

## Combining multiple sources of data to uncover the natural history of an endemic Andean hummingbird, the Peruvian Piedtail (*Phlogophilus barterti*)

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**ABSTRACT.** Endemic species with distributions restricted to narrow elevational ranges in the Andes are among the least-known tropical birds and are also among the most vulnerable to anthropogenic pressures of climate change and habitat fragmentation. One such species is the Peruvian Piedtail (*Phlogophilus barterti*), a hummingbird endemic to the Andean foothills of central and southern Peru. To obtain basic ecological information and estimate population densities, we studied Peruvian Piedtails over an 12-year period (2006–2017) along an elevational gradient in Manu National Park in Peru. We calculated a density of 57.9 (95% CI: 36.2–81.4) individuals per km<sup>2</sup>, which is similar to estimates reported for other range-restricted Andean hummingbirds. Peruvian Piedtails were found at elevations between 867–1545 m, but were more common in areas with undisturbed forest, dense vegetation, and bamboo patches in a narrow elevational band of 400 m (900–1300 m). All nests were in dense clumps of hanging moss, and clutches always consisted of two eggs. The duration of incubation (19 d) and nestling (23 d) periods was within the range reported for other hummingbirds of similar size, but the growth rate of nestlings ( $K = 0.28$ ) was relatively slow. Our observations suggest that Peruvian Piedtails are locally common, but only in specific habitats within their limited elevational range in southeastern Peru, and they may rely on patches of bamboo (*Guadua* sp.) for breeding. Thus, the broader extent of the occurrence and density of Peruvian Piedtails across their range should be evaluated to better inform their conservation status.

### RESUMEN. Combinando múltiples fuentes de datos para descubrir la historia natural del colibrí andino endémico, *Phlogophilus barterti*.

Las especies Andinas con distribuciones restringidas en estrechas bandas altitudinales están entre las aves tropicales menos conocidas y a su vez entre las más vulnerables al cambio climático y fragmentación. Una de estas especies es el *Phlogophilus barterti*, un colibrí endémico del Centro y Sureste de Perú. Estudiamos *P. barterti* por un período de doce años (2006–2017) para obtener información ecológica detallada y estimaciones de densidad poblacional en un gradiente altitudinal en el Parque Nacional Manu, Perú. Estimamos una densidad de 57.9 (95% CI: 36.2–81.4) individuos/km<sup>2</sup>, lo cual está dentro del rango estimado para otros colibríes andinos con distribución restringida. Encontramos *P. barterti* en elevaciones entre los 867–1545 m, pero fueron más abundantes en áreas con bosque conservado, vegetación densa y fragmentos de bambú entre los 900–1300 m. Los nidos ( $N = 34$ ) se encontraron en sustratos cubiertos con musgo y el tamaño de la nidada fue de dos huevos. Los periodos de incubación (19 d) y polluelos (23 d) están dentro del rango estimado para otros colibríes de igual tamaño, pero la tasa de crecimiento de polluelos basada en masa ( $K = 0.28$ ) fue relativamente lenta. Nuestras observaciones sugieren que *P. barterti* es localmente común, pero únicamente en hábitats específicos dentro de su limitado rango altitudinal en el Suroeste peruano, y que la especie puede depender de fragmentos de bambú para su reproducción. Por lo tanto, su área de ocurrencia global y densidad a lo largo de su rango deben ser revisados para evaluar su estado de conservación.

**Key words:** Andes, cloud forest, incubation rhythm, Manu National Park, nesting biology, population density, Trochilidae

With over 340 species and remarkable ecological, morphological, and taxonomic diversity, hummingbirds make up the second largest (McGuire et al. 2014), and possibly the most charismatic and iconic, family of

birds in the New World. More than two-thirds of all hummingbird species are found in South America (Remsen et al. 2018), with most occurring in the tropical Andean mountains from Colombia to Bolivia. In southeastern Peru, on the eastern slope of the Andes, Manu National Park harbors 66 species of hummingbirds along a forested elevational

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gradient from lowlands to treeline (Walker et al. 2006). Among the least studied of Andean hummingbirds is the Peruvian Piedtail (*Phlogophilus harterti*), a small and easily overlooked species endemic to the foothills and lower cloud forests of central and southern Peru. Peruvian Piedtails are found on the eastern slope of the Andes where they are restricted to a narrow range of habitats and elevations between 750 and 1500 m (Schuchmann 1999, Walker et al. 2006, Schulenberg et al. 2007). The other representative of this genus, the Ecuadorian Piedtail (*Phlogophilus hemileucurus*), is restricted to similar elevations, with a geographical range centered in Ecuador and including southern Colombia and northern Peru (Schuchmann 1999). The genus is phylogenetically nested within the diverse group of coquettes (Lophornithini), where it is basal to a clade including mostly Andean hummingbirds such as the sunangels (*Heliangelus*), sylphs (*Agelaiocercus*), and metal-tails (*Metallura*) (McGuire et al. 2014). Both *Phlogophilus* species are little-studied, with little published information about their natural history (Schuchmann 1999).

