easily accessible to snakes. There are at least four species of snakes on Barro Colorado that may depredate nest contents (Sieving 1992). Although terrestrial, they may swim to reach flycatchers' nests. Skutch (1966, 1985) reported that snakes are the main cause of mortality of bird broods and clutches in Neotropics. Robinson & Robinson (2001) witnessed 14 nest predation events in central Panama including four by snakes.

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