



Avian Behavior, Ecology, and Evolution

Molt patterns, aging, and sexing criteria for ten temperate Neotropical bird species: an important resource for bird monitoring programs

Patrones de muda, edad y criterios de sexado para diez especies de aves Neotropicales de zonas templadas: un recurso importante para los programas de monitoreo de aves

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ABSTRACT. Within avian biology, molt represents a crucial and energetically demanding process that involves the periodic replacement of plumage. A comprehensive understanding of molt patterns enables bird monitoring programs and conservation efforts. We analyzed the timing, duration, and extent of molt for 10 bird species in central Argentina, and established sex and age determination criteria based on molt patterns and morphometric measurements. We confirmed the center of Argentina as molting grounds for nine species, except *Elaenia albiceps*, despite 69 captures over 51 months. Our analysis revealed distinct molting seasons, with eight species exhibiting a temporally restricted molt toward the end of summer following breeding, while *Columbina picui* displayed a prolonged molting season. The preformative molt extent varied from partial to complete for eight species, but incomplete to complete for *Sporophila caerulea* and *C. picui*. Wing chord was significantly longer in males than in females in all 10 study species but was not entirely reliable as a sexing criterion. We present the first description of molt patterns for birds in central Argentina, which addresses the knowledge gap in the natural history of southern South America bird species. The identified patterns will facilitate field-based age and sex determination, thereby enhancing bird monitoring programs.

RESUMEN. Dentro de la biología aviar, la muda representa un proceso crucial y energéticamente exigente que implica el reemplazo periódico del plumaje. Un entendimiento exhaustivo de los patrones de muda permite llevar a cabo programas de monitoreo de aves y esfuerzos de conservación. Analizamos el momento, la duración y la extensión de la muda en 10 especies de aves del centro de Argentina, y establecimos criterios de determinación del sexo y la edad basados en patrones de muda y mediciones morfométricas. Confirmamos el centro de Argentina como un área de muda para nueve especies, excepto *Elaenia albiceps*, a pesar de las 69 capturas realizadas a lo largo de 51 meses. Nuestro análisis reveló distintas estaciones de muda, con ocho especies mostrando una muda temporalmente restringida hacia el final del verano siguiente a la reproducción, mientras que *Columbina picui* mostró una estación de muda prolongada. La extensión de la muda preformativa varió de parcial a completa en ocho especies, pero de incompleta a completa en *Sporophila caerulea* y *C. picui*. La cuerda alar fue significativamente más larga en los machos que en las hembras de las 10 especies estudiadas, pero no fue del todo fiable como criterio de sexado. Presentamos la primera descripción de los patrones de muda de las aves del centro de Argentina, que aborda el vacío de conocimiento en la historia natural de las especies de aves del sur de Sudamérica. Los patrones identificados facilitarán la determinación de la edad y el sexo en campo, mejorando así los programas de monitoreo de aves.

Key Words: *age determination; central Argentina; molt patterns; morphometric measurements*

INTRODUCTION

Within avian biology, molt is a critical energetically demanding life history stage in which birds undergo the periodic replacement of their plumage (Howell et al. 2003). Knowledge about molt patterns yields profound insights into the natural history of birds, ecological dynamics, and the factors that influence avian populations (Jarrett et al. 2021). These insights facilitate the implementation of effective bird monitoring programs, thereby improving our capacity to track, assess, and contribute to well-informed conservation strategies for natural bird populations (Albert et al. 2016).

The Nearctic and Palearctic regions possess well-established documentation regarding molt patterns of many species (Jenni and Winkler 2020, Pyle 2022). The Neotropical region and South America in general, however, historically lacked comprehensive analysis and research that assessed bird molt patterns (Ryder and Wolfe 2009, Rueda-Hernández et al. 2018). Nevertheless, in recent years, there has been an increase in research efforts dedicated to addressing this knowledge gap (Pyle et al. 2004, 2015, Guallar et al. 2009, 2016, 2018, 2020, Wolfe et al. 2009, Moreno-Palacios et

al. 2017, Díaz et al. 2020, 2022, Carnes and Ash 2023, Ferreira et al. 2023). Yet, it is worth noting that no such studies have been conducted within the temperate southern region of South America, and specifically in Argentina.

