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NESTING AND FORAGING ECOLOGY OF THE RUFOUS-BREASTED FLYCATCHER (*LEPTOPOGON RUFIPECTUS*)

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Resumen. – Anidamiento y ecología de forrajeo del Mosquerito Pechirrufo (*Leptopogon rufipectus*). – Se encontraron 17 nidos activos del Mosquerito Pechirrufo (*Leptopogon rufipectus*) entre Marzo a Mayo y Septiembre a Noviembre, en el oeste de la Provincia de Napo, Ecuador. Los nidos presentaron una forma semiglobular y pendulante, compuestos principalmente de musgo y raicillas, situadas en las pendientes a lo largo de arroyos dentro del bosque. Los huevos presentaron un color blanco sin marcas; el número de puesta fue dos. El período documentado de anidación de los polluelos fue entre 21 y 23 días. El forrajeo de estas aves estuvo basado en la búsqueda de insectos ubicados en el anverso de las hojas localizadas principalmente en el estrato medio del bosque, atrapando desde su percha a los insectos por medio de ataques directos o manteniéndose suspendidos en el aire antes de atraparlos. El anidamiento y la ecología de forrajeo del Mosquerito Pechirrufo son generalmente muy similares a lo que ya es conocido de otras especies de *Leptopogon*.

Abstract. – Seventeen Rufous-breasted Flycatcher (*Leptopogon rufipectus*) nests were active from March to May, and from September to November, in western Napo Province, Ecuador. Nests were semiglobular and pendant, composed primarily of moss, and located beneath stream banks. Eggs were white and unmarked; clutch size was two. Documented nestling periods were 21–23 days. Foraging birds searched for insects located on the undersides of live leaves from perches located primarily in the mid-story, and attacked insects by making upward sally-hovers and sally-strikes. Nesting and foraging ecology of Rufous-breasted Flycatchers appears generally similar to that which is known for other *Leptopogon* species. *Accepted 16 November 2005.*

Key words: Andes, Ecuador, eggs, foraging behavior, *Leptopogon rufipectus*, montane forest, nest, Rufous-breasted Flycatcher.

INTRODUCTION

The genus *Leptopogon* consists of four species of Neotropical forest flycatchers that replace each other along an elevation gradient on the eastern slope of the Andes (Bates & Zink 1994, Ridgely & Tudor 1994, Fitzpatrick 2004). Inhabiting higher elevations than the widespread and more familiar Sepia-capped (*Leptopogon amaurocephalus*) and Slaty-capped (*L. superciliaris*) flycatchers, the Rufous-breasted (*L. rufipectus*) and Inca (*L. taczanowskii*) flycatchers occur in humid upper montane (i.e., subtropical and lower temperate) forest, where they remain little known ecologically (Fitzpatrick 2004). All aspects of the breeding biology of the Rufous-breasted/

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Inca Flycatcher complex remain undescribed, and published information on their natural history (e.g., foraging ecology) is limited to anecdotal and qualitative descriptions.

The Rufous-breasted Flycatcher occurs between 1500 and 2700 m elevation, primarily 1900–2400 m a.s.l., from western Venezuela to northern Peru, where the Río Marañon drainage separates it from the Inca Flycatcher, its sister species of the Peruvian Andes farther south (Parker *et al.* 1985, Bates & Zink 1994, Ridgely & Tudor 1994, Fitzpatrick 2004). Locally fairly common in Ecuador, Rufous-breasted Flycatchers often occur in pairs within mixed-species flocks, within which they typically forage inconspicuously in the mid-story of primary forest and forest borders (Hilty & Brown 1986, Ridgely & Greenfield 2001, Fitzpatrick 2004). Rufous-breasted Flycatchers perch upright in shady areas below the canopy while searching for prey and, like other *Leptopogon* species, exhibit the characteristic habit of wing-lifting, an habitual quick raising and lowering of one wing over the back while perched (Hilty & Brown 1986, Ridgely & Tudor 1994, Fitzpatrick 2004). Here we describe the nesting and foraging ecology of the Rufous-breasted Flycatcher in northeastern Ecuador and, where possible, provide comparisons with other *Leptopogon* species to examine intrageneric variation along the eastern Andean elevation gradient.

