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NESTING BIOLOGY OF THE BLUE-AND-WHITE SWALLOW (*PYGOCHELIDON CYANOLEUCA*) IN NORTHEASTERN ECUADOR

Ethan B. Linck[1] · Heidi C. Huber[1] · Harold F. Greeney[2] · Kimberly S. Sheldon[3]

[1] Department of Biology and Burke Museum of Natural History & Culture, University of Washington, Seattle, WA 98195, USA.

[2] Yanayacu Biological Station & Center for Creative Studies, Cosanga, Ecuador, c/o 721 Foch y Amazonas, Quito, Ecuador.

[3] Department of Ecology & Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA.

E-mail: Ethan B. Linck · elinck@uw.edu

Abstract · The Blue-and-white Swallow (*Pygochelidon cyanoleuca*) is found in open country from Costa Rica to Patagonia. With a broad geographic range and both migratory and resident subspecies, *P. cyanoleuca* likely exhibits substantial variation in life history and breeding biology. Here, we present data on its nesting in northeastern Ecuador. From the years 2003–2009 we made general observations of breeding biology and detailed observations at 16 nests. We measured dimensions of four nests, took a time series of size and mass measurements on 12 eggs and five nestlings, and videotaped 110.5 hours of behavior at one nest. We found that nesting activity occurred from June to January, with no records in July. Mean measurements (cm ± SD) of four nests were: outer diameter, 11.3 ± 1.0; outer height, 3.5 ± 0.7; inner diameter, 5.3 ± 0.5; inner depth, 2.6 ± 0.3. Clutch size was always three eggs that were a plain white color or had very small, light brown speckles. Twenty-seven eggs of unknown age had mean measurements of 17.4 ± 0.6 mm long, 12.7 ± 0.3 mm wide. A subset of 12 eggs with accurate mass data weighed 1.4 ± 0.1 g. Based on observations of two color-banded birds at a nest, both adults provisioned young. We recorded a feeding rate at the nest of 6.1 feeds per nestling-hour. These data are largely consistent with previous studies of *P. cyanoleuca* and Hirundinidae more broadly.

Resumen · Biología de nidificación de la Golondrina Azul y Blanco (*Pygochelidon cyanoleuca*) en el noreste de Ecuador
La Golondrina Azul y Blanco se distribuye en campo abierto desde Costa Rica hasta la Patagonia. Debido a este amplio rango geográfico y a que existen tanto subespecies migratorias como residentes, es probable que *P. cyanoleuca* muestre una variación sustancial en su biología básica e historia de vida. En el presente estudio presentamos datos de la biología reproductiva de esta especie en el noreste de Ecuador. Durante los años 2003–2009 hicimos observaciones generales sobre la biología reproductiva de 16 nidos. Tomamos mediciones de las dimensiones de cuatros nidos, mediciones de series cronológicas de doce huevos y cinco pichones, y grabamos en video comportamiento en un nido por 110,5 horas. Encontramos actividad reproductiva entre Junio y Enero, sin registros en Julio. Las dimensiones (media ± DE, cm) para los cuatros nidos fueron 11,3 ± 1,0 en el diámetro exterior, 3,5 ± 0,7 en altura, 5,3 ± 0,5 en el diámetro interior, y 2,6 ± 0,3 en profundidad. El tamaño de puesta fue tres huevos en todos los nidos, y los huevos fueron completamente blancos o presentaron pequeños puntos café claro. Las dimensiones de 27 huevos sin fechas fueron 17,4 ± 0,6 mm en el largo, 12,7 ± 0,3 mm en ancho. Para una submuestra de huevos con datos de peso precisos la media fue 1,4 ± 0,1 g. En base a dos adultos anillados, observamos que los dos sexos proveyeron alimento al nido. Los pichones fueron alimentados a razón de 6,1 visitas por hora. Estos datos son consistentes en gran parte con investigaciones anteriores de *P. cyanoleuca* y la familia Hirundinidae en general.