In the southern region of the Neotropics, the absence of comprehensive avian life history knowledge has delayed the progress of population monitoring programs and field surveys because they rely heavily on accurate methods for determining the age and sex of avian species. To compensate for this issue, two primary approaches for establishing age and sex criteria have gained prominence in recent years: the analysis of molt patterns (Mulvihill 1993, Jenni and Winkler 2020, Pyle 2022, Pyle et al. 2024) and the use of morphometric differences (Pyle 2022).

In this context, the Wolf-Ryder-Pyle age classification system has provided a universal framework for age classification by scrutinizing molt patterns, and has enabled the categorization of birds into discrete age groups (Wolfe et al. 2010, Johnson et al. 2011, Pyle et al. 2022). Additionally, morphometric measurements are commonly used as a supplementary method

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for avian sex determination, especially in species with monochromatic plumage between the sexes (Bell 2020, Pyle 2022, Leys and Grieves 2023).

The study of feather molt has also demonstrated its substantial impact across various scientific disciplines. This is due primarily to the fact that molt demands a considerable energetic cost and exerts a direct influence on individual fitness (Nilsson and Svensson 1996). For instance, the proportion of yearling individuals, aged through the analysis of molt patterns, has been correlated with habitat quality (Pyle et al. 2020, Jarrett et al. 2021). Moreover, molt analysis serves as a valuable tool for evaluating anthropogenic influences on natural populations, such as urbanization and global warming (Hope et al. 2016, Kiat et al. 2019).

None of these population dynamics analyses would have been possible if it was not for previous clear descriptions about molt patterns. Due to the lack of basic descriptions of molt patterns in the temperate zone of South America, our goal was to determine the timing, duration, and extent of molt patterns for 10 common bird species of central Argentina. We also aimed to establish aging and sexing criteria using molt patterns and morphometric measurements.

METHODS

Study area

This study was conducted in the National University of Río Cuarto permanent bird banding station in the protected area “El Espinal” (33°6'54.90" S, 64°18'2.84" W; 424 m ASL) in the southern region of Córdoba, Argentina. The study area is represented by the Espinal biogeographic district (Arana et al. 2021) and the Espinal phytogeographic region (Burkart et al. 1999), a deciduous xerophytic forest, where the dominant trees are *Neltuma alba*, *N. nigra*, and *N. caldenia*, accompanied by *Vachelia caven*, *Geoffroea decorticans*, *Celtis tala*, and *Schinus fasciculatus*. However, in the past years, there has been an increase in the prevalence of exotic species such as *Morus* spp. and *Ulmus minor*. The region has a temperate sub-humid climate with highly marked climatic seasons, including precipitation during the spring and summer, from September to March (Seiler et al. 1995).

Data collection

The sampling encompassed the period from December 2018 to February 2023. The sampling array consisted of six to eight mist nets (12 × 2.5 m, 36-mm mesh) spaced approximately 50 m apart. Bird banding sessions were executed from one to four times per month, contingent upon weather conditions (i.e., mist nets were not operated on rainy or highly windy days). In each sampling day, the mist nets were opened during sunrise and closed around midday, approximately. This systematic approach was consistently applied over the entire sampling duration, and yielded a total of 72 sampling days and 1740 mist-net hours. Each bird captured was banded with a uniquely numbered aluminum band. For the analyses, we selected 10 species based on their abundance and data availability (captures/recapture) (Table 1).

