

The enigmatic Rothschild's Swift (*Cypseloides rothschildi*): Natural history, distribution, and seasonality

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ABSTRACT—Rothschild's Swift (*Cypseloides rothschildi*) is among the least known South American swifts. Here we clarify its distribution and seasonality, and provide detailed natural history data and breeding information. We compiled 197 records of Rothschild's Swifts (museum specimens, citizen science initiatives, literature, and field observations) from Argentina and Bolivia; most from the breeding season (Oct–Mar, 177 records; 44 documented), a few thought to be on migration (Apr and Sep, 15 records; 3 documented), and fewer during the nonbreeding period (May–Aug, 5 records; 1 documented) with no records from July/August. Rothschild's Swifts are migratory, but the wintering quarters remain unknown. The distribution during the breeding season is broadly overlapping with the Austral Yungas of Argentina and Bolivia, with sparse records in Andean and extra-Andean ranges with forested and non-forested waterfalls. Our breeding distribution model indicated high presence probabilities in the Austral Yungas of Bolivia and Argentina. The breeding season during the austral spring and summer (late Oct/mid-Nov to mid-Mar/early Apr in northwest Argentina) began roughly with the early rains as in other Neotropical swifts. Our data from 8 breeding sites and from 8 nests that we studied in northwest Argentina regarding nest placement (near waterfalls), nest features (moss or moss and mud cups), eggs (single and white), and on the protracted development of Rothschild's Swift nestlings (~55–60 d) and the sequence of plumage acquisition and behavior were coincidental with what is known from other *Cypseloides*. We provide behavioral information from a temporarily captive individual, which provided the first sound recordings of nestling/fledgling vocalizations of Rothschild's Swift—presumably the first available for any *Cypseloides*. It is unclear whether these vocalizations, recorded in captivity, represent developmental precursors of adult sounds or begging calls. Received 24 July 2020. Accepted 1 December 2020.

Key words: Andes, Apodidae, Black Swift, migration, phenology, Sooty Swift, Yungas endemic.

El enigmático vencejo pardo (*Cypseloides rothschildi*): historia natural, distribución y estacionalidad

RESUMEN (Spanish)—El Vencejo Pardo (*Cypseloides rothschildi*) es uno de los vencejos sudamericanos menos conocidos. Aquí esclarecemos su distribución, estacionalidad, y proveemos datos detallados de reproducción e información de historia natural. Compilamos 197 registros de vencejos pardos (especímenes de museo, iniciativas de ciencia ciudadana, literatura y observaciones de campo), todos de Argentina y Bolivia; la mayoría en época reproductiva (octubre–marzo, 177 registros; 44 documentados), unos pocos posiblemente en migración (abril y septiembre, 15 registros; 3 documentados), menos en época no reproductiva (mayo–agosto, 5 registros; 1 documentado) y ningún registro en julio/agosto. Los vencejos pardos son migratorios, pero sus sitios de invernada siguen siendo desconocidos. Su distribución en la época de cría se superpone ampliamente con las Yungas Australes de Argentina y Bolivia, con registros dispersos en cordones Andinos y extra-Andinos, en cascadas boscosas o desprovistas de bosque. Nuestro modelo de distribución indicó alta probabilidad de presencia en las Yungas Australes de Argentina y Bolivia. La época reproductiva durante la primavera y verano australes (octubre tardío/mediados de noviembre a mediados de marzo/abril temprano en el noroeste argentino) comenzó aproximadamente con las lluvias tempranas, como en otros vencejos neotropicales. Nuestros datos de cría de 8 localidades y de 8 nidos que estudiamos en el noroeste argentino muestran que los sitios para anidar (cerca de cascadas), características de los nidos (tazas de musgo o barro), huevos (únicos y blancos), el prolongado período de desarrollo de los vencejos pardos (~55–60 d) y la secuencia de adquisición de plumaje y comportamiento coinciden con lo que se sabe de otros *Cypseloides*. Proveemos información del comportamiento de un individuo momentáneamente cautivo que proveyó las primeras grabaciones de vocalizaciones de pichón/volantón de vencejo pardo; presumiblemente la primera disponible para *Cypseloides*. No está claro si estas vocalizaciones representan precursores ontogenéticos de los sonidos de adultos o voces de pedido de alimento.

Palabras clave: Andes, Apodidae, endémico de las Yungas, fenología, migración, vencejo negro, vencejo negruzco.

Swifts are among the most enigmatic birds worldwide. The genus *Cypseloides* currently comprises 8 species, 3 of which were described in the last 75 years (Zimmer 1945, Eisenmann and Lehmann 1962, Navarro S. et al. 1992). Rothschild's Swift (*Cypseloides rothschildi*) is the least

known South American species. It has been considered as an Austral Yungas endemic of northwest Argentina and southern Bolivia (Stattersfield et al. 1998), but has frequently been thought to breed or overwinter farther north up to southern Peru (Zimmer 1945, 1953; Short 1975, Chantler 1999, Chantler and Driessens 2000; but see Roesler et al. 2009) or even Colombia (von Sneider 1955; but see Eisenmann and Lehmann 1962). Distributional data is meager and widely scattered in different sources, leading to an unsatisfactory understanding of its seasonality and distribution, and while it has been considered

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as possibly migratory (Olrog 1963, Short 1975), rigorous analyses are missing. Similarly, breeding information is scarce, lacks detail, and has been published in seldom-read sources, therefore leading to a poor understanding in the mainstream literature. For example, despite old reports of nests and eggs (Dabbene 1918, Smyth 1928), an influential paper on swift biology mentioned that nothing was known of its breeding biology (Marín and Stiles 1992; see also Pearman et al. 2010). Indeed, there is no precise information documenting basic aspects such as breeding season, nest sites and placement, nesting materials, and characteristics of nestlings.