Key words: Andes · Egg dimensions · Feeding rates · Hirundinidae · Life history · Nesting biology · Nestlings

INTRODUCTION

The four swallows in the genus *Pygochelidon* are found from Mexico to the tip of South America, spanning a variety of habitats from tropical montane forest to arid grassland (Turner & Rose 1989, Stiles & Skutch 1989). Across this vast geographic range, members of the genus inhabit disparate niches and exhibit varied migratory behavior: the Pale-footed Swallow (*P. flavipes*) is a rare cloud-forest resident on the eastern slope of the Andes, but the Blue-and-white Swallow (*P. cyanoleuca*) is found primarily in open country from Costa Rica to Patagonia, and contains both migratory (ssp. *patagonica*) and nonmigratory subspecies (ssp. *cyanoleuca* and *peruviana*) (Goodall et al. 1946, Stiles & Skutch 1989, Turner & Rose 1989). *Pygochelidon* swallows are conspicuous across their range and are frequently associated with human settlement (Skutch 1952, Ridgely & Greenfield 2001, Restall & Freile 2018), making them useful taxa for understanding how life-history traits and breeding biology alternatively vary or are conserved across large geographic and ecological distances.

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Previous researchers have documented the basic natural history of the Blue-and-white Swallow in several regions across its extensive range. In Costa Rica, nominate *cyanoleuca* builds a shallow, cup-like nest of straw and weeds lined with feathers, choosing such diverse sites as "cavities in trees, holes in banks, niches in masonry bridges, crevices in house walls, and beneath roofs of thatch" (p. 406), often utilizing their nest sites year-round for sleeping, safety from predators, and as shelter from inclement weather (Skutch 1952). In the arid landscape surrounding Lima, Peru, subspecies *peruviana* prefers to nest in earthen burrows (Koepcke 1970). Blue-and-white Swallows in Costa Rica lay ´ 2–4 eggs from March to June, rearing up to two broods per year (Skutch 1952, Stiles & Skutch 1989). In northern Venezuela (*cyanoleuca*), breeding activity extends from April to June (Schäfer & Phelps 1954, Collins 2010), and 1200 km to the west in Colombia, the species apparently breeds year-round (Miller 1963). South of the Equator, the migratory subspecies *patagonica*, which occurs in Chile and Argentina, breeds from October to January in the early Austral summer and spring (Goodall et al. 1946, de la Peña 2013).

In Ecuador, where both resident breeding (*cyanoleuca*) and migratory non-breeding (*patagonica*) subspecies of Blue-and-white Swallows are found (Ridgely & Greenfield 2001), breeding data are scant. Here, we contribute additional data on both nest architecture and seasonal breeding biology of the Blue-and-white Swallow (ssp. *cyanoleuca*) in northeastern Ecuador.

METHODS

We conducted fieldwork at Yanayacu Biological Station and Center for Creative Studies (00°35.95'S, 77°53.40'W, 2100 m a.s.l.) and the nearby area of Las Palmas in Napo Province, Ecuador (00°32'23'S, 77°52'W, 1900 m a.s.l.). Detailed descriptions of the study area can be found in Greeney et al. (2006) and Guayasamin et al. (2006). Three observers (HCH, HFG, KSS) aided by several trained field techs collected data on nest location and architecture, egg size and mass, nestling size and mass, and breeding biology both methodically and on an opportunistic basis from 2003–2007. We recorded qualitative observations on the position, substrate, and composition of all nests encountered during the study. In several cases, we estimated nest height, basing our figure on the consensus of two observers whenever possible. We measured and weighed all eggs from a majority of nests using a Mitutoyo 500-784 Absolute Digital Caliper (accuracy 0.02 mm) and a KEEGH High-Precision Digital Milligram Pocket Scale (accuracy 0.001 g). For four nests, we made successive measurements of the mass of each egg for a minimum of 8 and maximum of 14 days, marking each egg uniquely with indelible ink. All data are presented throughout the manuscript as mean ± SD. We additionally used a tripod-mounted video camera (Sony video Hi8) at one nest at Yanayacu to quantify parental behaviors over an 11-day period (2–12 October 2006). First, we color-banded two adult birds coming to the nest to allow us to quantify individual behaviors. We then recorded a total of 110.5 hours of video between approximately 05:50 and 18:30 h, quantifying feeding, brooding, excretion, nest sanitation, and other behaviors for each color-banded parent. In some cases, we report these behaviors per nestling-hour (total observations / total number of nestlings / hours of observation).