Molt analysis

To analyze molts and molt strategies, we used Humphrey and Parkes' (1959) terminology as revised by Howell et al. (2003) (e.g., prejuvenile, preformative, prebasic, and prealternate molts; and complex basic and complex alternate molt strategies). When we

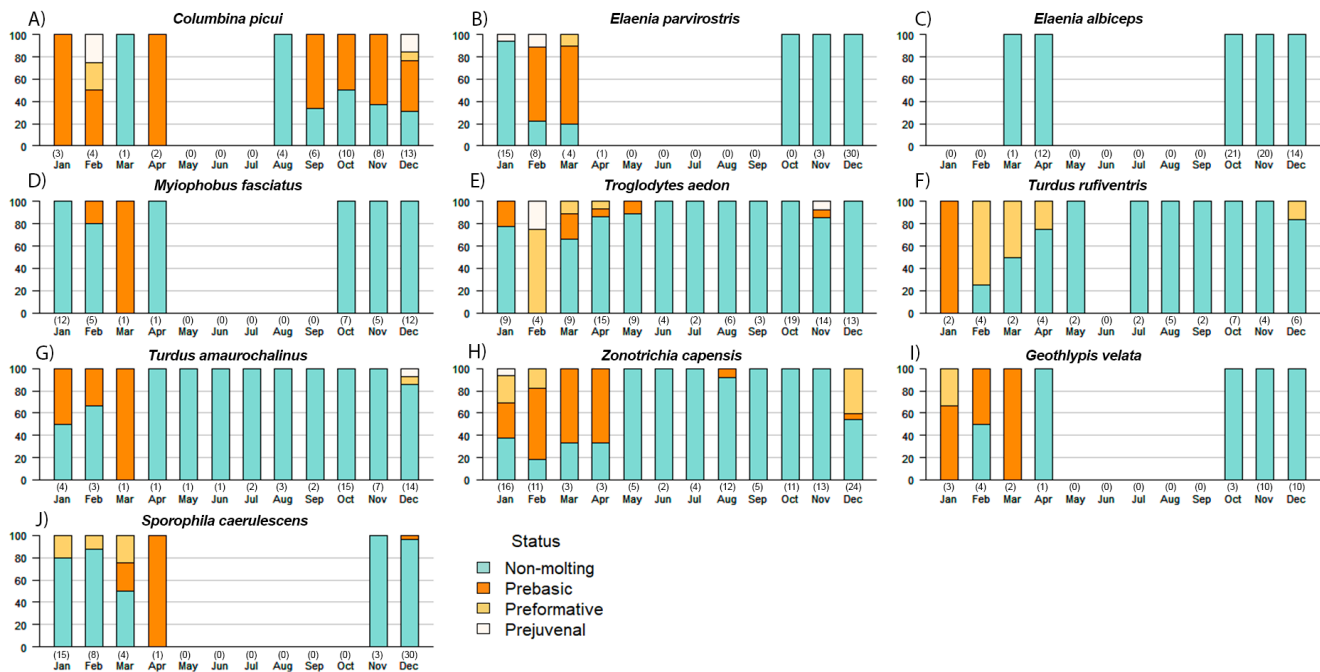
Table 1. Molt extent and number of captured individuals (*N*) of the analyzed species. Molts analyzed were preformative (PF), prebasic (PB), and prealternate (PA). The molt extents described here are absent (-), limited (L), partial (P), incomplete (I), incomplete eccentric (IE), and complete (C). Molts exhibiting a variable extent are specified in range (lesser feather replacement extent – higher feather replacement extent).

| Species | Molt extent | | | |
|--|-------------|-------|----|----|
| | <i>N</i> | PF | PB | PA |
| Picui Ground Dove (<i>Columbina picui</i>) | 52 | I – C | C | – |
| Small-billed Elaenia (<i>Elaenia parvirostris</i>) | 97 | IE | C | – |
| White-crested Elaenia (<i>Elaenia albiceps</i>) | 69 | IE | C | L |
| Bran-colored Flycatcher (<i>Myiophobus fasciatus</i>) | 44 | IE | C | – |
| House Wren (<i>Troglodytes aedon</i>) | 110 | P | C | – |
| Rufous-bellied Thrush (<i>Turdus rufiventris</i>) | 40 | P | C | – |
| Creamy-bellied Thrush (<i>Turdus amaurochalinus</i>) | 54 | P | C | – |
| Rufous-collared Sparrow (<i>Zonotrichia capensis</i>) | 108 | P | C | L |
| Southern Yellowthroat (<i>Geothlypis velata</i>) | 40 | P | C | – |
| Double-collared Seedeater (<i>Sporophila caerulea</i>) | 66 | P – C | C | L |