The taxonomic status of Rothschild's Swift is not settled. Historically considered identical to Sooty Swift (*C. fumigatus*; Dabbene 1917), it was later described as a paler and larger subspecies, under the name *C. fumigatus major* by Rothschild (1931). The then novel inclusion of Great Dusky Swift (*C. senex*) in the genus *Cypseloides* caused a clash between the name *Chaetura major* of Bertoni (1900) (a junior synonym of *C. senex*) and *C. fumigatus major* of Rothschild (1931), leading Zimmer (1945) to propose the replacement name *C. fumigatus rothschildi* for the latter. Full species status was afforded for the first time when Rogers (1939) considered "the bird described by Rothschild as *C. f. major*, from Argentina, a valid species. It is not only much larger (wing, 148–158 mm, one 163), but has actually smaller (relatively much smaller) feet (tarsus, 12–14 mm, one 15), the tarsus and toes more slender; *fumigatus* has a wing only 139–142 mm., tarsus, 15–16. *C. major* further differs from *fumigatus* in its mummy-brown instead of brownish black coloration, the crown as well as the forehead scaly, the throat not paler than the rest of the under parts, and no white chin, and still further in its rounded rectrices with normal shafts compared with the stiff shafts and at least sometimes tapering tips of the rectrices of *fumigatus*." These distinctions have been repeatedly mentioned in the literature and form the basis of its modern recognition as a separate species (Meyer de Schauensee 1966, Chantler and Driessens 2000, Rensen et al. 2020). Rothschild's Swift has also been considered to form a superspecies with Sooty, Black (*C. niger*), and White-chested (*C. lemosi*) swifts (Short 1975). Additionally, Marín and Stiles (1992) suggested that Rothschild's Swift might not be a valid species, while

suggesting that Sooty Swift was possibly conspecific with White-chinned Swift (*C. cryptus*), but genetic data contradicts the latter (Biancalana et al. 2017).

In this contribution, we synthesize the breeding distribution and seasonality of Rothschild's Swift based on a larger database than heretofore available. We also report for the first time detailed breeding information, including nest site, nest description and placement, breeding habitat, nestling development and vocalizations, and timing of the breeding season in northwest Argentina.

Methods

Distribution and seasonality

We compiled presence localities for Rothschild's Swift using literature sources, personal or photographic examination of museum specimens and labels, sound archives, eBird data, documented records from other online sources, and our own personal data (Supplemental Table S1). We used these data to assess the geographic distribution and seasonality and to obtain potential distribution models. To assess seasonality, we plotted the number of records per month and mapped their geographical distribution. To avoid biasing, we eliminated eBird duplicates by deleting the repeated "group identifiers" and left only the record of the author whose surname was first in alphabetical order; we only included the first visit to nesting sites that we visited repeatedly (see Supplemental Table S1).

To model habitat suitability, we used maximum entropy modeling using Maxent 3.4.1 (Phillips et al. 2017). The Maxent algorithm has been shown to be robust for modeling presence-only occurrence data, even with very low numbers of occurrence records, outperforming many other techniques (Elith et al. 2006). According to our biological question and the extreme flight capability of *Cypseloides* swifts, we set our background area as South America (latitude 13.4 to -56.7 , longitude -81.6 to -34.05). Models were fitted using the 19 bioclimatic variables available in CHELSA 1.2 (30 arcsec, ~ 1 km; Karger et al. 2017; <http://chelsa-climate.org/>), an EarthEnv Shannon diversity of Enhanced Vegetation Index (EVI; 30 arcsec, ~ 1 km; Tuanmu and Jetz 2015; <http://www.earthenv.org/>), and a topographical CGIAR-CSI SRTM 90m Digital Elevation Model

(DEM) 4.1 (30 arcsec, ~1 km; Jarvis et al. 2008; <http://srtm.csi.cgiar.org>).

Environmental variables are frequently intercorrelated (Graham 2003), causing problems of multicollinearity, with models providing incorrect estimations of a given variable in the presence of collinear variables (Dormann et al. 2008). To deal with this, a variable selection process was performed removing highly correlated predictors using principal components analysis (PCA). The PCA consisted of all environmental variables for 1,000 random points within the background area. Encompassing 98% of the environmental variability, we selected CHELSA variables of mean diurnal range, temperature seasonality, mean temperature of the driest quarter, precipitation of the driest month, precipitation of the wettest quarter, precipitation of the warmest quarter, precipitation of the coldest quarter, the CGIAR-CSI DEM, and the EarthEnv Shannon EVI. We further diminished spatial autocorrelation for ecological niche modeling of the breeding distribution of Rothschild's Swifts by reducing the number of data points using the following protocol. First, we included only points known to fall within the breeding period of the species according to our data, which extends from early October to late March. Second, we decided to leave all data points of confirmed nesting records regardless of the distance between them, since these constitute the best information we have on the breeding grounds of the species. Third, we applied a 20 km radius buffer around each data point and eliminated points falling within this radius, prioritizing documented records over undocumented ones. This reduced our database to 50 points, which were used to model the breeding distribution.