Peruvian Piedtails are poorly known because of their small size, inconspicuous behavior, restricted range, and preference for forest interior. This species is listed by the IUCN as near threatened, with the population expected to decline in the future due to habitat loss (BirdLife International 2018). As a result, basic ecological information and estimates of population densities are urgently needed for this endemic species to aid in developing adequate management plans. Here, we present data collected across 12 yr in Manu National Park to describe the local distribution, habitat use, nesting biology, vocalizations, and behavior of Peruvian Piedtails.

## METHODS

We studied Peruvian Piedtails along an elevational gradient in Manu National Park, Department of Cuzco, Peru. Our study area extended > 70 km from lowland rain forest (~400 m) to treeline (3400 m) (Jankowski et al. 2013, Londoño et al. 2015), but all detections of Peruvian Piedtails were in the foothills and lower montane forest between 800 and 1600 m. We conducted surveys and

searched for nests along this gradient based at field stations in Villa Carmen (12.8955°S, 71.4038°W; 600–1200 m), Tono (12.9568°S, 71.5641°W; 800–1100 m), and San Pedro (13.0553°S, 71.5466°W; 1200–1600 m), with forest trails near these stations spanning the broader elevation range. This area consisted of pristine premontane and montane cloud forest with extensive stands of bamboo (*Guadua* spp.), a canopy height of up to 30 m (David and Londoño 2013), and was close to fast-flowing mountain rivers. Forest in these areas was mostly continuous, with some gaps and patches of vegetation in various successional stages caused by natural landslides or tree falls.

**Population density.** We conducted point-count surveys along the elevational gradient from July to November 2006–2017. We established 331 survey points that ranged in elevation from 400 to 3400 m, including 162 survey points from 600 to 1700 m where Peruvian Piedtails were predicted to occur. Points were 130 m apart along trails and were visited 4–8 times from 2006 to 2017. On each sampling day, one of us (JEJ) conducted 10-min counts at each of 10 points between 05:00 and 09:00. During each count, all individuals detected were identified by sight and sound, and their distances from the point were estimated using a laser range finder. All counts were digitally recorded for later species confirmation (see Jankowski et al. 2013 for details).

We estimated population density using point-transect sampling in the “Distance” package (Miller 2017) in R (R Development Core Team 2017). We fit eight commonly used models (key function plus adjustment terms) to our data truncated at 5% of the greatest distances (Buckland et al. 2001) and used Akaike’s Information Criterion (AIC) to select the best model for the detection function (Buckland et al. 2001, Miller et al. 2016). For models that were equally parsimonious ( $\Delta\text{AIC} \leq 2$ ), we used the model-averaging procedure estimating the variance and confidence interval by bootstrap with 999 randomizations (Buckland et al. 2001), using multiple analyses on distance data in the “mads” package (Marshall 2017). In total, 103 detections were used to calculate detection function and density for the study area after the truncation.

**Elevational range and habitat.** We complemented point-count surveys with mist-net captures to describe the elevational range of Peruvian Piedtails. Mist-netting was conducted from July to November 2005–2007 and 2011–2016 using 10 nets each at an average of five or six locations in each 250-m elevational zone between 400 and 3100 m. At each location, mist-nets were placed along or near trails at forested sites for 3 d from 06:00 to 17:00.

We collected vegetation data at survey points with detections using a protocol adapted from Martin et al. (1997). Forest vertical structure variables were estimated in 20-m  $\times$  20-m plots surrounding each survey point and included mean canopy height, number of trees  $>$  10-cm dbh, and percent canopy cover. Understory variables were estimated in 10-m  $\times$  10-m plots and included the number of small stems ( $<$  2.5-cm dbh), large stems ( $>$  2.5-cm dbh), and percent bamboo cover (Jankowski et al. 2013).

