

**RECOMMENDED BAND SIZES AND A NOVEL TECHNIQUE FOR SEXING IMMATURE GREEN-BACKED FIRECROWN HUMMINGBIRDS (*SEPHANOIDES SEPHANIODES*)**Tyler N. McFadden<sup>1</sup> · Gabriela Biscarra<sup>2</sup> · Jorge Ruiz<sup>2</sup> · Juan G. Navedo<sup>2,3</sup><sup>1</sup> Department of Biology, Stanford University, Stanford, CA 94305, USA.<sup>2</sup> Bird Ecology Lab, Instituto de Ciencias Marinas y Limnológicas, Universidad Austral de Chile, Valdivia, Chile.<sup>3</sup> Estación Experimental Quempillén, Facultad de Ciencias, Universidad Austral de Chile, Ancud, Chile.

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**Abstract** · The Green-backed Firecrown (*Sephanoides sephaniodes*; Trochilidae) is one of the most important pollinators in the temperate rainforests of southern South America, yet its life history, including migratory behavior, population dynamics, and pollination biology remain poorly studied. Furthermore, juvenile firecrowns are sexually monochromatic, making them difficult to sex, which limits understanding of sex-related ecological differences that are common in hummingbirds. Here, we report the first banding of firecrowns in mainland Chile, propose ideal band sizes, and describe a technique for sexing immature individuals using the ratio of bill length to body mass. We place our results in the context of other studies of firecrowns and discuss possible ecological and behavioral implications of sexual dimorphism. In February–June 2018, we banded 71 firecrowns in Los Ríos Region, Chile (40°S). We recommend cutting bands to 8.2 mm in length for banding birds. Sexual dimorphism is clear, with large, short-billed males, and smaller, longer-billed females. Immature males and females can be distinguished based on the ratio of bill length to body mass, which in our sample does not overlap between the two adult sexes. This ratio separated all immature individuals at the 99% confidence level ( $< 3.09 \text{ mm g}^{-1}$  classified as male,  $> 3.36 \text{ mm g}^{-1}$  as female), and so should be tested elsewhere in the firecrown range. The incorporation of Green-backed Firecrowns in ongoing banding programs in the region has the potential to contribute important new information about the species' ecology and evolution as well as its role in ecosystem processes.

**Resumen** · Tamaños de anillas recomendados y una nueva técnica para el sexaje de individuos inmaduros en el Picaflor Chico (*Sephanoides sephaniodes*)

El Picaflor Chico (*Sephanoides sephaniodes*; Trochilidae) es uno de los polinizadores más importantes en el bosque templado austral de Sudamérica, pero su historia natural, incluyendo comportamiento migratorio, dinámica poblacional, y biología de polinización, sigue siendo poco estudiado. Además, los juveniles son monocromáticos, lo cual los hace difícil de sexar y limita el conocimiento de las diferencias ecológicas relacionadas con el sexo, que son comunes en colibríes. En este estudio reportamos los primeros anillamientos de picaflor chico en Chile continental, proponemos los tamaños de anillas ideales, y describimos una técnica para determinar el sexo de los individuos inmaduros utilizando el cociente entre la longitud del pico y el peso corporal. Ponemos nuestros resultados en el contexto de otros estudios del picaflor chico, y consideramos posibles implicaciones del dimorfismo sexual en la ecología y el comportamiento. En febrero–junio 2018 anillamos 71 picaflores chicos en la Región Los Ríos, Chile (40°S). Recomendamos cortar las anillas a 8,2 mm de largo (longitud preformada) para anillar los picaflores. Dimorfismo sexual es claro: los machos son grandes con picos cortos, mientras las hembras son más pequeñas con picos más largas. Los machos y hembras inmaduros se distinguieron por el cociente entre la longitud del pico y el peso corporal, que en nuestra muestra no superpone entre los adultos de cada sexo. Este cociente separó todos los individuos inmaduros al nivel de confianza de 99% ( $< 3,09 \text{ mm g}^{-1}$  clasificado como macho,  $> 3,36 \text{ mm g}^{-1}$  como hembra), y debe ser evaluado en otras partes del rango de distribución de la especie. La incorporación del picaflor chico en los programas de anillamiento en la región tiene la potencial de aportar nueva información importante sobre su ecología y evolución, tanto como su rol en los procesos ecológicos.