refer to the different molt extents and feather tracts, we followed Pyle's (2022) terminology; i.e., limited extent: only some body feathers replaced; partial: some to all body feathers replaced (including wing coverts: lesser, median, and greater coverts) but no flight feathers (primaries and secondaries); incomplete: all body feathers and some but not all flight feathers (with flight feather replacement starting in primary and secondary number one); incomplete eccentric: the same as incomplete but with a lack of replacement of inner primaries and secondaries; and complete: all body and flight feathers (no retained feathers). Lastly, to age birds, we used the Wolf-Ryder-Pyle system (Wolfe et al. 2010, Johnson et al. 2011, Pyle et al. 2022).

To differentiate between plumages and identify first cycle birds, we used two criteria. We first searched for molt limits, defined as an interruption in a molt episode that is arrested, where the molt does not continue later, resulting in feathers from different molt episodes next to each other (Pyle 1997). A molt limit can occur within a single feather tract (e.g., primary coverts) or between adjacent feather tracts (e.g., primary coverts versus greater or secondary coverts). We considered the preformative molt as the molt episode during which the juvenile plumage is replaced (Howell et al. 2003). In contrast with formative and basic feathers, juvenile feathers are less dense, remiges and rectrices present pointier tips, and wing coverts tend to be shorter and are often light-colored edged (Pyle 1997, Lehnardt et al. 2012, Jenni and Winkler 2020, Pyle 2022). As a complementing aging criteria, we analyzed ossification patterns of the skull, which typically does not completely ossify until after the eighth month of age in most passerines (Nero 1951, Pyle 2022). We also searched for signs of prealternate (PA) molts and the presence of alternate plumages. To do so, we considered an alternate plumage to be present when first cycle individuals exhibited three feather generations (juvenile, formative, and alternate) and adults exhibited two (definitive and alternate). We searched for alternate molt limits on the body and/or tertials, since the PA molt extent in passerines typically ranges from partial to limited (Ryder and Wolf 2009, Johnson and Wolf 2017, Diaz et al. 2020). This information was then used to elucidate the molt strategies of each of the 10 species.

Fig. 1. Percentage of individuals undergoing feather molt (prebasic, preformative, and prejuvenile molt) captured per month from December 2018 to February 2023. Numbers in brackets (*n*) indicate the total number of captures.



Molt periods

First, we determined the prejuvenile (PJ), preformative (PF), and prebasic (PB) molt periods throughout the year for each of the target species. We considered birds to be molting when they exhibited at least one of the following characteristics: (1) the simultaneous growth of at least three groups of body feathers from distinct feather tracts (each tract with at least three sheaths/growing feathers), and/or (2) the symmetric replacement of flight feathers (Pyle 2022). For each species, we then quantified the proportion of individuals undergoing each type of molt, relative to the total number of captures recorded each month throughout the sampling period.

Preformative molt extent

We assessed the extent of the PF molt and its variability within species in terms of wing feather replacement. To ensure robust and representative data, we selected those species with at least five formative-plumaged individuals. To calculate the feather replacement during the PF molt, we quantified how many individuals had replaced each wing feather. For the greater coverts, primary coverts, tertials, secondaries, and primaries, we quantified each feather. For the inner and median coverts, we were not able to count feathers individually, so considered the tract as a unit. We then calculated the percentage of individuals that had replaced each wing feather or tract.