STUDY AREA AND METHODS

We observed Rufous-breasted Flycatchers and their nests between 2000 and 2200 m a.s.l. in the vicinity of the Yanayacu Biological Station and Center for Creative Studies (00°35.9S, 77°53.4W), 3 km southwest of Cosanga, Napo Province, Ecuador. We encountered nests during the course of general field work from May 2001 to November 2003, throughout which time we worked in suitable nesting habitat (i.e., primary forest riparian areas; see below) and thus likely found most nests present. Due to variation in nest accessibility, we were not able to provide equitable attention to all nests. At a subset of nests we measured nest (to the nearest 0.1 cm) and egg (to the nearest 0.1 mm) dimensions, and monitored nests regularly to determine the duration of incubation and nestling periods, and nest fate. At all active, as well as inactive (unoccupied) nests, we measured nest height and noted nest site characteristics (e.g., nest substrate, location, and habitat).

We also weighed eggs at two nests to measure egg mass. Because little is known regarding the degree of egg-mass loss (i.e., water loss) during incubation in tropical forest-breeding birds, we reweighed eggs at these two nests to provide preliminary data for the Rufous-breasted Flycatcher. We used a microgram balance to measure egg mass, and recorded egg mass as the average value of three consecutive mass readings. We weighed each of two clutches two times, one clutch 8 days apart and the other 14 days apart. We calibrated the scale with a standard weight prior to weighing eggs.

A single observer (RCD) collected foraging data during April 2002, January–February 2003, and July–August 2003. After encountering birds while walking through the study area along streams, trails, or small roads, the observer followed individuals and described their behavior vocally into a micro-cassette tape recorder in order to maintain visual contact (continuous, focal animal sampling; Martin & Bateson 1993). Upon locating a foraging flycatcher, the observer waited 5 sec before commencing data collection to prevent bias toward conspicuous behaviors, and then recorded up to five consecutive prey attack attempts. Upon observing the first prey attack attempt for a given bird, the observer visually estimated the bird's height, average canopy height within a 5-m radius of the bird,