**Key words:** Banding · Chile · Sexual dimorphism · Trochilidae · Valdivian Rainforest Ecoregion

**INTRODUCTION**

The temperate rainforests of southern South America (TRSSA) in southern Chile and Argentina comprise a highly threatened global biodiversity hotspot, recognized for its rich plant diversity and endemism (Heilmayr et al. 2016, Myers et al. 2000, Carvajal et al. 2018). One striking characteristic of the TRSSA is the predominance of plant species that have vertebrate-mediated pollination and seed dispersal syndromes, despite the relatively depauperate community of animal mutualists (Aizen et al. 2002, Armesto et al. 1996). Most notably, almost 20% of the woody plant genera in the TRSSA have ornithophilous (red and tubular) flowers, yet there is only one hummingbird species: the endemic Green-backed Firecrown (*Sephanoides sephaniodes*; hereafter 'firecrowns') (Aizen & Ezcurra 1998, Smith-Ramirez 1993). This is the world's southern-most hummingbird species, breeding as far south as Isla Navarino at the southern tip of South America. Firecrowns are among the most abundant birds in

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the TRSSA during the breeding season, in which they occur from ~ 30–55°S latitudes. During the non-breeding season, firecrowns apparently migrate to lower latitudes where nectar is more available, but can be found year-round as far south as 42°S (Couve et al. 2016, Aizen et al. 2002). Due to their widespread distribution and role as the only legitimate pollinator for many plant species, firecrowns are believed to be critical for ecosystem functioning throughout the TRSSA (Rodríguez-Cabal et al. 2013, Valdivia et al. 2006, Chalcoff et al. 2012).

Despite the firecrown's ubiquity and ecological importance, population trends are poorly studied. BirdLife International lists the species as Least Concern because the firecrown is common throughout its large geographic range, although it is suspected that the population is decreasing (BirdLife International 2018). Widespread land-use change throughout its range, largely due to conversion of native forest to agriculture or exotic timber plantations (Heilmayr et al. 2016), combined with local evidence of land-use change associated population declines, suggest that the population may not be as stable as once thought. For example, despite being found in a wide range of habitat types, firecrown presence is strongly associated with forest cover (Vergara & Armesto 2009) and large trees (Díaz et al. 2005). Firecrowns have reduced functional connectivity across open habitats (Magrath et al. 2012) and are also more abundant in continuous than fragmented forests (Valdivia et al. 2006), and in native forests than pine plantations or open areas (Estades & Temple 1999).

Long-term population data for firecrowns are lacking, in part due to the specialized techniques and equipment required for banding hummingbirds – bands must be made by hand and are currently not available through the Chilean Servicio Agrícola y Ganadero (SAG), the government agency that oversees bird-banding in Chile. To our knowledge, long-term banding of firecrowns has only occurred in the extreme south in Tierra del Fuego, where large-scale habitat conversion has not yet occurred (Rozzi & Jiménez 2013). Because few studies have involved marked individuals, we have limited knowledge of firecrown morphology and molt/plumage characteristics. For example, while adult males and females are easily distinguished in the field based on the presence or absence of red crown feathers, these feathers do not develop until the pre-formative molt (during the Austral summer and fall; Pyle et al. 2015), making it impossible to reliably sex younger individuals using plumage characteristics. As such, researchers are unlikely to detect potential sex-related differences in juvenile survival rates, dispersal, site fidelity, migratory behavior, or foraging ecology, all key parameters to understanding population dynamics and ecosystem function. With the goal of stimulating further research on this emblematic and ecologically important bird, we provide a detailed protocol for banding hummingbirds, report appropriate band sizes for use with *S. sephaniodes*, and describe a novel morphometric-based technique for sexing immature individuals.

## METHODS

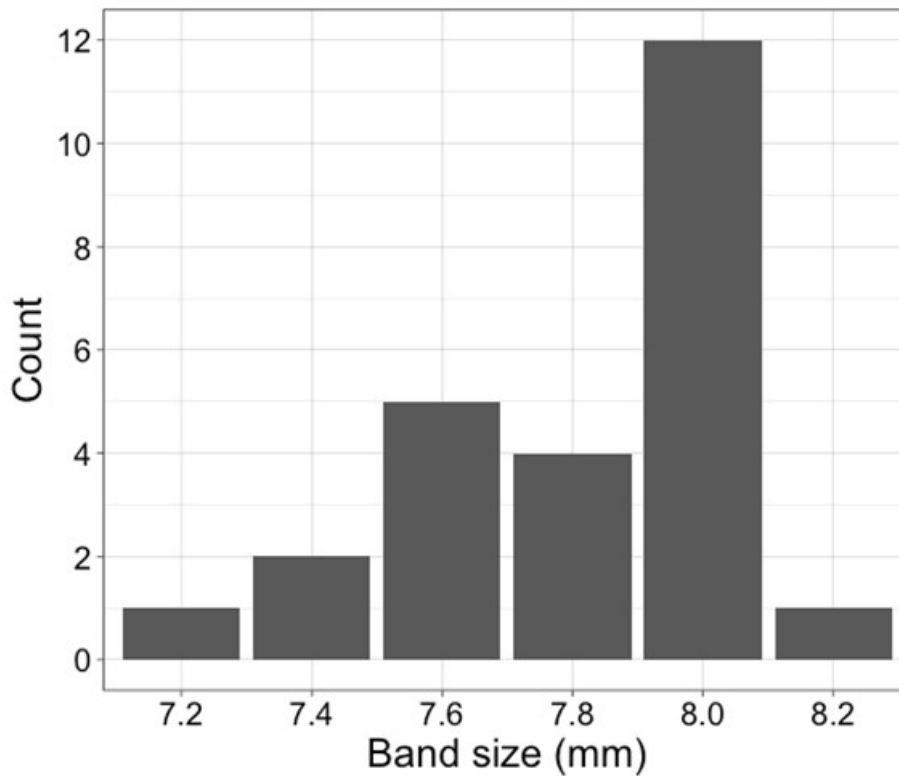
**Study area.** We captured hummingbirds during February–June 2018 in native forests and exotic timber plantations in and adjacent to the Llancahue Forest Reserve in Los Ríos