We obtained an initial set of 10 models, setting Maxent to select at random 75% of the occurrence localities at each run for training, and leaving the remaining 25% for testing. This initial set was used to identify variables with minimal or no contribution to the overall model. Maxent jackknife test of variable importance was used to evaluate the relative strength of each predictor variable (Yost et al. 2008). Shannon EVI variable was deleted from the set of variables selected from the PCA. We tested for features shapes (linear, quadratic, and hinge) and regularization multipliers (0.1, 1, 5, 10) using ENMTools 1.3. We

selected the best model based on AIC_c. Finally, to assess the robustness of our model, we ran 10-fold cross-validation and assessed variable importance through a jackknife estimation of variable contribution (Phillips and Dudík 2008).

Breeding

We surveyed 4 creeks in the province of Salta, northwest Argentina, looking for nests of Rothschild's Swifts in which we knew about or suspected the possible presence of waterfalls: Quebrada de Tilián, Río Corralito, Quebrada de Escoipe, and Quebrada del Toro (see Supplemental Table S1 for initial visit dates). For each nest found we took notes on nest placement (height from the ground, substrate, distance and placement from waterfall, and distance from other nests if present) and materials used for nest construction. When possible, we also measured the nest's inner and outer height and diameter to the nearest 0.5 mm. We measured nestling bill length and bill width at the anterior end of nares, tarsus length, and unflattened wing length using digital and dial calipers (precision 0.01 mm), and weight using a digital MH500g scale (precision 0.1 g).

Nestlings were photographed during each visit to document the progression of plumage acquisition. The age of nestlings was estimated based on features of nestlings of known age of Sooty (Biancalana 2015), Black, and White-fronted swifts (*C. cherriei*) (Marín and Stiles 1992). Additionally, we sought breeding information from the literature, consulted third parties, and searched for nests and eggs in natural history collections (Supplemental Table S1). Finally, we took notes on the behavior of one nestling we held in captivity. We sound-recorded its presumed begging calls (using a Marantz PMD-661 MKII sound recorder with a Telinga Pro 6 microphone on a Telinga Universal Parabola at 48 kHz and 24 bit, and a Canon EOS T1i camera), and obtained measurement and weight data as described above for nestlings. Spectrograms shown were built in Raven Pro 1.5 (<http://www.birds.cornell.edu/raven>) using the following spectrogram parameters: Window-Type: Hann, Size: 512 samples (= 10.7 ms), 3dB Filter Bandwidth: 135 Hz; Time grid-Overlap: 50%, Hop size: 256 samples (= 5.33 ms); Frequency grid-DFT size: 512 samples, Grid spacing: 93.8 Hz. All the recordings are deposited

at the Macaulay Library of Natural Sounds (Cornell Lab of Ornithology, Ithaca, New York, USA).

Results

Distribution and seasonality

We obtained 197 records of Rothschild's Swifts all from Argentina and Bolivia, 48 of which were documented (Fig. 1, Supplemental Table S1). The vast majority of records came from the breeding season (Oct–Mar, 177 records; 44 documented), with fewer records of birds thought to be on migration (Apr and Sep, 15 records; 3 documented), a handful of records during the nonbreeding period (May–Aug, 5 records; 1 documented), and no records at all in July or August (Fig. 1, Supplemental Table S1). The spatiotemporal distribution of records clearly show that Rothschild's Swifts are migratory (Fig. 1), breeding during the austral spring and summer, and migrating to hitherto unknown wintering quarters. The species basically disappears from the ornithological radar during the nonbreeding period, with 4 out of 5 records lacking documentation and therefore here treated with caution.

Our distribution model using breeding records and a geographically spread sample of records from the breeding season indicated high presence probabilities in the Austral Yungas of Bolivia and Argentina, south to eastern Catamarca in the latter country (Fig. 1). It also showed high probabilities in the humid Sierras de Guasayán in southwest Santiago del Estero (with influence of Yungas), but more reduced probabilities for the drier and colder Sierras de Córdoba, and virtually null probabilities in flat areas below mountains and in mountainous terrain above Yungas forest (Fig. 1). Our model was broadly consistent with the plotting of raw data, but it also showed high-presence probabilities in the Andes and eastern foothills of southern Bolivia, in a large area that currently constitutes a gap with no records between a southern and a northern cluster (Fig. 1).

Breeding

All known breeding data pertains to 8 localities within the Austral Yungas of northwest Argentina (Fig. 1, Supplemental Table S1), although the species conceivably breeds in the Austral Yungas

and possibly Intermontane Valleys of Bolivia based on the timing and number of records (Fig. 1; see Remsen and Ridgely 1980, Hennessey et al. 2003). Breeding seems likely also in other Andean and extra-Andean ranges with waterfalls in Argentina, such as the Sierra de Guasayán. Documented breeding records came from 2 historical localities in Tucumán province (Tafi Viejo and Taficillo; ~650–850 m a.s.l.) and 5 newly found sites at 4 localities in Salta province (2 sites at Quebrada de Tilián, Finca La Vida at Quebrada de Escoipe, Chorro Blanco at Río Corralito, and Parque Nacional El Rey; 950–1,875 m a.s.l.), while undocumented records come from 1 locality in Jujuy province (Río Yala) and 1 in Catamarca province (Río Las Cañas) (Fig. 1, Supplemental Table S1). Although we saw Rothschild's and White-collared swifts (*Streptoprocne zonaris*) during our visit to Chorro Azul in the Quebrada del Toro on 27 January 2017, we did not find any nests in the first waterfall. However, we failed to reach a second waterfall due to the broken relief, where breeding is likely to occur (Supplemental Table S1).