RESULTS

Nest sites and habitat. We found and recorded location information for 16 nests. Thirteen of these nests were located in the eaves of buildings and residences at Yanayacu Biological Station while the remaining nests were located on cliff faces in the vicinity of nearby Las Palmas. Nests located in the eaves of buildings were found 4.7 ± 2.1 m off the ground, while the nests on cliff faces were 10.8 ± 13.1 m off the ground and were protected by crevices or overhangs in the rock.

Nest construction and nest architecture. On three occasions, we observed adult Blue-and-white Swallows during the building phase of nesting. We recorded pairs flying to and from the nest site carrying unidentified material. Nests typically featured a well-formed cup, and were constructed with pale rootlets, fibers, moss, grass blades and thin sticks, usually well-lined with feathers (Figure 1). Measurements (cm) for four nests were: outer diameter 11.3 ± 1.0; outer height; 3.5 ± 0.7; inner diameter 5.3 ± 0.5; inner depth 2.6 ± 0.3.

Eggs. Eggs were typically of plain white color with no pattern, though some had a small amount of pale brown flecking (Figure 1). Among the nests (n = 9) we observed that had eggs or nestlings, clutch size was always three. The average size of eggs (n = 27) was 17.4 ± 0.6 x 12.7 ± 0.3 mm. Twelve eggs were weighed and had a mean mass of 1.4 ± 0.1 g. Our detailed monitoring of four nests revealed a decreasing trend in egg mass over time (Figure 2).

Banded birds. On 3 October 2006, one day after filming commenced, we used a mist-net to catch a female coming to the nest. She had a full brood batch and no cloacal protuberance, and we gave her color bands to identify her. We recorded the following measurements: tarsus 11.6 mm, wing chord 92.6 mm, and mass 11.8 g. On 8 October 2006, we caught and color-banded a male arriving to the nest. He had a full cloacal protuberance and no brood patch. We made the following measurements: tarsus 12.0 mm and wing chord 95.0 mm. The male had no body molt or flight-feather molt. He was missing the right outer most rectrices (two of them), but there was no visible regrowth of these feathers.

Nest visitation. Combined, the two color-banded adults visited the nest at least 2081 times over 11 days for an average of 6.3 visits per nestling-hour. The average duration of a visit was 6 s. Of the total visits, 11% lasted 10 s or more, and 68% lasted only 1 s, and consisted of the adult touching down and lifting off from the nest rim in quick succession. In all recorded instances (100%), adults approached the nest from the same direction, being restricted in their approach by the location of the nest. We were able to determine a bird's band color on 60% of recorded visits during the period in which they were banded, with the female adult visiting a much greater proportion of total visits than the male (80% vs. 20%, respectively). During the 1.9 h an identifiably color-banded adult spent standing on the nest, the female also

Figure 1. Typical Blue-and-white Swallow (*Pygochelidon cyanoleuca*) nest of pale rootlets, fibers, moss, grass blades, thin sticks, and a feathered lining. This nest was located under the eaves of Yanayacu Biological Station and Center for Creative Studies, Napo Province, Ecuador. Note the pale brown flecking on the eggs. Photograph by H. F. Greeney.

spent considerably more time compared to the male (1.3 vs. 0.6 h, respectively).

Nestling provisioning and growth. Our videotaped nest revealed adults provisioned three nestlings 2034 times during 110.5 h of filming; 6.1 ± 0.3 feeds per nestling-hour across all 11 days. Nestling provisioning varied from 3.7 to 6.5 feeds per nestling-hour, with the lowest rate likely unrepresentative as it occurred on a day in which we only filmed the nest for 43 minutes. The earliest recorded feeding occurred at 05:57 h and the latest feeding occurred at 18:05 h. For two nests where we measured nestling mass for each individual over the course of 8 and 15 days, respectively, we found an linear relationship between growth and time (Figure 3; slope = 0.69, $p < 0.001$, $R^2 = 0.88$).

Sanitation. The three nestlings produced a total of 385 fecal sacs during 110.5 h of observation for a rate of 1.2 ± 0.2 fecal sacs per nestling-hour. Adults almost always carried fecal sacs away from the nest, in most cases dropping them 10–30 m from the nest. They consumed the fecal sac at the nest on only two occasions. In the instances where fecal sacs were not produced in the presence of adults (69% of fecal sacs), the chicks deposited fecal sacs on or over the edge of the nest.