Region, Chile (39°50'S, 73°08'W, 1300 ha). This reserve is located in the Intermediate Depression from 50 to 360 m a.s.l., and contains ~ 700 ha of old-growth Valdivian Temperate Rainforest and an additional ~ 400 ha of secondary native forest corresponding primarily to the mixed evergreen broadleaf and *Nothofagus dombeyi* (Nothofagaceae)-dominated forest types (Donoso et al. 2014). Annual rainfall averages 2100 mm, occurring mostly from April–October (Donoso et al. 2014). Temperatures are moderate, with maximum and minimum temperatures at the weather station in Valdivia (25 m a.s.l.) averaging 22.9 and 10.4°C in January, and 11.2 and 4.5°C in July (Climate-data.org, 2019). Surrounding the reserve is a heterogeneous mosaic of exotic timber plantations (primarily *Pinus radiata*, Pinaceae and *Eucalyptus* spp., Myrtaceae), pastureland, and remnant patches of native forest. We captured birds in old-growth and secondary native forests, a 14-year-old *Eucalyptus nitens* plantation, and an 11-year-old *Pinus radiata* plantation.

**Hummingbird banding.** Aluminum hummingbird bands were provided through the United States Geological Survey Bird Banding Lab and used with permission from SAG. Bands were provided uncut in sheets of 300 bands, each with its own 6-digit alphanumeric code. Bands were sliced using a bench-shear to widths of < 1.5 mm, and individually cut to length using a custom-made jig. We initially made bands ranging in length from 6.4–8.4 mm to allow for variation in hummingbird tarsus widths. After cutting, bands were carefully sanded with 400 grit sandpaper to remove any sharp edges, and formed into open 'C' shaped bands using a custom-made band-forming tool (Figure S1, Supplementary Material online; all custom-made tools manufactured by Lee Rogers, Hummingbird Monitoring Network).

In the field, hummingbirds were captured with mist nets (9 x 2.5 m nets, 16 mm mesh, 5–11 nets per day) in the forest understory. Nets were opened one hour after sunrise, operated for 5 hours, and checked every 15 minutes. Hummingbirds were removed from the nets and placed in nylon mesh draw-string bags (mesh size: ~ 5.5 mm) for processing and banding. To determine the appropriate band size for each bird, we measured the width of the tarsus at its widest point by carefully extracting its leg from the mesh bag and inserting it into a custom-made tarsus gauge (Figure S2). Once the appropriate size was determined, a band was placed on the right tarsus and gently closed using the 2.0 mm aperture on standard banding pliers (Figure S3). The appropriate fit was confirmed by checking that the band could slide up and over the tibiotarsal joint, but could not fall off (following Russell & Russell, 2001). Once banded, we removed the bird from the mesh bag and measured the standard variables: mass ( $\pm$  0.1 g, electronic balance), wing chord ( $\pm$  0.5 mm, rule), bill length (exposed culmen;  $\pm$  0.01 mm, caliper), and tail length ( $\pm$  0.5 mm, rule). All birds were provided 20% sucrose nectar (v/v in water) from a glass dropper prior to release.

**Ageing and sexing.** Firecrowns were aged and sexed in the field based on plumage characteristics and the presence of bill striations, following Pyle et al. (2015). We used the Wolfe-Ryder-Pyle (WRP) molt-based ageing system (Wolfe et al. 2010), which is preferable in tropical or Austral regions where breeding and fledging occur across calendar years.