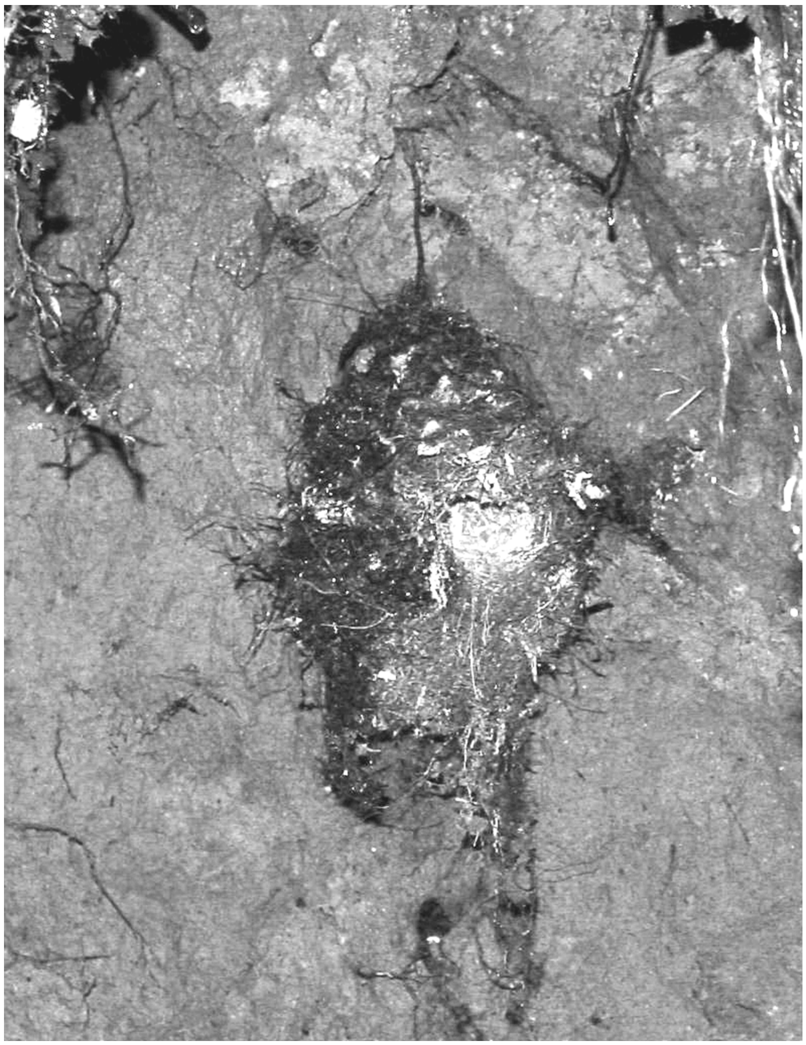

FIG. 1. Nest of the Rufous-breasted Flycatcher in western Napo Province, Ecuador, October 2002.

foliage density within a 1-m radius of the bird (0–5 scale with 0 indicating that all light passes through, and 5 that no light passes), and horizontal position in the tree (if applicable) where the attack occurred [see Remsen & Robinson (1990) for additional details]. For all prey attack attempts, the observer recorded attack maneuver, prey substrate, and, where possible, approximate size of the prey substrate (where applicable). For sally-type attacks, the observer also visually estimated angle and distance of the sally flight. Attack maneuvers follow Remsen & Robinson (1990), except that we lumped sally-stall with sally-hover and sally-glide with sally-strike, due to their respective similarities.

To supplement our field data on Rufous-breasted Flycatcher breeding biology, we examined gonad data included on labels of both Rufous-breasted and Inca flycatcher specimens (measurements made during specimen preparation) housed at the Louisiana State University Museum of Natural Science (LSUMNS). Because ovary size is not necessarily a good indicator of breeding condition (Marra 1990) and because few measurements of the largest ovum (a better indicator of breeding condition) were reported on specimen labels, we considered only male gonad measurements (i.e., size of the largest testis) to investigate seasonality of breeding activity (following Marra 1990). In one case where testes size was classified as "testes minute" on a specimen label, we placed it in a 2 mm size category.

RESULTS

Nesting ecology. We observed active nests (N = 17) during two distinct periods: March–May (3 nests) and September–November (14 nests); we also observed a pair with at least one dependent fledgling in November. We discovered most nests (70%) during incubation; clutch size was two at all nests (N = 12). Three nests discovered during the nestling stage contained two nestlings each. The nestling period (number of days from hatching to fledging) was 21 days at one nest and 22 or 23 days at another nest.

Eggs were immaculate white, showing no variation and no markings, and measured (mean ± SD) 20.3 ± 0.9 x 14.5 ± 0.5 mm (N = 19 eggs; 10 clutches). Mean egg mass was 2.23 ± 0.045 g (N = 4 eggs; 2 clutches) early in incubation. The average rate of mass loss due to water loss was 0.020 ± 0.004 g/day (N = 4 eggs; 2 clutches).