**Pollen collection and identification.** We collected pollen from 12 Peruvian Piedtails captured in mist-nets by passing a non-toxic adhesive sliver of gelatin over the forehead and bill of birds. The gelatin was made from a solidified mixture of gelatin, glycerol, and distilled water. The piece of gelatin, with attached pollen grains, was transferred to a microscope slide, melted by slowly heating the bottom of the slide with a lighter, and sealed with a glass cover slip to preserve and protect the pollen grains. Pollen samples were photographed and identified to family or genus in the Neotropical Paleocology Research Lab at the Florida Institute of Technology in Melbourne, FL, USA (M. Bush, pers. comm.).

**Vocalizations.** We recorded vocalizations opportunistically with a microphone (ME-66; Sennheiser Electronic Corporation, Old Lyme, CT) and digital recorder (Edirol R-09; Roland Corporation U.S., Los Angeles, CA) as 32-bit wav stereo files at a sampling frequency of 44.1 kHz. Low frequency cut-off was used on the microphone to dampen ambient noise (e.g., nearby fast-flowing rivers).

Peruvian Piedtails used several perches in their territories to sing, and visited these perches in succession. Once a singing perch

was identified, observers sat quietly and waited for the individual to return and sing, thus obtaining recordings from a distance of 10 to 12 m. Spectrograms were generated from sound files in Raven Pro 1.5 (Program Research Bioacoustics 2014). We describe the songs of Peruvian Piedtails and, using Raven, quantified several acoustic variables, including song duration, duration of note types, minimum and maximum frequency, and duration of silent intervals.

**Nesting biology.** We searched for nests of Peruvian Piedtails from August to December 2008–2014, following the protocol of Martin and Geupel (1993) for nest searching and monitoring. We measured nest and egg dimensions ( $\pm$  0.1 mm) using calipers, and wing chord of nestlings ( $\pm$  1 mm) using a ruler. We weighed eggs and nestlings ( $\pm$  0.05 g) using a digital pocket scale (Flip-scale F2; Phoenix, AZ). We monitored incubation behavior at five nests using thermal sensors placed both inside nests under the eggs and outside nests for environmental temperatures. Sensors were connected to a data logger (U-12 HOBO; Onset Computer Corporation, Pocasset, MA) placed near nests and camouflaged, and temperatures were recorded every minute (Cooper and Mills 2005, Londoño 2009). We used changes in temperature to estimate incubation behavior (i.e., number and duration of incubation bouts) and nest microclimate, and calculated nest attentiveness at nests as the percentage of time birds were on nests incubating eggs (Martin 2002). Means are reported  $\pm$  SE. Sample sizes are number of nests, unless otherwise indicated.

The duration of incubation periods was calculated as the number of days between the last egg laid and the last egg hatched, and nestling period was estimated as the number of days between when the last egg hatched and the last nestling left the nest (Martin 2002). We estimated nestling growth rate ( $K$ ) by fitting a logistic, Gompertz and von Bertalanffy function to the average nestling mass over the nestling period (Ricklefs 1967). We then used Akaike's Information Criterion (AIC) to select the best function to describe the growth in mass. All statistical analyses were performed in R (R Development Core Team 2017).

## RESULTS

**Population density.** We detected 107 Peruvian Piedtails at 45 points across all surveys. All detections were made aurally, with some accompanied by visual records. Of those detections, 51 were individuals singing and 56 were individuals giving calls. The maximum number of individuals detected at a point (in the duration of one count) was two ( $N = 15$  points). The average of models considered equally plausible according to AIC values estimated a density of 57.9 (95% CI: 36.2–81.4) individuals per km<sup>2</sup> (Table 1).

**Elevational range and habitat.** Peruvian Piedtails were found primarily in the interior of mature forests. The lowest elevation where they were detected was a nest at 867 m, and the highest was an adult captured at 1545 m. However, most captures, detections, and nests were in a narrow 400-m elevational range between 900 and 1300 m (Fig. 1).

Peruvian Piedtails were most common in areas of undisturbed premontane forest in extensive patches of bamboo (*Guadua* spp.). These areas were often near small creeks or rivers, with dense vegetation covered by moss and lichens that are ideal locations for nests (see below). The mean canopy height of survey points where Peruvian Piedtails were detected was  $16 \pm 6.8$  m ( $N = 25$ ), with a

mean percent canopy cover of  $87 \pm 3.2\%$  ( $N = 19$ ) and an average of  $21 \pm 8$  trees  $> 10$  cm dbh ( $N = 26$ ). Understory vegetation at these points was also moderately dense, with an average of  $39 \pm 26.8$  ( $N = 26$ ) small stems and  $19.8 \pm 12.8$  ( $N = 26$ ) large stems. Bamboo cover was present at most survey points with detections (21 of 26  $10 \times 10$ -m plots, or 81%), with an estimated average bamboo cover of  $28 \pm 20\%$  ( $N = 26$ ).