**Figure 1.** Recommended band sizes based on measured tarsus widths in 32 Green-backed Firecrowns (*Sephanoides sephaniodes*) in Los Ríos Region, Chile. Band size corresponds to the length in mm of the unformed aluminum bands.

Firecrowns follow a Complex Basic Molt Strategy, and can be reliably assigned to one of several age classes in the field: juvenile plumage, pre-formative molt, formative plumage, pre-basic molt, basic plumage. Adult (late pre-formative molt and older) males and females were sexed in the field based on the presence or absence of red crown feathers. Younger individuals that could not be sexed in the field are hereafter referred to as immatures.

**Statistical analysis.** We tested the ratio of bill length to body mass (bill:mass ratio) as a potential metric for sexing immature individuals, because females appeared to have longer bills than males relative to their body size (pers. obs.). To test this relationship, we attempted a binomial generalized linear model with sex as the response variable and the ratio of bill length to body mass as the predictor variable. The model achieved perfect separation (all individuals were sexed accurately by this single predictor variable), indicating there was zero overlap in bill:mass ratio between males and females, which precluded the use of a GLM for describing the relationship. Instead, we sexed immature individuals based on their bill:mass ratios alone. To reduce the risk of type I errors (erroneously assigning an individual to a given sex), we conservatively used the 99% confidence intervals of male and female bill:mass ratios to sex the immature individuals. Following this method, an immature individual was assumed to be male only if its bill:mass ratio was less than the lower 99% bound for females, and assumed to be female only if its bill:mass ratio was greater than the upper 99% bound for males.

Morphological differences between sexes were compared using two sample *t*-tests. Wing chord was log-transformed to comply with the *t*-test normality assumption. For the purposes of this analysis, we only included individu-

als which were sexed unequivocally in the field based on plumage (i.e., adults).

## RESULTS

We captured and banded 71 individuals. Band sizes based on measured tarsus widths for 32 hummingbirds (10 male, 10 female, 12 immature) averaged  $7.82 \pm 0.04$  mm and ranged from 7.2–8.2 mm (Figure 1). Based on these measurements, we used 8.2 mm bands for all subsequent captures. We have subsequently recaptured 24 individuals banded following this protocol (as part of this and other studies) and observed no band problems.

Adult males and females displayed clear sexual dimorphism (Table 1) in all measured morphological variables ( $p < 0.001$ ). Males were on average 32% heavier than females and had longer wings and tails, while females' bills were 7% longer. This difference in bill length was even more notable when evaluated in relation to body mass (female bills were 43% longer relative to mass). Males and females displayed zero overlap in bill:mass ratios, averaging 2.61 and 3.74 mm  $g^{-1}$ , respectively (Figure 2A, Male 99% CI: 1.86–3.36, female 99% CI: 3.09–4.38). The bill:mass ratios of all immature individuals closely aligned with either male or female values (Figure 2B), allowing all immature individuals to be sexed at the 99% confidence level (Table S1, Supplementary Material online).

## DISCUSSION

Clear sexual dimorphism in adult firecrowns suggests that morphometrics may provide a rapid and cost-effective tool for sexing immature birds that have not yet developed dichromatic plumage. Indeed, our proposed sexing method,