We found 8 nests at 4 sites in 3 localities: solitary nests were found at Quebrada de Tilián and Chorro Blanco, and two 3-nest colonies were found, 1 at a second site in Quebrada de Tilián and another at Finca La Vida (Fig. 2, Supplemental Table S2). Additionally, a nest with a large nestling was photographed on 3 January 2013 by Rocío Lapido at the Salto de Los Loros waterfall in Parque Nacional El Rey, Salta, Argentina (Supplemental Table S2). All the nests that we found were cups or half-cups placed behind or close (0.7–10 m) to waterfalls, 2.2–12 m above the water level and placed on rocky ledges or small rocky cavities in vertical walls (Fig. 2, Supplemental Table S2). All but 1 nest had a mud base topped by green bryophytes conforming the lining and were subjected to direct waterfall spray (Fig. 2, Supplemental Fig. S1). New nests had soft, fresh, green and spongy lining, which became flat and browner as nesting advanced. The dry nest that we found at Chorro Blanco was placed in an unusual place, a rocky slab on a small cavity below the roots of a tree, 10 m away and in front of a waterfall; it had no apparent mud base and seemed instead to be made by bryophytes that were dry by the time we found it (Fig. 2, Supplemental Table

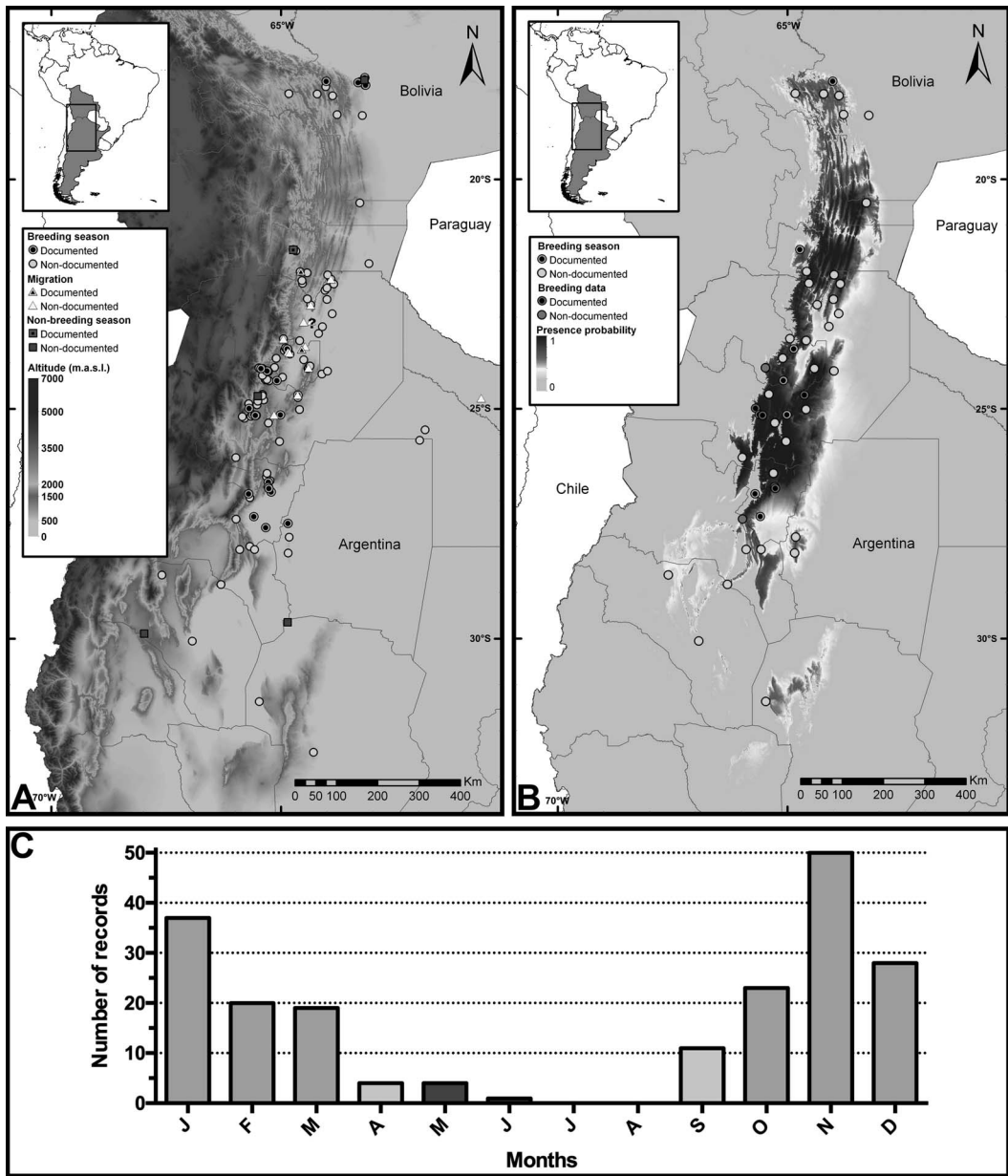


Figure 1. Geographic distribution and seasonality of Rothschild’s Swift (*Cypseloides rothschildi*). (A) Breeding, migration, and nonbreeding season records. (B) Distribution modeling based on concrete breeding localities and geographically separate breeding season records (see Methods). (C) Histogram showing seasonal distribution of records; note the abundance of records during the breeding season (gray; Oct–Mar), reduced number of records during presumed migration after and before breeding (pale gray; Apr and Sep), and almost complete absence of records during the nonbreeding season (dark gray; May–Aug).

S2). Most nests were inaccessible, but we were able to examine and measure the 2 solitary nests: the Quebrada de Tilián one was 140 mm tall, 72 × 72 mm wide and was flat, while the dry Chorro

Blanco nest was 124.5 mm tall, 119 × 90 mm wide and had a shallow 18 mm depression.