Nine plant families were identified in pollen samples obtained from 12 adults (Table 2). Of these families, the most common were Asteraceae, Campanulaceae, and Gesneriaceae.

**Vocalizations.** We documented two distinct vocalizations for Peruvian Piedtails, including songs and a call. Songs consisted of a series of high-frequency notes with a total duration of 5 to 7 s and a frequency range of 7 to 11 kHz (Fig. 2). Songs began with a two-note introduction (0.53-s duration), followed by a single high-frequency and slightly shorter-duration note (0.44 s), then a series of five to seven repeated two-note parts, with each part 0.5–0.6 s in duration. Songs were sung either once or repeated 2–3 times in succession followed by 3–8 s silent intervals (Fig. 2A). When songs were repeated in succession (with a much shorter silent interval of 0.25 s), the initial two-note introduction was

Table 1. Density estimates (individuals per km<sup>2</sup>) and 95% confidence intervals for Peruvian Piedtails in Manu National Park, Cusco, Peru. Estimates based on different models (key function plus adjustment terms) using the “Distance” package in R. Models are ranked by ascending value of Akaike’s Information Criterion (AIC), with mean of models considered equally plausible ( $\Delta\text{AIC} \leq 2$ ) obtained after model-averaging by bootstrap (999 randomizations).

Model	Density estimate	95% CI	AIC ( $\Delta\text{AIC}$ )	CV	AIC <sub>wi</sub>	ER
Hazard rate	57.5	37.2–88.9	727.37 (0)	0.22	0.54	
Uniform + Cosine	57.9	27.9–119.7	728.80 (1.43)	0.38	0.26	2.04
Hazard rate + Cosine	57.5	18.5–178.2	729.37 (2.00)	0.62	0.20	2.72
Half-normal + Cosine	60.3	24.4–149.2	729.96 (2.59)	0.48	–	–
Half-normal	67.7	44.4–103.1	730.41 (3.04)	0.23	–	–
Hazard rate + Simple polynomial	58.5	23.1–148.8	730.54 (3.17)	0.50	–	–
Uniform + Simple polynomial	71.0	46.2–109.1	730.62 (3.25)	0.23	–	–
Half-normal + Hermite polynomial	57.6	25.6–129.6	730.72 (3.35)	0.43	–	–
Mean of models with $\Delta\text{AIC} \leq 2$	57.9	36.2–81.4	–	0.20	–	–

CV, coefficient of variation; ER, evidence ratio; *wi*, weight.

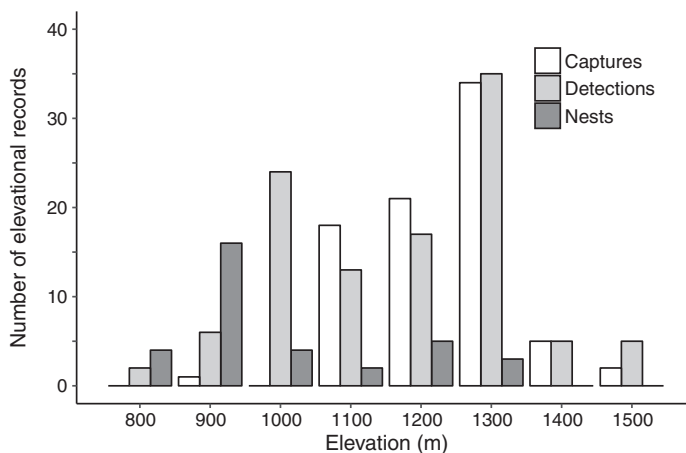


Fig. 1. Number of elevational records for captures ( $N = 81$ ), survey point detections ( $N = 107$ ), and nests ( $N = 34$ ) of Peruvian Piedtails along an elevational transect in Manu National Park, Peru. Nest searching and mist-netting were conducted for 3 yr at elevations < 1000 m, and for 7 and 9 yr, respectively, for all other elevations. Effort was similar for survey points (4–8 visits) across elevations.

Table 2. Plant families recorded in pollen samples from 12 adult Peruvian Piedtails (*Phlogophilus harterti*) in Manu National Park, Peru. Number of records and percent of samples are shown for each plant family.