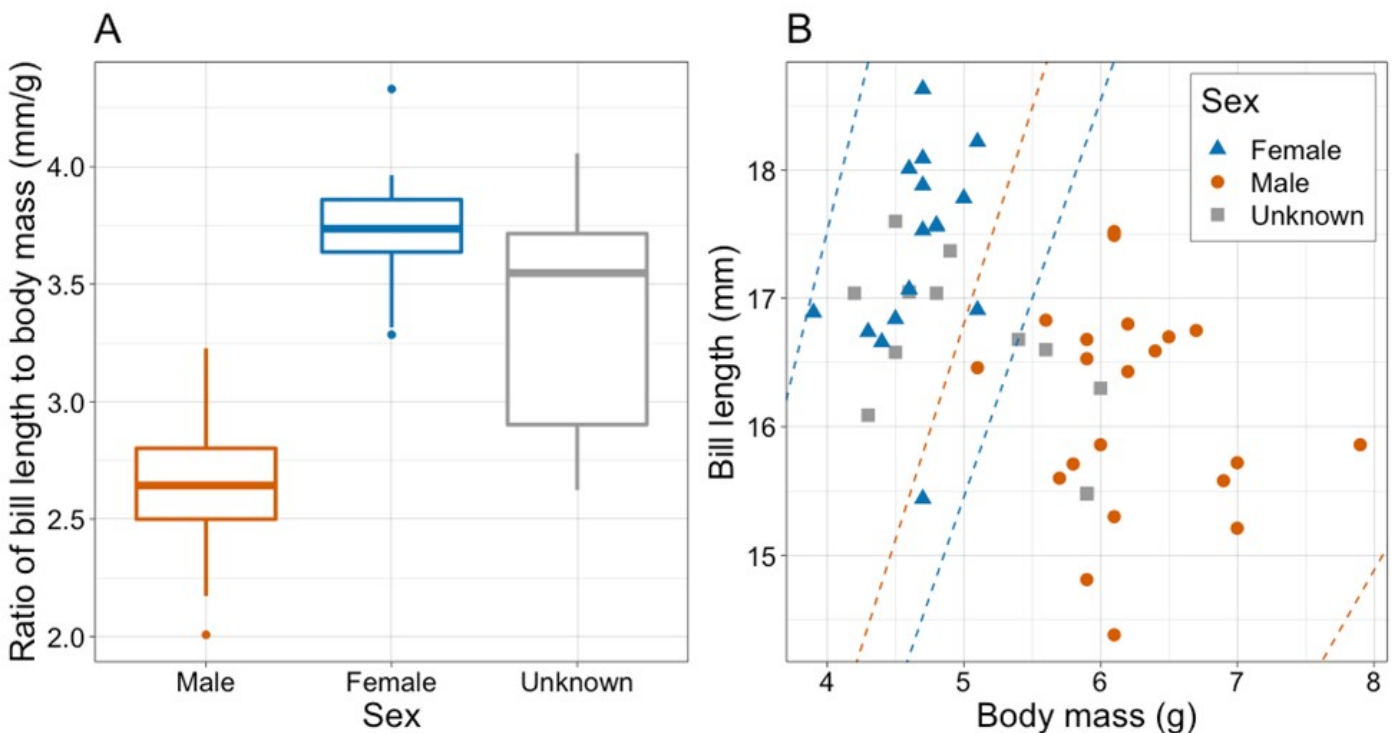
**Table 1.** Morphometric data for 71 Green-backed Firecrowns (*Sephanoides sephaniodes*) captured in Los Ríos Region, Chile. Sex was assigned in the field based on plumage. Immature individuals were unable to be sexed in the field due to non-sexually dimorphic plumage. All differences between males and females are significant at  $p < 0.001$ . All values reported as mean (SE).

	Males	n	Females	n	Unknown	n
Body mass (g)	6.2 (0.1)	24	4.7 (0.1)	29	5.2 (0.2)	17
Wing chord (mm)	62.6 (0.3)	24	56.9 (0.3)	29	59 (0.9)	16
Bill length (mm)	16.13 (0.18)	21	17.30 (0.19)	17	16.61 (0.20)	12
Tail length (mm)	37 (0.3)	19	34 (0.4)	26	36 (0.9)	10

based on the ratio between bill length and body mass, appears to be highly effective. This simple ratio of standard morphological measurements perfectly separated 21 males and 16 females, and permitted sexing of all 12 immature individuals (at the 99% confidence level). To our knowledge this is the first description of using relative bill length to sex immature hummingbirds, though dimorphisms in bill size and shape are common in many species of hummingbirds (Berns & Adams 2013), and are sometimes used for sexing adults (e.g., Temeles & Kress 2003). Relative bill length may be a useful tool for sexing other immature hummingbirds, since many sexually dimorphic species have monochromatic juvenile plumage (Berns & Adams 2013). It is important to note that we assume sex-specific bill:mass ratios to be similar among adult and immature individuals. As such, it will be important to corroborate the accuracy of this method through molecular methods (e.g., Shibuya et al. 2018) or the recapture of marked individuals once they have developed adult plumage.

Male firecrowns in our study were consistently larger and heavier, while females had longer bills, especially relative to their body mass. These broad patterns were similar to those

found in other studies of firecrowns (Pyle et al. 2015, González-Gómez & Estades 2009, Rozzi & Jiménez 2013), though the absolute measurements vary somewhat, possibly due to measurement error or, more plausibly, real differences associated with latitude, elevation, or climate, as are commonly found in other birds (e.g., Ashton 2002, Perктаş 2011, Sun et al. 2017). Indeed, when comparing measurements in four studies (including this one) there is some evidence for a positive latitudinal trend in body mass (Table 2; Fraga et al. 1997, González-Gómez et al. 2009, Rozzi & Jiménez 2013). This regional variation is unlikely related to pre-migratory fattening in migratory populations, since firecrowns do not appear to store measurable amounts of fat – in 367 captures across all seasons we have never observed a firecrown with more than trace amounts of fat (authors, unpubl. data). Instead, this variation may be explained in part by Bergmann's Rule, which indicates that endotherm body size increases in colder regions, especially given the high thermoregulatory costs firecrowns experience at low temperatures (Victoria López-Calleja et al. 1997, Salewski & Watt 2017). Given documented morphological variation throughout the firecrown range, caution should be used in applying our proposed sexing tech-