Nests were nearly-spherical, pendant balls with a centrally located, visored side entrance (Fig. 1). Occasionally a small amount of material hung below the nest and usually an "inverted tail" of material rose above the nest, fixing it to the attachment point. Different types of material comprised nests. The entrance "visor" and outer shell were composed of dry moss and brown and black rootlets, woven together with spider webs. This enclosed an inner chamber of dry moss. At one nest, cut in half to view construction details, the inner chamber of moss was roughly 5.5–6 cm thick below the cup and 1–2 cm thick on the walls and sides. Within this, a thick egg cup was composed of pale brown plant fibers, pale seed down, and spider silk. At this nest the cup was 2.25 cm thick on the bottom, 0.5–1 cm thick on the sides, and a thin layer of lining material covered rest of the inner chamber. All nests had a large number (> 20) of empty spider (Theridiidae) egg sacs on the exterior. These egg sacs were small yellow or whitish balls that occur naturally in situations similar to those where we found nests (i.e., beneath overhanging clay banks; HFG pers. obs.). Nests were suspended from single roots or vines, either at the tip (N = 14) or from the center of a U-shaped portion of the stem (N = 3). One nest was broadly attached to the bottom of an old nest of this species. Considering both active and inactive nests, all nests (N = 32) were located beside (i.e., within 0–6 m of) small mountain streams, well inside mature forest. The majority of nests (88%) hung below overhanging clay banks cut by forest streams, three nests (9%) hung beneath large fallen or strongly leaning tree trunks, and one (3%) beneath a rock overhang. Average nest height (± SD) was 1.7 ± 1.0 m (range 0.8–4.5 m; N = 18), with only two nests located above 1.9 m. Average (± SD) nest measurements were: inside (chamber) width 6.1 ± 0.6 cm, inside (chamber) height 9.0 ± 2.8 cm, cup depth 4.3 ± 0.7 cm, overhang above entrance (visor) 5.8 ± 1.2 cm, entrance width 4.0 ± 0.6 cm, entrance height 3.4 ± 0.3 cm, outside (structure) width 12.0 ± 0.7 cm, outside (structure) height 14.6 ± 1.5 cm, outside (structure) front to back 11.3 ± 1.5 cm, extra material above nest 5.8 ± 3.0

cm, extra material below nest (tail) 3.3 ± 2.4 cm (N = 4 nests).

We found one nest 26 days prior to the laying of the first egg. At this time it consisted of an unformed conical clump of dry rootlets and spider egg sacs twisted around a hanging root. Similar material was added until a ball was formed and, 10 days later a crudely formed nest, with an inner chamber and partially-visored entrance. At this point there was already a small amount of moss inside the rootlet shell, but no seed down had been added. Twelve days later the inner ball of moss was mostly in place, and seed down was being added. We were unable to determine if one or both adults participated in nest building. During building, adults approaching the nest while an observer was present immediately dropped the material they were carrying and began calling. These birds remained 3–6 m above the ground, calling repeatedly for 5–10 minutes before leaving the area.

As far as we could determine, only one adult incubated the clutch, while both adults attended the nestlings. Incubating adults never flushed from the nest until an approaching human observer was less than 1 m from the nest, and within view of the incubating adult. Brooding adults were very reluctant to leave the nest, often doing so only after some coaxing by the observer (e.g., gently tapping the nest or nearly touching the adult). An adult flushed from a nest during incubation typically flew swiftly and silently away. In contrast, an adult flushed from a nest containing nestlings, or an adult approaching its nest (during any stage) while an observer was near, typically remained 5–10 m above the observer giving repeated "skwee!" calls. In such situations, this adult was quickly joined by a second adult, presumably its mate, and both continued calling until the observer left the area.

Among five nests whose outcome was determined, two fledged successfully two young each, yielding a nesting success of 40% or an average of 0.8 nestlings per nest. Of the three nests known to fail, one nest (with eggs) was torn down, presumably by a predator, one nest (with nestlings) was depredated by a long-tailed (Andean) weasel (*Mustela frenata*), and one nest (with nestlings) failed when heavy rains caused a leak in the sheltering clay bank, soaking the nest and nestlings.