Plant family	Number of records (percent of samples)
Asteraceae	11 (92%)
Campanulaceae	10 (83%)
Gesneriaceae	8 (67%)
Cyatheaceae	4 (33.3%)
Apocynaceae	1 (8%)
Betulaceae	1 (8%)
Lythraceae	1 (8%)
Melastomataceae	1 (8%)
Poaceae	1 (8%)

often omitted. An example of this vocalization has been uploaded to xeno-canto (catalog number: XC17394). Songs were typically sung in patches of *Guadua* bamboo by individuals that flew between several different perches in a territory, singing for several minutes at each perch at heights between 1.5 and 3 m above ground. Often, two and sometimes three individuals could be heard singing simultaneously within a 60-m radius. Peruvian Piedtails were never detected singing outside of patches of *Guadua* bamboo.

A second vocalization was a call, typically given in flight. This call consisted of the same

two notes used in the introduction of the song (Fig. 2B). Calls were detected both inside and outside of patches of *Guadua* bamboo.

**Nests and eggs.** We found 34 nests between 2008 and 2014 at elevations ranging from 867 to 1370 m (mean = 1049 m,  $N = 26$ ). The earliest date a nest was found was 26 August and the latest was 7 December; in both cases, nests contained eggs. For 19 nests where initiation dates (date first egg was laid) were known, 89% were initiated in September and October. However, we did not search for nests from late December to July.

Nests were tiny open cups composed of green and dry moss and lichens, with an inner lining of fine soft light green and white pieces of lichen (Fig. 3A). All nests were in dense clumps of hanging moss located on small sticks, trunks, or vines so that nests were cryptically attached to the mossy vegetation of the substrate. Mean nest height was  $1.8 \pm 0.7$  m above ground. Mean inner diameters of nest cups were  $36.2 \pm 8.5$  mm by  $26.3 \pm 9.1$  mm. Mean wall thickness and cup depth were  $15.9 \pm 4.8$  and  $29.7 \pm 11.7$  mm, respectively. Mean external diameters were  $57.2 \pm 8.3$  mm by  $48.7 \pm 10.3$ , and mean nest height was  $61.8 \pm 16.3$  mm ( $N = 30$  for all nest variables).



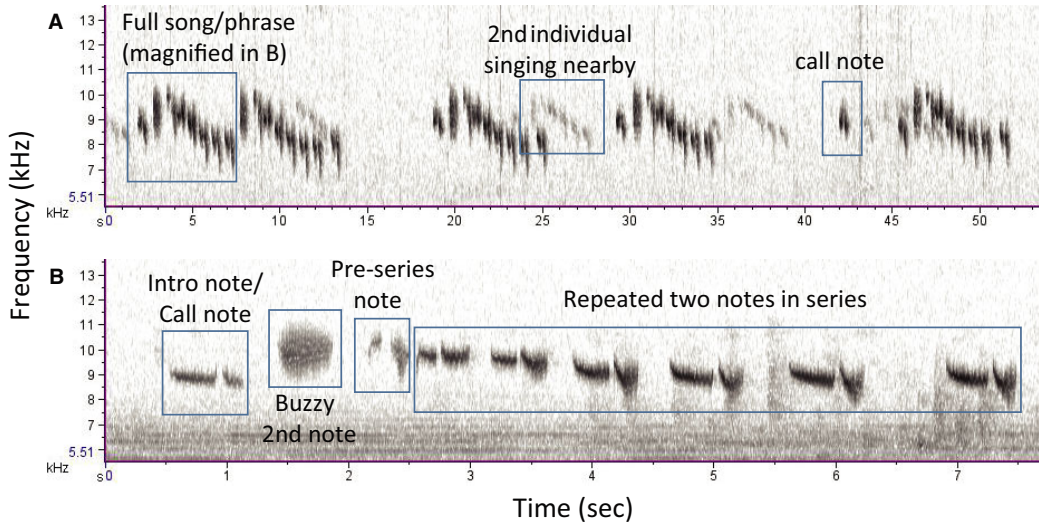


Fig. 2. Examples of vocalizations of Peruvian Piedtail recorded in Manu National Park, Peru. (A) Series of five complete song phrases recorded in *Guadua* sp. bamboo forest habitat. Song phrases separated by more than 0.5–1 s are initiated with introductory “call notes.” The songs of a second Peruvian Piedtail can also be seen in the sonogram, demonstrating that multiple individuals can be found singing 20–30 m apart. (B) A complete song phrase consists of an introductory two-note part, followed by a buzzy note, a pair of “pre-series” notes, then a series of two notes, repeated 5–7 times, with increasing inter-note intervals between successive repetitions. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