**Figure 2.** A) Boxplot showing the ratio of bill length to body mass (bill:mass ratio;  $\text{mm g}^{-1}$ ) separated by sex for 21 female, 16 male, and 12 unknown sex Green-backed Firecrowns (*Sephanoides sephaniodes*) in Los Ríos Region, Chile. B) Scatterplot of bill length vs. body mass. Dashed lines indicate 99% confidence intervals for bill:mass ratios. Individuals of unknown sex were classified *post hoc* as male if bill:mass ratio was less than the lower female 99% bound (right of blue line), or female if bill:mass ratio was greater than the upper male 99% bound (left of orange line).

**Table 2.** Mean body mass, wing chord, and bill length of Green-backed Firecrowns (*Sephanoides sephaniodes*) from four locations across a latitudinal gradient in the Temperate Rainforests of Southern South America. All values reported as mean  $\pm$  SE (n).

Source	Latitude	Body mass (g)		Wing chord (mm)		Bill length (mm)	
		Male	Female	Male	Female	Male	Female
González-Gómez & Estades 2009	~35-36°S	5.925 $\pm$ 0.068 (106)	4.736 $\pm$ 0.033 (344)	62.29 $\pm$ 0.25 (106)	56.70 $\pm$ 0.15 (344)	14.26 $\pm$ 0.16 (106)	15.77 $\pm$ 0.08 (344)
This study	39°50'S	6.2 $\pm$ 0.1 (24)	4.7 $\pm$ 0.1 (29)	62.6 $\pm$ 0.3 (24)	56.9 $\pm$ 0.3 (29)	16.13 $\pm$ 0.18 (21)	17.30 $\pm$ 0.19 (17)
Fraga et al. 1997	40°52'- 41°02'S	6.01 $\pm$ 0.06 (28)	5.43 $\pm$ 0.19 (8)	63.62 $\pm$ 1.02 (11)	60.35 $\pm$ 0.81 (2)	15.58 $\pm$ 0.15 (29)	15.66 $\pm$ 0.24 (9)
Rozzi & Jiménez 2013	54°57'S	7.1 $\pm$ 0.4 (12)	6.1 $\pm$ 0.4 (9)	62.7 $\pm$ 0.9 (12)	58.6 $\pm$ 1.2 (9)	15.9 $\pm$ 0.32 (12)	16.4 $\pm$ 0.49 (8)

nique and our specific bill:mass ratios across large geographic scales (Ellrich et al. 2010).

Despite clear sexual dimorphism in firecrown plumage and morphology, the evolutionary origins or ecological implications of these traits are poorly studied (but see González-Gómez & Estades 2009, González-Gómez et al. 2014). Hummingbird bill length is typically linked to foraging behavior: longer bills increase foraging efficiency at flowers with long corollas and are typically associated with non-territorial or traplining foraging strategies (*sensu* Janzen 1971), whereas shorter bills are typical of territorial species (Paton & Collins 1989, Temeles & Roberts 1993, Temeles 1996). Both male- and female-biased bill dimorphisms are common in hummingbirds, with females typically having longer bills in species with territorial males (Bleiweiss 1999). Male firecrowns are highly territorial, while females are not, and instead make brief forays into male territories to forage (González-Gómez & Estades 2009). Therefore, longer bills may be advantageous for females (González-Gómez & Estades 2009), allowing them to extract nectar more quickly, or access leftover nectar that the shorter-billed males cannot (Bleiweiss 1999, Temeles & Roberts 1993). Differences in bill length, territoriality, and foraging behavior have the potential to influence pollination processes either through sex-specific resource selection (Temeles & Kress 2003) or differential pollen movement (Betts et al. 2015). However, little is known about sex-specific diet in firecrowns. One study of pollen loads in Argentina suggests there may be some diet differentiation, at least in the case of *Tristerix corymbosus* (Loranthaceae; Fraga et al. 1997), a hemi-parasitic mistletoe that is one of the only winter-blooming flowers available to the firecrown in much of its range (Smith-Ramirez 1993, Rodríguez-Cabal et al. 2013). Fraga et al. (1997) reported that many male, but few female firecrowns carried *T. corymbosus* pollen, which could be due to territorial males monopolizing this important resource. This hypothesis is supported by winter observations in Chile of extremely male-biased sex ratios and territorial behavior in a small forest patch containing dozens of *T. corymbosus* plants in full bloom (authors, unpubl. data).