We were unable to find nests with eggs, but museum searches and old published records show

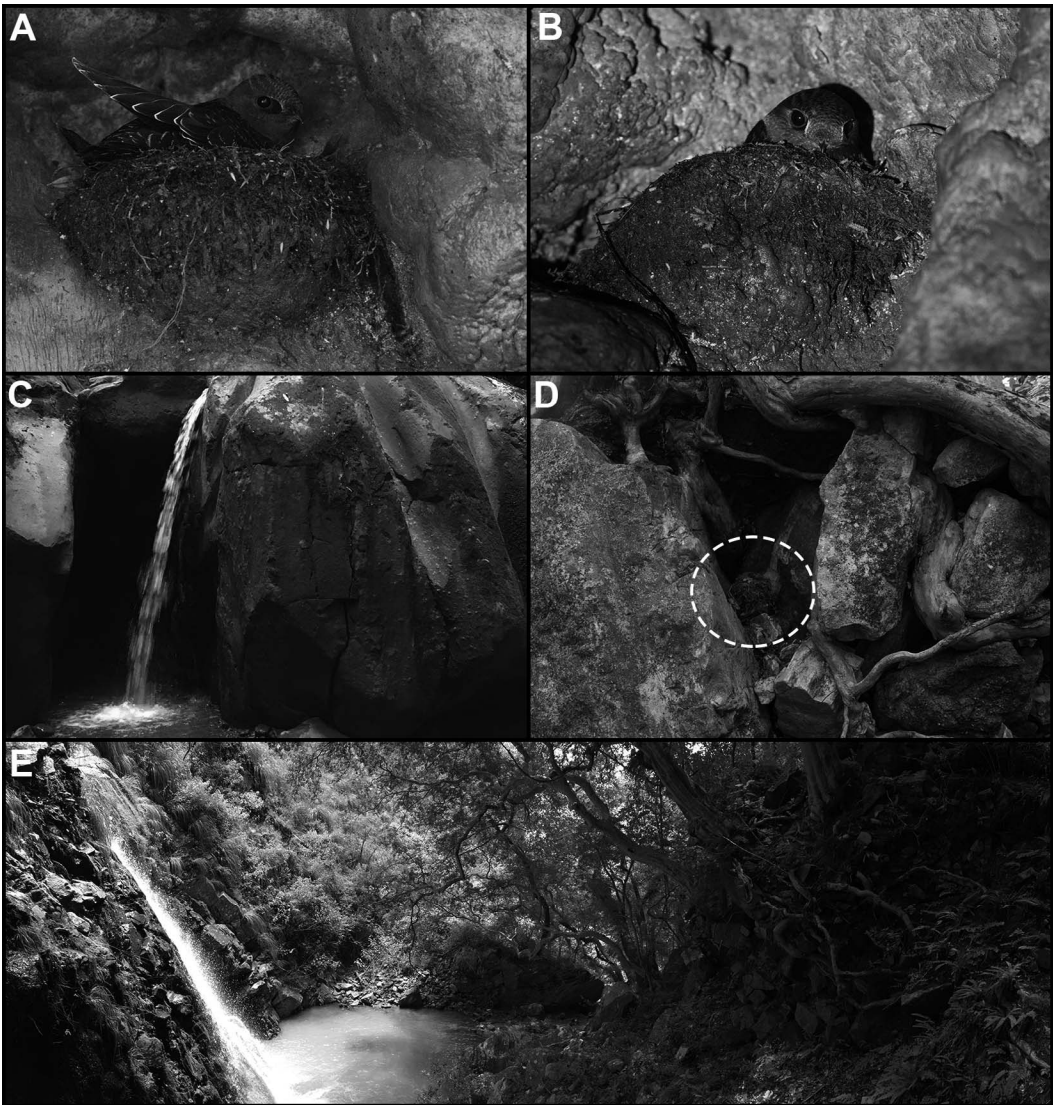


Figure 2. Nestlings, nests, and breeding habitat of Rothschild's Swift (*Cypseloides rothschildi*) in Salta, Argentina. (A) Lateral view of a large and contrastingly marked nestling at nest, Quebrada de Tilián colony, 25 January 2017; photograph JIA. (B) Frontal view of a large and little marked nestling at nest, Quebrada de Tilián colony, 25 January 2017; photograph JIA. (C) Nesting habitat at Quebrada de Tilián waterfall, 25 January 2017; photograph EAD. (D) Unusual nest (dashed line) placed in a dry area under the roots of a *Eugenia* tree near a waterfall, Chorro Blanco, 31 January 2017; photograph JIA. (E) Nesting habitat at Chorro Blanco, 31 January 2017; photograph EAD.

that eggs (all from Tañi Viejo and Taficillo in Tucumán) are white, without gloss, and measure 28.1 ± 1.4 mm ($n = 3$) \times 18.4 ± 0.5 mm ($n = 4$) (see Supplemental Table S1 for measurements).

The breeding season seems to extend from late October/mid-November to mid-March/early April in northwest Argentina. The earliest documented

egg record was from 18 November at Taficillo, but an undocumented record suggests an early start of incubation by 7 November at Río Yala, and the latest documented egg was from 23 December at Tañi Viejo (Supplemental Table S1). Documented nestling records span 26 December to 12 March at the Quebrada de Tilián (Supplemental Table S1).

The 2 sites at Quebrada de Tilián were considerably out of phase; for example, on 25 January 2017 the solitary nest had an 8- to 9-day-old nestling (Supplemental Fig. S2), while the 3 nestlings at the colony were at least an estimated 40–45 d old (Fig. 2). The next breeding season all these nests were reused: the solitary nest was renewed and ready to be used by 20 November 2017, while the 3 colony nests had nestlings of unknown age by 26 December 2017 (Supplemental Table S2).