Fig. 3. Nest, eggs, and nestlings of Peruvian Piedtails in Manu National Park, Peru. (A) Adult incubating eggs, (B) vertical view of the eggs inside a nest, and (C) nestling at 12 days of age. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

Clutches ( $N = 25$ ) always consisted of two eggs; four nests were found with one egg and were confirmed as abandoned, possibly after predation of the other egg. Eggs were completely white (Fig. 3B), with dimensions averaging  $12.1 \pm 1.6$  mm by  $7.9 \pm 1$  mm and

an average mass of  $0.43 \pm 0.04$  g ( $N = 54$  eggs). Mean egg mass represented 16% of adult body mass ( $2.68 \pm 0.16$  g,  $N = 32$  adults).

**Incubation behavior and nestling period.** We only confirmed an incubation

period of 19 d for one of 30 nests because most nests were either predated before eggs hatched (63%) or were found with eggs of unknown ages (33%). Thermal sensors recorded a total of 503.25 h of incubation data from five nests. Eggs were incubated for 452.2 h overall (89.9% of the time), with a diurnal nest attentiveness of  $69.3 \pm 1.1\%$  ( $N = 5$  nests). Incubating birds averaged  $19 \pm 1.1$  foraging trips/day (range = 12–26), with an average duration of  $12 \pm 0.7$  min per trip (range = 1–37 min). Incubation bouts averaged  $29.5 \pm 2.4$  min in duration (range = 3–108 min). Mean nest temperature during diurnal incubation bouts was  $29.8 \pm 0.9^\circ\text{C}$  (range =  $23.3$ – $35.6^\circ\text{C}$ ) and decreased to  $25.7 \pm 0.9^\circ\text{C}$  (range =  $18$ – $31^\circ\text{C}$ ) during incubation recesses. Nocturnal on-bouts averaged  $12 \pm 0.1$  h in duration (range =  $11.4$ – $12.9$  h), with an average nest temperature of  $28.9 \pm 1.2^\circ\text{C}$  (range =  $23.7$ – $33.3^\circ\text{C}$ ). Adults initiated nocturnal incubation bouts between 16:48 and 17:43 ( $N = 5$  nests, 14 days of sampling for all incubation parameters above).

Eleven of 34 nests had nestlings at some point, but young fledged from only four nests (11.8%). Three of these nests were found with nestlings and one with one nestling was monitored throughout a 23-d nestling period. On the day of hatching, nestlings had pink skin, downy feathers on their backs, and weighed  $0.36 \pm 0.09$  g ( $N = 7$ ). Pins on wings started to emerge by day 7 or 8 post-hatching when nestlings weighed  $1.98 \pm 0.23$  g ( $N = 7$ ), their eyes were open, and the skin on their backs was dark gray. Primary feathers broke through their sheaths by day 14 or 15 post-hatching when pins averaged  $19.6 \pm 4.1$  mm in length, and nestlings weighed  $3.07 \pm 0.18$  g ( $N = 10$ ; Fig. 3C). Nestlings gained an average of 0.2 g per day during the first 14 days of development, and their wing chords grew an average of 1.2 mm per day during the nestling period (Fig. 4). Growth rate ( $K$ ) based on average nestling mass was 0.28 ( $N = 18$  nestlings). Mean nestling mass on the day they fledged was  $3.02 \pm 0.19$  g ( $N = 4$ ), which exceeded adult mass ( $2.68 \pm 0.16$  g,  $N = 32$  individuals) by 12%.

## DISCUSSION

Detailed knowledge of life history traits, reproductive biology, and habitat requirements

for rare and narrowly endemic Andean hummingbirds have increased in recent years (Fierro-Calderón and Martín 2007, Tinoco et al. 2009, Freile et al. 2011, Baldwin and Londoño 2016, Guevara et al. 2017). Most species, however, are still understudied, limiting our understanding of variation in the life history traits of hummingbirds, and our assessment of anthropogenic effects such as fragmentation and climate change on species in the Andes region.