Morphometric analysis

Lastly, we tested for differences in morphometric measurements between the sexes. The morphological measurements analyzed were (1) wing chord (distance from the carpal joint to the tip of the longest primary, without flattening the wing), (2) tail length

(distance between the tip of the longest rectrix and the point where the two central tail feathers emerge from the skin), (3) tarsus length (distance from the depression at the anterior intertarsal joint to the distal edge of the last scale on the leg before the toes diverge distally), and (4) bill length (distance from the distal part of the nares to the tip of the bill) (Ralph et al. 1996). For the analysis, we considered only the six species that had at least five captures per sex (Kennedy et al. 2018). The classification by sex was conducted using morphological characteristics such as plumage (when the species exhibited marked sexual dichromatism) and presence of cloacal protuberance or brood patch. To test for differences between the sexes, we used the Student's *t* test for two samples and applied the Bonferroni correction to eliminate the multi-testing error. In the cases that did not meet the requirements for the *t* test in terms of normality of the data, we performed Wilcoxon rank sum tests (Table 1).

RESULTS

During this study, we captured and banded a total of 511 birds and recaptured 169 of them (680 total captures) (Table 1). Our analysis revealed distinct patterns in the timing of PF and PB molts throughout the year, with eight species displaying a concentration of molt episodes toward the end of the summer (Fig. 1). In contrast, no molting individuals of *Elaenia albiceps* were recorded despite 69 captures over 51 months, and *Columbina picui* exhibited a prolonged molting season (Fig. 1A). The PB molt was complete for all 10 species (Table 1). The extent of the PF molt was partial for five species (Table 1), incomplete eccentric for the three tyrant flycatcher species (Table 1), and variable, from partial to complete and from incomplete to complete, for *Sporophila caerulescens* and *C. picui*, respectively.

Species account and molt analysis

Columbina picui ($n = 52$): The Picui Ground Dove exhibited a complex basic strategy. The PF molt was incomplete to complete, and occurred from December to February (Fig. 1A, Table 1). Formative individuals ($n = 2$) could be identified by light-edged retained juvenile body feathers and/or shorter retained flight feathers. The PB molt was complete ($n = 27$) and exhibited a prolonged molt season from September to April (Fig. 1A). Note that the accurate identification of formative individuals was possible only when the individual presented retained juvenile feathers due to an incomplete PF molt.

Elaenia parvirostris ($n = 97$): The Small-billed Elaenia appeared to follow the complex basic molt strategy. The formative plumage displayed an eccentric replacement pattern (Fig. 2A, Fig. 3A). During the PF molt, this species did not replace the inner primaries (P1–P3 0% of replacement), secondary 1 (0% of replacement), or inner primary coverts (0% of replacement) (Fig. 2A). We recorded the PF molt only in March, when one individual was captured in the middle of its molt (Fig. 1B). The PB molt was complete for this species and occurred from the beginning of February to March (Fig. 1B). We did not find any evidence of a PA molt for the species.

Elaenia albiceps ($n = 69$): The White-crested Elaenia exhibited a complex alternate strategy. The PF plumage of this species showed an incomplete and eccentric pattern (Fig. 2B, Table 1). Formative individuals ($n = 19$) had retained their inner primaries (P1–P2) and/or secondaries (S1) and some inner to all primary coverts during the PF molt (Fig. 3B). The PB molt extent was complete ($n = 38$), but definitive *Elaenias* showed molt limits within their tertials (T1 versus T2) due to a limited PA molt. We did not record any individual with active molt signs during the study (Fig. 1C).

Myiophobus fasciatus ($n = 44$): The Bran-colored Flycatcher followed a complex basic strategy. Similar to the two other tyrant species, the extent of its PF molt was incomplete eccentric ($n = 9$) (Fig. 2C). All formative-plumaged individuals had retained primaries 1 and 3 (P1,3) (Fig. 3C). The six outer primaries and secondaries six and five were replaced in all individuals (Fig. 3C). One formative individual exhibited an arrested molt pattern, where it retained primaries one and three (P1,3), and replaced primary two (P2) as well as the rest of the feathers. During our study, we did not capture any individuals undergoing their PF molt (Fig. 1D). The PB molt, however, was complete and occurred from February to March (Fig. 1D).