Foraging ecology. Rufous-breasted Flycatcher pairs typically foraged together in mixed-species flocks, perching on relatively exposed branches from the under-story to the subcanopy. The birds almost always perched on live tree branches, diagonal or horizontal, moss-covered or bare, that averaged (± SD) 4.0 ± 2.4 cm in diameter (range 1–15; N = 21); birds rarely perched on the tops of large leaves (e.g., *Cecropia*). Mean foraging height was 10.4 ± 3.5 m above the ground (range 2.4–15.2; N = 72 events, 72 birds); birds foraged an average of 8.1 ± 4.0 m below the canopy (range 3.0–21.3; N = 72 events, 72 birds). Relative foraging height (bird height/canopy height) was 0.57.

Rufous-breasted Flycatchers were completely insectivorous and attacked prey using primarily sally-hover (48.7 %) and sally-strike (46.2 %) maneuvers, and rarely sally-pounce (4.2 %) or glean (0.8 %) techniques (N = 119 attacks, 76 birds). Although the flycatchers occasionally attacked flying insects in the air (4.2 %), their prey were located mainly on live leaves (87.3), followed by bark or bare stem (5.0 %), moss (2.5 %), and flowers (0.8 %) (N = 119 attacks, 76 birds). Rufous-breasted Flycatchers searched for prey while perched, often remaining on a perch 10–20 sec before making an attack or flying to a new perch. While perched, the birds primarily scanned upwards, presumably searching for insects on the undersides of live leaves. Of 87 live leaf substrates where leaf surface was determined, 82.7% of attacks were toward undersides,

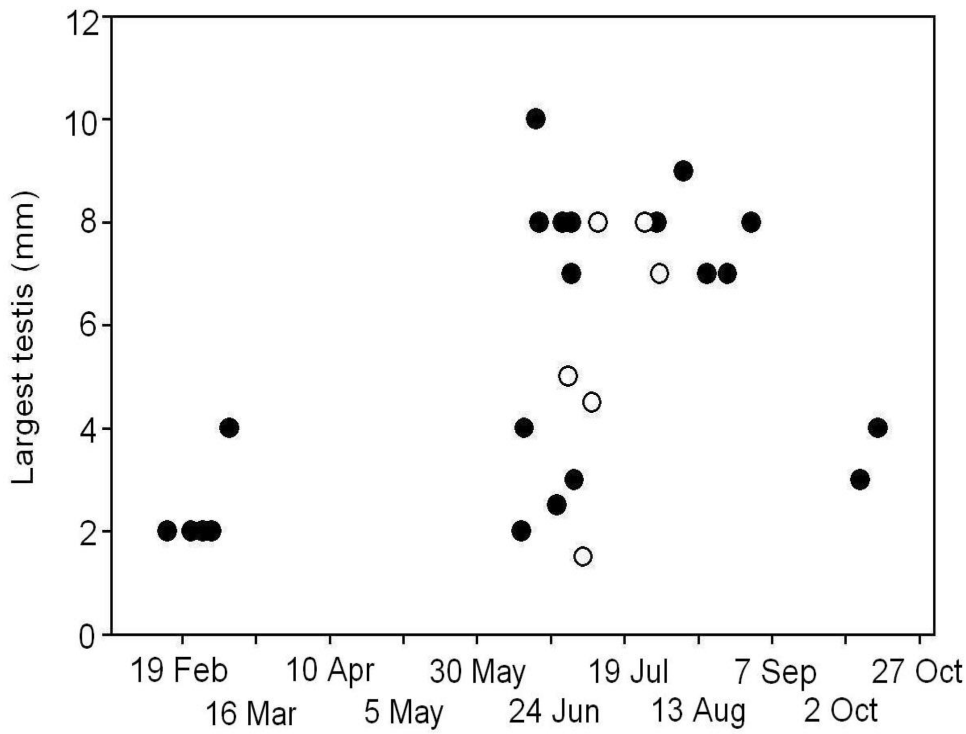

FIG. 2. Gonad data indicate that Rufous-breasted Flycatchers (open circles) exhibit high breeding activity during July in northern Peru, in the extreme southern portion of its geographic range. A larger sample size for Inca Flycatcher (closed circles) suggests a breeding season during roughly the same period, extending from June through August, throughout its range in eastern Peru.