**Population density.** Using point-count surveys, we estimated a population density of 57.9 individuals per  $\text{km}^2$  (95% CI: 36.2–81.4) in our study area. Our estimate suggests a higher density of Peruvian Piedtails compared to other hummingbirds in the lowlands of southeastern Peru, but within the density ranges of other range-restricted Andean hummingbirds from Ecuador. Using mist-net captures and visual observations, Terborgh et al. (1990) estimated densities of  $< 10$  individuals per  $\text{km}^2$  for several species of low-elevation hummingbirds in Manu National Park in the Peruvian Amazon. However, Cresswell et al. (1999) used a distance-transect method to calculate densities of several Andean cloud-forest species, including range-restricted hummingbirds such as Black-thighed Pufflegs (*Eriocnemis derbyi*) and Golden-breasted Pufflegs (*E. mosquera*). Estimates for these two species in pristine and secondary habitats ranged from 60–160 individuals per  $\text{km}^2$ , and the value estimated in our study is at the lower end of this range. More broadly, density estimates are critical to understand the effects of a wide variety of ecological processes, such as human disturbances, on wild populations (Buckland et al. 2015). Our estimates serve as a point of comparison for future studies of this and other Andean hummingbirds.

**Elevational range and habitat.** Although the extent of occurrence of Peruvian Piedtails is estimated at  $\sim 100,000$   $\text{km}^2$ , their actual distribution is likely more limited. An elevational range of 750–1500 m above sea level has been reported for this species (Walker et al. 2006, Schulenberg et al. 2007). Our observations generally confirm this range, but our lowest and highest detections were at 867 and 1545 m, respectively, despite surveying points as low as 600 m along a contiguous forested gradient and to 400 m in Amazon forest

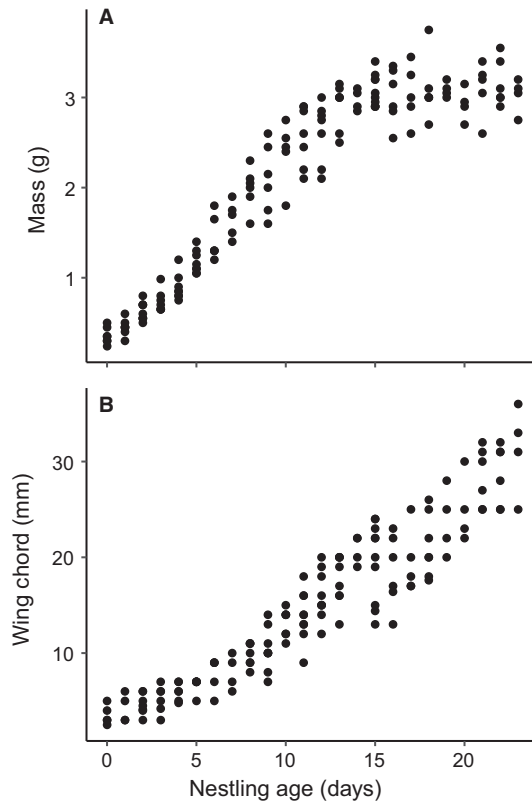


Fig. 4. Increasing mass and length of wing chords with increasing nestling age for Peruvian Piedtails in Manu National Park in southeastern Peru. Growth rate ( $K$ ) based on average nestling mass was 0.28 ( $N = 18$  nestlings).

connected to the Andes by long outlying foothill ridges (i.e., Pantiacolla). Nevertheless, Peruvian Piedtails appeared to be locally common within a narrow 400-m elevational band (900–1300 m). The difference in the low elevational range limit of Peruvian Piedtails between our observations and those reported in the literature may be due to undetected elevational migration occurring outside our study period (i.e., January–June). Although elevational migration has been reported for several Andean birds in Manu, Peruvian Piedtails are considered non-migrant residents with little evidence of elevational movements (Merkord 2010). Alternatively, this difference could reflect a recent elevational response to climate change. Range shifts at elevational limits have been widely recognized for a variety of taxa (Freeman et al. 2018), although precise historical data on elevational limits would be needed to confirm this for Peruvian Piedtails.

Availability of large patches of *Guadua* spp. bamboo surrounded by undisturbed, humid lower montane forest, appear to be important requirements for mating and breeding. For example, Peruvian Piedtails were not detected in our mist-netting or point-count surveys at low elevations in Villa Carmen (600–775 m), a protected forest area along the same elevational gradient that includes extensive patches of second-growth *Guadua* bamboo, but with little to no surrounding old-growth forest. However, these sites may also be located beyond the lower limit of the elevational range of Peruvian Piedtails.