Troglodytes aedon ($n = 110$): The House Wren molt strategy was complex basic. It exhibited a partial PF molt (Fig. 2D) that occurred from February to April (Fig. 1E). The inner greater coverts were always replaced (Fig. 3D), and in some cases, the outer ones were also replaced (60%) (Fig. 3D). Formative individuals were easily identified by examination of their wing bars. Because juvenile flight feathers are retained during the PF molt, their wing bars are perfectly aligned upward (Taylor 2012, Pyle 2022). The PB molt occurred between January and May (Fig. 1E) and was complete in all cases ($n = 60$). Due to the sequential replacement of flight feathers, the alignment of the wing bars was lost.

Fig. 2. Aspect of formative plumages (left column) for eight selected species and the corresponding wing (right column) for each individual. Molt limits between formative and juvenile feathers are marked with yellow arrows. Species included are (A) *Elaenia parvirostris*, (B) *Elaenia albiceps*, (C) *Myiophobus fasciatus*, (D) *Troglodytes aedon*, (E) *Turdus rufiventris*, (F) *Turdus amaurochalinus*, (G) *Zonotrichia capensis*, and (H) *Sporophila caerulea*.

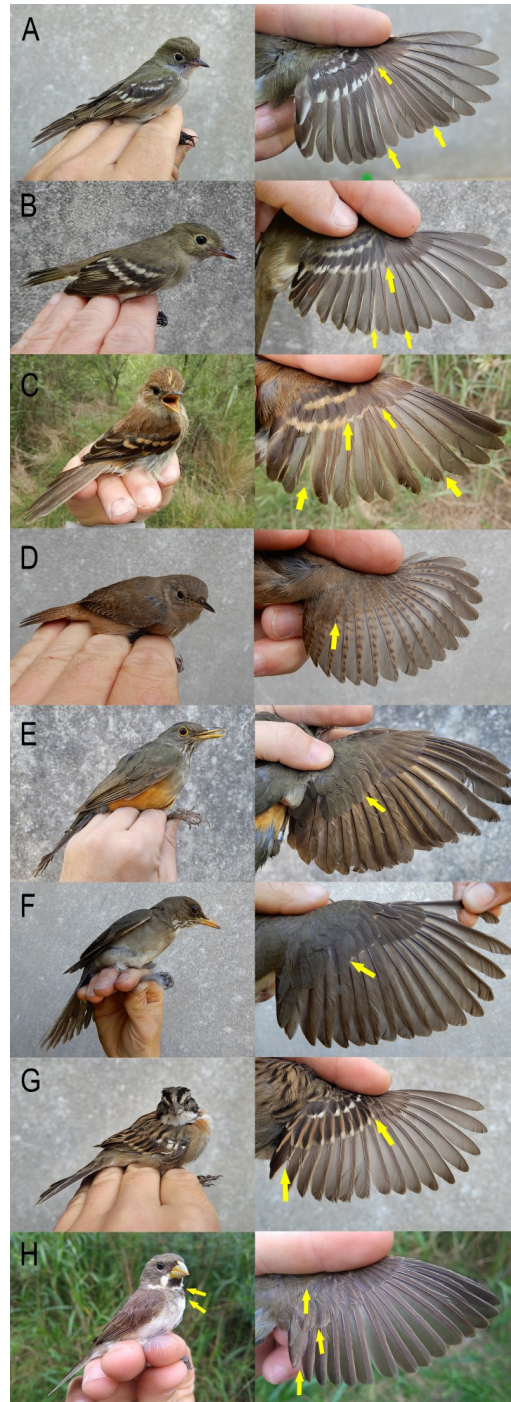
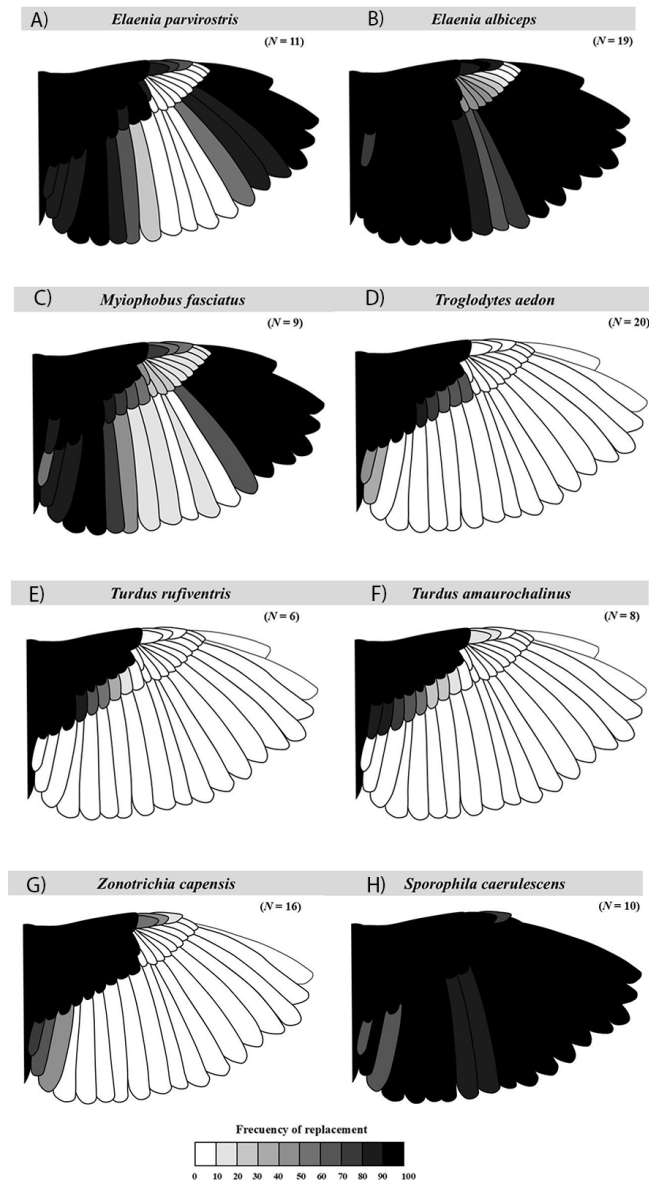