We observed adults brooding nestlings of 8–9 d but no adults were observed at nests after 14–15 d, perhaps because this is close to the boundary age at which nestlings acquire thermoregulation (Collins 1968a, Foerster 1987, Marín 1997a).

Nestling development

We were able to follow one nestling at the solitary nest at Quebrada de Tilián across almost the entire nestling period from an age of ~8–9 d (25 Jan 2017) until it fledged at ~54–65 d (after 12 Mar and before 24 Mar 2017). Measurements, detailed plumage descriptions, and information on nestling behavior can be found in Supplemental Table S2 and photographs in Supplemental Fig. S2.

Captive nestling/fledgling

On 22 January 2017, Marlene Sánchez Palacios serendipitously found a nestling of Rothschild's Swift near a waterfall in the Quebrada de Tilián. She posted an image of the bird on social media seeking help and Gabriel Núñez called our attention to her request. On 24 January we took the nestling to JIA's home. We attempted, without success, to find the empty nest to which it might have belonged on 25 January 2017, and thus decided to take care of it. On 31 January 2017, it was released at the exact place in which it was found.

The nestling was ~60 d old on 24 January 2017. The contour feathers were fully developed, without visible areas of semiplumes. The wings were approaching full length, ~83% of the adult size, exceeding the length of the body and kept backward at rest. The contour feathers, except for the lores, collar, and tail, had narrow, pale white fringes at the tip. The feathers between the forehead and nostrils also had narrow, pale white

fringes at the tip, whereas feathers of a small area on the chin were pale white, leading to dark feathers posteriorly on the nape and neck, and the throat. Tarsi and toes were pinkish-gray, and claws were black.

The nestling was held on a soft clean and dry cloth inside a 20 × 30 cm cardboard box with numerous breathing holes, which was placed in dark and cool rooms. We fed it with an assortment of ants (mostly flightless and flying *Camponotus mirabilis*) and undetermined flies that were macerated in water for 30 min to 2–6 h periods. The bird swallowed insect balls (approximately 0.5 × 0.5 cm to 1 × 1 cm) that were put on our fingertips and gently rubbed against the bill commissure. This procedure was repeated once every 2–3 h during the daylight hours, and the bird was given periods of 10–15 min either in the hand or with the box open to lure it to fly inside a room with natural light. When periods of 2–3 h without feeding were approaching, the bird spontaneously gave high-pitched wailing calls and twitters (Fig. 3A, 3B). These vocalizations were also given between consecutive feeding events within a feeding bout, sometimes while preening, and sometimes without any clear specific context. The duration, rate of note delivery, and number and type of notes varied greatly (Fig. 3A, 3B). For example, arced or complex notes could be given alone and a bout could extend for more than 20 s (Fig. 3A, 3B). The bird frequently assumed a horizontal resting position with wings closed and pointing upward, the tail lowered and the feet thrust forward; the same position was assumed when clinging to us. After alighting on us, it climbed proficiently and looked for shelter (e.g., below an armpit, or above the neck, introducing its head in our hair). The bird was more active, fluttered its wings, and called more often at dawn and dusk than during the day. We noted an admirable complexity in the movements of the feathers above and in front of the eyes, which gave the bird a very expressive character, depending on whether the frontal tuft was raised or lowered and whether the line of feathers above the eye gave a straight or flexed upper bound.

During its stay in captivity, our feeding protocol and food types were insufficient to increase its mass, which decreased from 29 g (26 Jan) to 25.5 g (29 Jan), while its wing chord increased from 124.18 to 128.06 mm in this period (being