As one of the most abundant birds in South American temperate rainforests, and the primary pollinator for a rich assemblage of plants therein (Aizen et al. 2002, Valdivia et al. 2006, Chalcoff et al. 2012), Green-backed Firecrowns are an excellent model species for studying ecological function in this biodiversity hotspot. While many studies have examined firecrown behavior, physiology, and ecological interactions,

basic information on population trends, demography, migration, and spatial ecology is still lacking. Including hummingbird banding in current banding operations in Chile and Argentina will help fill these knowledge gaps and contribute to long-term bird monitoring in the region. Though approximate band sizes have been reported elsewhere (Anderson et al. 2002), one barrier to hummingbird banding in the region has been the lack of clear information about the techniques and equipment required. We hope that the band sizes and techniques we describe here will serve to stimulate further consideration of hummingbirds in local monitoring programs and regional conservation strategies.

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#### REFERENCES

- Aizen, MA & C Ezcurra (1998) High incidence of plant-animal mutualisms in the woody flora of the temperate forest of southern South America: biogeographical origin and present ecological significance. *Ecología Austral* 8: 217–236.
- Aizen, MA, DP Vásquez & C Smith-Ramírez (2002) Historia natural y conservación de los mutualismos planta-animal del bosque templado de Sudamérica austral. *Revista Chilena de Historia Natural* 75: 79–97.
- Anderson, C, R Rozzi, C Elphick & YS McGehee (2002) El Programa Omora de anillamiento de aves en los bosques subantárticos: la estandarización del tamaño de anillos apropiados para las aves de la Región de Magallanes. *Boletín Chileno de Ornitología* 9: 2–11.
- Armesto, JJ, C Smith-Ramírez & C Sabag (1996) The importance of plant-bird mutualisms in the temperate rainforest of southern South America. Pp 248–265 in Lawford, RG (ed). *High-latitude Rainforests and associated ecosystems of the west coast of the Americas*. Springer, New York, New York, USA.
- Ashton, KG (2002) Patterns of within-species body size variation of