Observed breeding dates. We observed nesting activity during 7 months of the year, including June and August–January. We observed nest building in September (2008) and December (2008). Incubation was observed in June (2006, 2008), August (2006), September (2004, 2006, 2007), October (2006, 2007), November (2007), December (2004), and January (2005). We recorded brooding in August (2007), September (2007), October (2003, 2004), November (2006), December (2003, 2004, 2007, 2009), and January (2005, 2008). Fledglings were observed in October (2007) and December (2009).

Fledging. Though we did not directly observe any instance of fledging, we inferred fledging of nestlings under observation from three nests when nestlings were observed flying around, including between 15 and 18 September 2007, 28 September and 1 October 2007, and on 6 December 2009.

DISCUSSION

We recorded nesting activity in seven months, spanning early June to late January. Our findings are therefore consistent with observed breeding for much of the same period in Colombia (Miller 1963, Willis 1988) and in October (Skutch 1952) in Costa Rica. Interestingly, we note a conspicuous

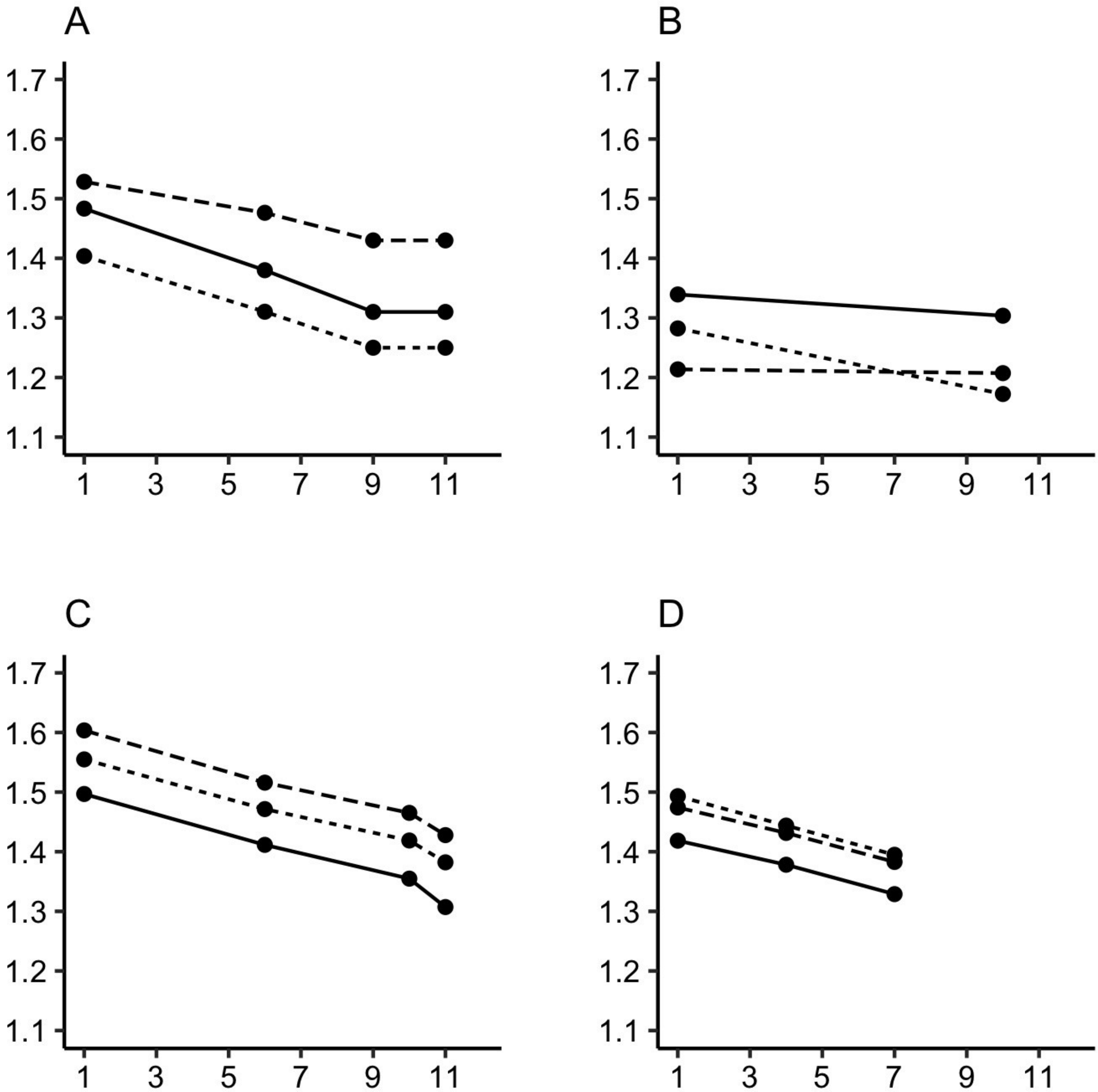

Figure 2. Changes in egg mass (g) over time (day of incubation as recorded from the beginning of the observation period) in four nests of Blue-and-white Swallow (*Pygochelidon cyanoleuca*) at Yanayacu Biological Station and Center for Creative Studies, Napo Province, Ecuador. (A-D). Each line represents mass for a given egg (n = 3 eggs per nest).