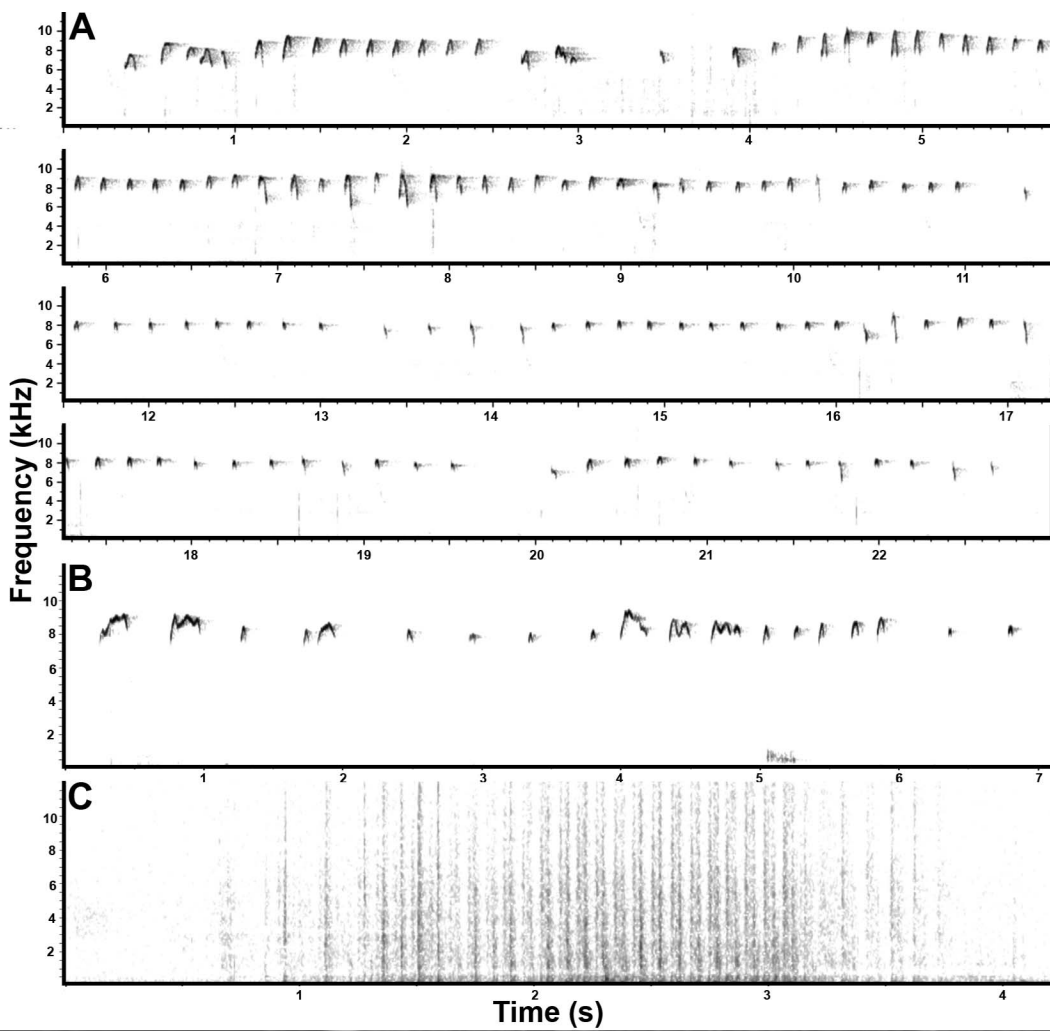


Figure 3. Vocalizations and appearance of a captive Rothschild's Swift (*Cypseloides rothschildi*) fledgling at an age of >60 d. (A) Full-length, long calling bout showing diverse note types. (B) Detail of a bout showing complex wailing and arced notes. (C) Heating wingbeats. (D) Lateral and (E) dorsal views in the field of the fledgling on its release date. Recordings from 28 January and photographs from 31 January 2017 by JIA.

considerably lighter than the ~36 g of a similarly sized nestling in nature; see Supplemental Table S2). Between 24 and 25 January the bird made its first short 3–4 m flights in straight line clinging to curtains; between 26 and 29 January it gave longer 6–8 m long flights maneuvering with difficulty in a 4 × 8 m room, sometimes softly hitting the walls without suffering any harm and trying to cling to walls, doors, or picture frames. However, by 30 January it could make long flights, maneuver inside this room moving back and forth and giving closed 360° turns in a 2 m radius, dodge people and other objects in its way, and even fly to adjacent rooms through the door spaces without touching any obstacle. At this point, the bird hovered briefly in front of different surfaces, and chose to cling to those that could support it (e.g., cotton curtains, wooden lintel, pillows). Before each flight, the swift typically raised, stretched, and fluttered its wings a variable number of times; during the last 2 d, this movement was frequently reduced to a quick shiver. After the longer flights, the pectoral muscles were noticeably warm. We obtained recordings of heating wingbeats and of a single flight. Wingbeat rate was 13.1 wingbeats/s for heating (Fig. 3C) and 12.4 wingbeats/s for proper flight. Given its mass loss, increased wing chord, newly gained flight abilities, and the regular evident intention of flying, we decided to release the bird on 31 January 2017 at the waterfall where it was found (Fig. 3D, 3E; <https://macaulaylibrary.org/asset/723345>). Upon release, it flew steadily and quickly along the Quebrada de Tilián creek and above the forest cover until we lost view of it.

Discussion

We have clarified the breeding distribution and seasonality of Rothschild's Swift based on a more extensive dataset than heretofore available, and provided detailed breeding information, including timing, nest description and placement, breeding habitat, nestling development, and behavior and vocalizations of a fledgling from northwest Argentina.

Distribution and seasonality

The distribution of Rothschild's Swift during the breeding season broadly overlaps with the Austral Yungas of Argentina and Bolivia, with

additional sparse records in Andean and extra-Andean ranges with forested and non-forested waterfalls (Fig. 1). Lowland records during the breeding season should be more properly considered as foraging individuals than as indicative of breeding activity, given the nearly complete dependence of *Cypseloides* swifts on waterfalls (Knorr 1961, Marín and Stiles 1992, Pearman et al. 2010, Biancalana 2015).

The breeding season of Rothschild's Swifts is coincidental with the rainy season in the Austral Yungas and commences together with or slightly before the first early rains as reported for other Neotropical swifts (Snow 1962, Collins 1968a, 1980; Rowley and Orr 1962, 1965; Ayarzagüena 1984, Marín and Stiles 1992, Pichorim 2002, Pearman et al. 2010, Passeggi 2011, Biancalana 2015). Rothschild's Swifts vacate the breeding grounds during the winter, but we were unable to assess the nonbreeding distribution, which remains a mystery. We know of a single documented record outside of the breeding season, a specimen collected at Tarija in May 1925 (Friedmann 1945; Supplemental Table S1), which may also pertain to a late migrant or to an individual that did not migrate for unknown reasons. We consider this record to be unusual and not representative of the true winter range of Rothschild's Swifts.

The paucity of documented records and the difficulty of identifying all-dark *Cypseloides* in flight may be an important factor leading to uncertainty on its wintering grounds. Specifically, some records of White-chinned Swift along the Andes and elsewhere may pertain instead to Rothschild's Swift, while overwintering (*borealis*) or even tropical breeding (*costaricensis*) Black Swifts (Stiles and Negret 1994, Beason et al. 2012) could also possibly overlap and be confused with nonbreeding Rothschild's.