14.9% were toward uppersides, and 2.3% were directed at leaf tips. Average leaf size was 29 x 37 cm (N = 90 attacks, 65 birds). Of 105 sally-type attack maneuvers where direction was noted, 60.9% were directly upward or upward-diagonal, 26.7% were horizontal, and 12.4% were downward or downward-diagonal. Average (± SD) sally distance was 82 ± 53 cm (range 5–300; N = 101 attacks, 67 birds). Most attacks occurred in the outer one-third (59%), followed by the middle (33%), of the tree's horizontal profile, where foliage is most abundant; Rufous-breasted Flycatchers rarely attacked prey on the trunk or inner branches (i.e., the inner one-third; 8%; N = 73 attacks, 73 birds). Foliage density around prey attack locations was relatively low, averaging 2.1 (mode = 2; N = 73 attacks, 73 birds) on a 0–5 scale, indicating that, on average, 75–95% of light passed through the 1-m diameter area surrounding the site.

Museum data. Data from LSUMNS specimen labels showed male Rufous-breasted Flycatchers (N = 6) in breeding condition during July in Dept. Cajamarca, northern Peru, at the southern edge of the species' range (Fig. 2). Similarly, LSUMNS data showed male Inca Flycatchers (N = 21) in breeding condition from 19 June to 31 August farther south in Depts. San Martin, Huanuco, Pasco, and Cusco, Peru (Fig. 2).

DISCUSSION

Limited breeding activity by Rufous-breasted Flycatchers during March–May, the peak of the rainy season at our site, was eclipsed by a major breeding effort during September–November, corresponding with the dry season. While we may have overlooked some nests during the March–May period, our effort was not greater during September–November, suggesting that the observed seasonal variation in nesting activity is real. Timing of breeding at our site in northeastern Ecuador is consistent with the few published data available from elsewhere in the species' range (i.e., breeding condition male in mid-October, eastern Boyacá, Colombia; Olivares 1971). Unpublished LSUMNS specimen data from northern Peru suggest that, at the southern edge of its range, the Rufous-breasted Flycatcher breeds during July, and probably June–August as is apparent for its sister species, the Inca Flycatcher, farther south in eastern Peru (Fig. 2). June–August is the driest period of the year on the eastern slope of the Peruvian Andes. High dry-season breeding activity of Rufous-breasted and Inca flycatchers in Peru is thus consistent with our pattern of Rufous-breasted Flycatcher dry-season breeding in northeastern Ecuador. It is important to note, however, that the specimen label data used to infer breeding activity of Rufous-breasted Flycatchers in northern Peru is very limited. Additional data are necessary to understand fully the seasonality of breeding in eastern Peru.

The nest and eggs of the Rufous-breasted Flycatcher are superficially similar to those described for its congeners, Sepia-capped and Slaty-capped flycatchers, which also build semiglobular nests with side entrances, suspended from a log, rock, or root in dark sheltered areas, and have unmarked white eggs (Belcher and Smooker 1937, Moore 1944, Skutch 1967, Hilty & Brown 1986, ffrench 1991, Aguilar & Marini 1997). Data from Sepia-capped Flycatchers breeding in semi-deciduous forest in Minas Gerais, southeastern Brazil (Aguilar & Marini 1997) allow for more detailed comparisons. Average nest height (1.2 m above the ground in Sepia-capped Flycatchers; 1.7 m in Rufous-breasted) and nest dimensions (outer height 13.4 cm in Sepia-capped, 14.6 cm in Rufous-breasted; outer width 10.1 cm in Sepia-capped, 12.0 in Rufous-breasted) of the two species appear to be generally similar, although Rufous-breasted may build slightly larger nests than Sepia-capped. Sepia-capped Flycatchers laid 2–3 eggs in Minas Gerais (Aguilar & Marini 1997), whereas we observed only 2-egg clutches in Rufous-breasted Flycatchers. Sepia-capped Flycatcher eggs (average 1.9 g; 18.5 x 13.7 mm; Aguilar & Marini 1997) appear to be smaller in mass and linear measurements than Rufous-breasted Flycatcher eggs (average 2.23 g; 20.3 x 14.5 mm; this study). Investigation of the statistical significance or biological importance of these differences is beyond the scope of this paper, but these comparisons may reflect variation in adaptations for breeding at two extremes of an elevation gradient.