absence of breeding records from February–May despite reports of incubation in April and May from northwest Ecuador and southwest Colombia (Fjeldså & Krabbe 1990), nesting from April-June in Venezuela (Schäfer & Phelps 1952, Gillard 1959), and year-round breeding in the Andes of Colombia (Miller 1963). Additional observations in northeast Ecuador and northwest South America are necessary and may reveal local variation in breeding seasons driven by variation in factors like precipitation regimes, altitude, and habitat type (Perrin 1970, Verhulst & Nilsson 2008).

Our general observations on nest architecture and habitat are consistent with detailed observations from Costa Rica (Skutch 1952, 1985; Stiles & Skutch 1989), as well as records from Argentina (de la Peña 1987), Brazil (Buzzetti & Silva 2005, Lopes et al. 2013), Colombia (Willis 1988), Peru (Koepcke 1970), Venezuela (Gillard 1959), and elsewhere in Ecuador (Greeney & Nunnery 2006, Ridgely & Greenfield 2001). These data suggest breeding behavior in *Pygochelidon cyanoleuca* is largely conserved among populations and subspecies, a conclusion that reflects the broader consensus on the evolutionary basis of behavioral ecology in swallows (Winkler & Sheldon 1993, Soler et al. 1998).

To the best of our knowledge, our measurements of egg mass and water loss represent a novel data set for *P. cyanoleuca*, though the basic values are similar to those reported in other swallow taxa (Rahn et al. 1977, Wiggins 1990, Whittingham et al. 2003, Whittingham et al. 2007). Our data on nestling growth are consistent with and complement