- birds: strong evidence for Bergmann's rule. *Global Ecology and Biogeography* 11: 505–523.
- Berns, CM & DC Adams (2013) Becoming different but staying alike: patterns of sexual size and shape dimorphism in bills of hummingbirds. *Evolutionary Biology* 40: 246–260.
- Betts, MG, AS Hadley & WJ Kress (2015) Pollinator recognition by a keystone tropical plant. *Proceedings of the National Academy of Sciences of the United States of America* 112: 3433–3438.
- Bleiwiss, R (1999) Joint effects of feeding and breeding behaviour on trophic dimorphism in hummingbirds. *Proceedings of the Royal Society B: Biological Sciences* 266: 2491–2497.
- Carvajal, MA, AJ Alaniz, C Smith-Ramírez & KE Sieving (2018) Assessing habitat loss and fragmentation and their effects on population viability of forest specialist birds: linking biogeographical and population approaches. *Diversity and Distributions* 24: 820–830.
- Chalcoff, VR, MA Aizen & C Ezcurra (2012) Erosion of a pollination mutualism along an environmental gradient in a south Andean treelet, *Embothrium coccineum* (Proteaceae). *Oikos* 121: 471–480.
- Couve, E, CF Vidal & J Ruiz (2016) *Aves de Chile, sus islas oceánicas y Península Antártica* 1st ed. FS Editorial, Punta Arenas, Chile.
- Díaz, IA, JJ Armesto, S Reid, KE Sieving & MF Wilson (2005) Linking forest structure and composition: avian diversity in successional forests of Chiloé Island, Chile. *Biological Conservation* 123: 91–101.
- Donoso, PJ, C Frêne, M Flores, MC Moorman, CE Oyarzún & JC Zavaleta (2014) Balancing water supply and old-growth forest conservation in the lowlands of south-central Chile through adaptive co-management. *Landscape Ecology* 29: 245–260.
- Ellrich, H, V Salewski & W Fiedler (2010) Morphological sexing of passerines: not valid over larger geographical scales. *Journal of Ornithology* 151: 449–458.
- Estades, CF & SA Temple (1999) Deciduous-forest bird communities in a fragmented landscape dominated by exotic pine. *Ecological Applications* 9: 573–585.
- Fraga, RM, AE Ruffini & D Grigera (1997) Interacciones entre el picaflor rubí *Sephanoides sephanioides* y plantas del bosque subantártico en el Parque Nacional Nahuel Huapi, Argentina. *El Hornero* 14: 224–234.
- González-Gómez, PL & CF Estades (2009) Is natural selection promoting sexual dimorphism in the Green-backed Firecrown hummingbird (*Sephanoides sephanioides*)? *Journal of Ornithology* 150: 351–356.
- González-Gómez, PL, N Madrid-Lopez, JE Salazar, R Suárez, P Razeto-Barry, J Mpodozis, F Bozinovic & RA Vásquez (2014) Cognitive ecology in hummingbirds: the role of sexual dimorphism and its anatomical correlates on memory. *PLoS ONE* 9: e90165.
- Heilmayr, R, C Echeverría, R Fuentes & EF Lambin (2016) A plantation-dominated forest transition in Chile. *Applied Geography* 75: 71–82.
- Janzen, DH (1971) Euglossine bees as long-distance pollinators of tropical plants. *Science* 171: 203–205.
- Magrath, A, AR Larrinaga & L Santamaría (2012) Effects of matrix characteristics and interpatch distance on functional connectivity in fragmented temperate rainforests. *Conservation Biology* 26: 238–247.
- Myers, N, RA Mittermeier, CG Mittermeier, GAB Da Fonseca & J Kent (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- Paton, DC & BG Collins (1989) Bills and tongues of nectar-feeding birds: a review of morphology, function and performance, with intercontinental comparisons. *Australian Journal of Ecology* 14: 473–506.
- Perktaş, U (2011) Ecogeographical variation of body size in Chaffinches *Fringilla coelebs*. *Bird Study* 58: 264–277.
- Pyle, P, A Engilis & DA Kelt (2015) *Manual for ageing and sexing birds of Bosque Fray Jorge National Park and northcentral Chile, with notes on range and breeding seasonality*. Special Publication of the Occasional Papers of the Museum of Natural Science, Louisiana State University, Baton Rouge, Louisiana, USA.
- Rodriguez-Cabal, MA, M Noelia Barrios-García, GC Amico, MA Aizen, NJ Sanders & DS Simberloff (2013) Node-by-node disassembly of a mutualistic interaction web driven by species introductions. *Proceedings of the National Academy of Sciences* 110: 16503–16507.
- Rozzi, R & JE Jiménez (2013) (eds) *Magellanic Sub-Antarctic ornithology: first decade of long-term bird studies at the Omora Ethnobotanical Park, Cape Horn Biosphere Reserve, Chile*. Univ. of North Texas Press, Denton, Texas, USA.
- Russell, SM & RO Russell (2001) *The North American banders' manual for banding hummingbirds*. The North American Banding Council, Point Reyes Station, California, USA.
- Salewski, V & C Watt (2017) Bergmann's rule: a biophysiological rule examined in birds. *Oikos* 126.
- Shibuya, FLS, FT Presti, SAC. Lopes, PG Mota & JJ Roper (2018) Molecular sex determination in neotropical monochromatic hummingbirds. *Ornitología Neotropical* 29: 225–228.
- Smith-Ramirez, C (1993) Los picaflor y su recurso floral en el bosque templado de la isla de Chiloé, Chile. *Revista Chilena de Historia Natural* 66: 65–73.
- Sun, Y, M Li, G Song, F Lei, D Li & Y Wu (2017) The role of climate factors in geographic variation in body mass and wing length in a passerine bird. *Avian Research* 8(1), <https://doi.org/10.1186/s40657-016-0059-9>
- Temeles, EJ (1996) A new dimension to hummingbird-flower relationships. *Oecologia* 105: 517–523.
- Temeles, EJ & WJ Kress (2003) Adaptation in a plant-hummingbird association. *Science* 300: 630–633.
- Temeles, EJ & WM Roberts (1993) Effect of sexual dimorphism in bill length on foraging behavior: an experimental analysis of hummingbirds. *Oecologia* 94: 87–94.
- Valdivia, CE, JA Simonetti & CA Henríquez (2006) Depressed pollination of *Lapageria rosea* Ruiz et Pav. (Philesiaceae) in the fragmented temperate rainforest of southern South America. *Biodiversity and Conservation* 15: 1845–1856.
- Vergara, PM & JJ Armesto (2009) Responses of Chilean forest birds to anthropogenic habitat fragmentation across spatial scales. *Landscape Ecology* 24: 25–38.
- Victoria López-Calleja, M, F Bozinovic & C Martínez del Río (1997) Effects of sugar concentration on hummingbird feeding and energy use. *Comparative Biochemistry and Physiology* 118A: 1291–1299.
- Wolfe, JD, TB Ryder & P Pyle (2010) Using molt cycles to categorize the age of tropical birds: an integrative new system. *Journal of Field Ornithology* 81: 186–194.