Although little information is available for comparison, the duration of the nestling period may also vary among highland and lowland *Leptopogon* species. The 21–23 day nestling period documented for the Rufous-breasted Flycatcher (this study) is longer than the 18–21-day nestling period documented for the Sepia-capped Flycatcher (Aguilar and Marini 1997) and the 20-day nestling period documented for the Slaty-capped Flycatcher (ffrench 1991). While further data are needed to describe robustly the duration of the nestling period and its variation in these three species, a longer nestling period for the Rufous-breasted Flycatcher in humid montane forest than for Sepia-capped and Slaty-capped flycatchers in humid lowland forest makes intuitive sense given cooler conditions at higher elevations.

Nest composition of the Rufous-breasted Flycatcher, being primarily rootlets on the exterior, moss on the interior, and a nest cup of soft plant fibers, is generally similar to that described for the Sepia-capped Flycatcher (Moore 1944, Sick 1993) and the Slaty-capped Flycatcher (Belcher and Smooker 1937, Skutch 1967). The use of spider egg sacs to decorate the outside of Rufous-breasted Flycatcher nests appears to be similar to the "parti-coloured cocoons on the outside..." of Slaty-capped Flycatcher nests (Belcher and Smooker 1937) and the "tiny white and tan-colored fluffs of thistle-down bound into the outer surface…" of Sepia-capped Flycatcher nests (Moore 1944). It thus appears that this trait, well-known in the lowland *Leptopogon* species, is also characteristic of their Andean congener. The function of spider egg sacs is not known, but they may aid in camouflaging the nest. In reviewing literature and museum nest collections, Hansell (1996) concluded that arthropod cocoons (typically spider egg sacs) adorning the outside of birds' nests function to conceal nests through crypsis. Pale cocoons on a dark nest, and against a variable background, are thought to reflect light such that the entire nest resembles a random sample of the background, thus allowing the nest to blend into the background (Hansell 1996).

While foraging, Rufous-breasted Flycatchers typically perch on relatively exposed branches in the mid-story of the forest, scanning the undersides of leaves of the sub-canopy above, and often remain on individual perches for extended periods of time before making relatively long sally-flights to attack insects. In contrast, the 10–12 species of tyrant-flycatchers that regularly co-occur with Rufous-breasted Flycatchers in the same mixed-species flocks at our study site tend to change perches frequently, move through thicker vegetation, and make shorter sally-attacks to foliage (RCD pers. obs.). Rufous-breasted Flycatcher foraging ecology is generally similar to that of other *Leptopogon* species, based on anecdotal descriptions for each species (see Fitzpatrick 2004) and quantitative data for the Slaty-capped Flycatcher in Bolivia (Remsen 1984). Similar to our observations for Rufous-breasted, the Slaty-capped Flycatcher searched for prey in the middle story of forest, attacked insect prey using primarily (only) sally-type attack maneuvers, and made sally flights just under 1 m in distance (Remsen 1984).

The nesting and foraging ecology of the Rufous-breasted Flycatcher appears to be generally similar to that of its congeners, Sepia-capped and Slaty-capped flycatchers, based on currently available information. Additional quantitative natural history data for *Leptopogon* species will allow us to investigate more thoroughly how life histories of congeneric species reflect evolutionary history and current ecological relationships. Most interesting will be comparable natural history information for the other taxon comprising this Andean superspecies, the virtually unknown Inca Flycatcher.

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