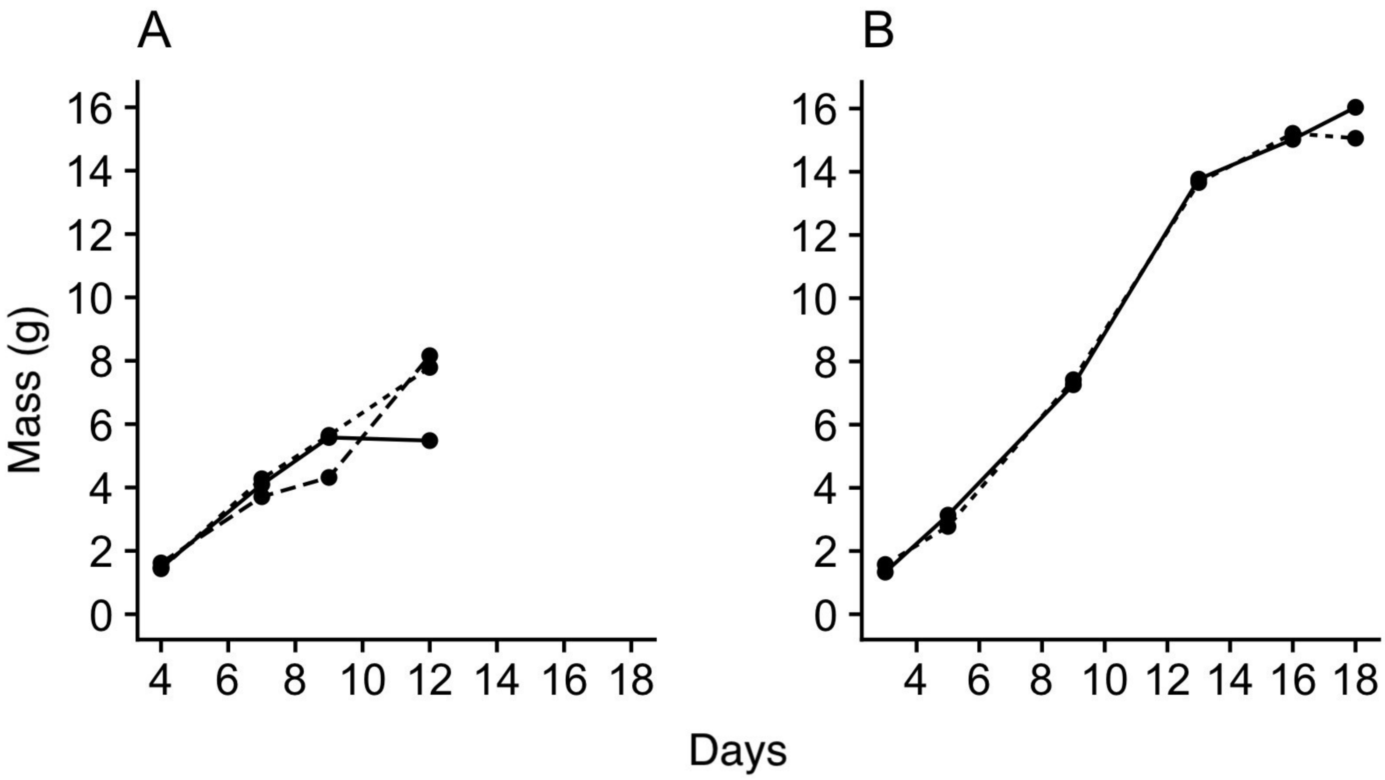

Figure 3. Nestling growth over time in two nests of Blue-and-white Swallow (*Pygochelidon cyanoleuca*) that were observed in A) November (n = 3 nestlings), and B) January (n = 2 nestlings - one egg in this clutch did not hatch) at Yanayacu Biological Station and Center for Creative Studies, Napo Province, Ecuador.

Collins' (2010) results from a similar study in Venezuela, and, taken together, represent the start of a potentially valuable resource for future studies exploring hypotheses about 'reduced growth curves in nestlings of tropical populations versus higher latitude conspecifics (e.g., Ricklefs 1976). We encourage researchers with regular access to nesting *P. cyanoleuca* across its full range and spectrum of habitats to build on these comparative data.

Our results are also largely consistent with previous studies of breeding biology in the Blue-and-white Swallow and the Hirundinidae more broadly. Skutch (1953) describes *P. cyanoleuca* as one of only five species of birds in Central America where he has recorded incubation by the male. Our video recordings of one *P. cyanoleuca* nest confirmed attendance (but not incubation) by male and female color-banded adults. Nestling provisioning rates (6.1 feeds per nestling-hour) were higher than those recorded in similar studies on Tree Swallows (*Tachycineta bicolor*) (~ 2–3 feeds per nestling -hour: Leonard & Horn 1996, Wittingham et al. 2003). The clutch size in our study (3 eggs per nest) is comparable but less variable than the 2–4 eggs reported by Skutch (1952) in Costa Rica, and smaller than the clutch size of 4–5 eggs from the migratory subspecies *P. c. patagonica* in Argentina (de la Peña 1987). These data are consistent with the widely-reported trends of increasing clutch size with latitude in many taxa (Lack 1947, Slavsgold 1975, Owen 1977, Ricklefs 1980, Perrins & Birkhead 1983), and suggest that even the moderate difference in latitude between Yanayacu (~ 0°) and Costa Rica (8°–11° N) may affect commonly cited clutch-size determinants (e.g., day length, nest predation: Soler & Soler 1992). Further study of the biology of *P. cyanoleuca* and its congeners may help establish a mechanism for this intriguing pattern.

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