**Nesting biology.** A cup-shaped nest built with soft material and clutch sizes of two white eggs are typical among tropical hummingbirds (Schuchmann 1999, Fierro-Calderón and Martin 2007). However, materials and placement of nests of Peruvian Piedtails differ from those of Ecuadorian Piedtails,



their only congener. Schuchmann (1999) described the nests of Ecuadorian Piedtails as tiny cups of fine rootlets and pieces of fern leaf built in vines or under dense thickets overhanging steep roadsides. In contrast, the nests of Peruvian Piedtails in our study were composed of green and dry moss and lichens with an inner lining of fine soft light green and white pieces of lichen. The use of lichen as lining material is atypical for hummingbirds, and we are not aware of other hummingbird species that use lichen in this manner. Lichen is commonly placed on the exterior of nest walls in other species. We hypothesize that the lichen may serve as camouflage for eggs and nestlings when adults are not on nests.

Incubation and nestling periods of 19 and 23 d, respectively, for Peruvian Piedtails are within the range reported for other hummingbirds of similar size (17–22 d for incubation; 21–25 d for nestlings, ~3 g; Aldrich 1945, Skutch 1961, 1964, Fierro-Calderón and Martin 2007). A relatively high daily nest attentiveness (69.3%) is also common among temperate and tropical hummingbirds (60–80%), but the K growth rate of 0.28 for nestling Peruvian Piedtails is on the lower end reported for other hummingbird species (0.26–0.47; Fierro-Calderón and Martin 2007).

Nest success in our study was low (~12%), with most nests being predated (20/34). Human disturbance could potentially reduce nesting success. However, we followed recommendations for locating and monitoring nests to minimize this effect on predation rates (Martin and Geupel 1993). High predation rates have also been reported for other cup-nesting species along this elevational gradient (Valdez-Juarez and Londoño 2012, David and Londoño 2013, Sánchez-Martínez and Londoño 2016) and for tropical birds overall (Skutch 1985).

**Other natural history notes.** Forest-dwelling hummingbirds, such as Peruvian Piedtails, are notoriously difficult to observe, particularly when trying to determine movements and spatial use patterns. We detected the calls of Peruvian Piedtails in a range of forest habitats, including old-growth cloud forest and patches of *Guadua* sp. bamboo. However, Peruvian Piedtails were only observed singing in stands of *Guadua*,

suggesting that *Guadua* habitat may be an important and possibly essential component of their breeding ecology.

Individuals rotated among several (3–4) designated perches between singing bouts, and singing perches appeared to be separated by at least 20 m. This behavior suggests that this species may form leks for mating. Lekking behavior has been described for at least 28 species of hummingbirds in two major clades, hermits, and emeralds (Skutch 1964, Stiles and Wolf 1979, Pizo and Silva 2001, Ramjohn et al. 2003, Pizo 2012), but mating systems are poorly documented for most Andean endemic species. Detailed observations of Peruvian Piedtails in potential leks are needed to confirm this behavior, and to understand daily activity patterns or other displays potentially associated with mating.

Peruvian Piedtails have been observed feeding on flowering epiphytes, shrubs, and small trees, such as those in the families Rubiaceae, Ericaceae and Gesneriaceae (Schuchmann 1999). In addition to these families, we identified Asteraceae and Campanulaceae as potentially common nectar sources for this species based on pollen swabbed from the bills of captured individuals. Interestingly, spores of Cyatheaceae were found in 33% of the samples, suggesting that tree ferns are used as a source for small arthropods or nesting material.

**Conservation implications.** The Peruvian Piedtail is currently classified as Near Threatened (NT) with a suspected decrease in global population due to habitat loss (Birdlife International 2018). Our observations were made in relatively intact areas along the elevational gradient in and around Manu National Park. Here, forested habitats in the park and adjacent conservation concession areas remain protected, but development of foothill forest outside protected areas is ongoing with the sprawling and development of foothill towns and villages. Moreover, mining and oil and gas extraction have been rapidly increasing in southeastern Peru, contributing to forest loss and representing a serious threat to regional biodiversity (Finer et al. 2008, Asner et al. 2013). Whether Peruvian Piedtails will be able to persist in fragmented habitat remains to be determined, but their preference for undisturbed forest, dense vegetation, and patches of *Guadua* bamboo at elevations

between 900–1300 m suggests that their distribution and extent of occurrence are probably substantially narrower than previously estimated and should be evaluated. A full distribution modeling analysis based on occurrence data and detailed ecological information is needed for this species to evaluate its current conservation status.

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