Indeed, specimen records attributed to Rothschild's Swift were later found to pertain to White-chinned Swifts in Peru (Roesler et al. 2009) and to immature White-chested Swifts in Colombia (Eisenmann and Lehmann 1962). Similarly, presumed records of Sooty Swift from Ecuador were later regarded as White-chinned Swifts (Collins 1968b, Marín 1993, Freile et al. 2019). Undocumented records, especially those outside of the documented geographic and temporal ranges here described, must be taken with caution (Fig. 1). Future studies tracking Rothschild's Swifts should

help clarify their migratory routes, overwintering destinations, and possible confusion with other *Cypseloides*.

Breeding biology remarks

Our data on nest placement, nest features, eggs, the protracted development of Rothschild's Swift nestlings, and the sequence of plumage acquisition and behavior are coincidental with what is known from other *Cypseloides* (Smith 1928, Knorr 1961, Collins 1980, Marín and Stiles 1992, 1993; Marín 1997a, 1997b; Hirshman et al. 2007, Stopiglia and Raposo 2007, Whittaker and Whittaker 2008, Pearman et al. 2010, Biancalana 2015, Brito et al. 2015, Horvath and Bennet 2016). Our data is in particularly close agreement with what is known for the Sooty Swift, its sister taxon (Vasconcelos et al. 2006, Stopiglia and Raposo 2007, Pearman et al. 2010, Biancalana et al. 2012, Biancalana 2015).

A remarkable aspect of *Cypseloides* nesting biology is the invariance of clutch size: a single egg was laid in 6 out of 8 currently recognized species for which there are data (this work, Dabbene 1918, Smith 1928, Smyth 1928, Collins 1980, Ayarzagüena 1984, Marín 1997a, 1997b; Marín and Stiles 1992, 1993; Stopiglia and Raposo 2007, Whittaker and Whittaker 2008, Pearman et al. 2010, Brito et al. 2015). This is more notable given the wide latitudinal distribution spanning western Canada (subspecies *borealis* of the Black Swift), through the lowlands and highlands of the Neotropics, south to northwest (Rothschild's Swift) and northeast (Sooty Swift) Argentina. This suggests the existence of a deeply entrenched constraint in the life history of *Cypseloides* that merits further study. While *Streptoprocne* swifts routinely lay 2 eggs, syntopic *Cypseloides* nesting in the same sites lay just 1, despite lacking obvious differences in nest safety or food items (Marín and Stiles 1992; JIA pers. obs.). Their life histories have been likened to those of inshore seabirds (*Streptoprocne*) and pelagic ones (*Cypseloides*), with the prediction that *Cypseloides* would be more "pelagic" and thus may range farther from the nests in search for food with a consequently lower feeding rate for their nestlings, which in turn would explain the 1-egg clutches and longer nestling periods (Marín and Stiles 1992; see Ricklefs 1968, 1982). Our data on Rothschild's Swift shows that even in the cold, humid Andes of

northwest Argentina, near the southern latitudinal limit of the genus, the single-egg constraint continues to operate.

We have provided the first sound recordings of nestling/fledgling vocalizations of a Rothschild's Swift, which appear to be the first available for any *Cypseloides*. It is unclear what these vocalizations represent, as they could constitute developmental precursors of adult sounds or begging calls. The fact that the captive sound-recorded swift was losing weight and gave these vocalizations mostly, although not exclusively, when it was about to be fed, suggests that loud begging may occur more often when hunger is extreme. However, because these vocalizations were recorded during the nestling/fledgling transition, they may later develop into the adult twittering and chipping that constitute their flight voices. Begging "clicking" vocalizations have been reported, but not documented, for Black Swifts in North America (Smith 1928, Murphy 1951), which have otherwise been considered to beg in silence (Marín 1997b). Harper (1986) predicted that begging intensity should decrease with clutch size, and that little or no begging should be expected at nests with a single chick. Begging calls in Neotropical swifts seem to fit these predictions, where nestlings in species with larger clutches give noisy harsh begging calls (*Chaetura*, *Aeronautes*, *Panyptila*), those with 2-egg clutches utter softer calls (*Streptoprocne*) and those with 1 egg are silent or nearly so (*Cypseloides*) (Haverschmidt 1958, Sick 1959, Collins 1968a, Marín and Stiles 1992, Marín 1997b). Lack of intra-nest competition may make begging sounds generally unnecessary in the single-brooded *Cypseloides*, and silent begging has additionally been considered to minimize predation given their long incubation and nestling periods (Marín 1997b). Further work is needed to clarify when and how the vocalizations here recorded in captivity are used in nature.

Taxonomic comments

Our nestling data contradicts the widely held opinion that Rothschild's Swifts are brownish as our data shows instead dark sooty chicks (Fig. 2, Supplemental Fig. S2). Likewise, a recent specimen from Tucumán (IML 1746) is unique in its sooty black coloration, and contrasts markedly with other browner (older) specimens from

Santiago del Estero, Tucumán, and Salta (see Supplemental Table S1; AMNH 477443 to 477446; FMNH 302353, 302354; IML 679, 7227, 9383, 15793, 15799, 15800; LSUMZ 83925; MACN 9647, 38147, 41525; MLP 0761). Recently, Biancalana et al. (2017) provided mitogenomic data of a Sooty Swift, but no genetic information is available for Rothschild's. We obtained blood samples from the nestlings/fledgling herein shown and are actively pursuing clarification of the taxonomy of Rothschild's Swifts based on molecular phylogenetic, vocal, and morphological data.

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