Fig. 3. Frequency of wing feather replacement during the preformative molt for eight selected species. Numbers in brackets (*N*) indicate the number of individuals analyzed.



Turdus rufiventris ($n = 40$): The Rufous-bellied Thrush exhibited a complex basic molt strategy. Similar to the Creamy-bellied Thrush, the extent of the PF molt was partial, but we did not find any replacement of alulas (Fig. 3E). This molt occurred from December to April (Fig. 1F). The retained buffy tips of the juvenile feathers also facilitated aging of the Rufous-bellied Thrush. Its PB molt was complete and was recorded only in January ($n = 2$) (Fig. 1F).

Turdus amaurochalinus ($n = 54$): The Creamy-bellied Thrush exhibited a complex basic molt strategy. The extent of the PF molt was partial (Fig. 2F). Both alulas and the outer greater coverts showed relatively low percentages of replacement (Fig. 3F).

Formative individuals were recognizable due to the buffy tips of the retained juvenile feathers. We captured only a single individual in December that was undergoing its PF molt. The PB molt was complete ($n = 33$) and occurred from January to March (Fig. 1G).

Zonotrichia capensis ($n = 108$): The Rufous-collared Sparrow exhibited a complex alternate molt strategy. The PF molt occurred from December to February (Fig. 1H) and was partial (Fig. 2G). The PB molt was complete ($n = 27$) and was recorded from January to April (Fig. 1H). It is worth noting that definitive-plumaged individuals exhibited a pseudolimit between the primary coverts and the greater coverts (secondary coverts), which made them difficult to age. We also found evidence of a limited PA molt, where one to two tertials had been replaced, as well as a few body feathers in the head and collar.

Geothlypis velata ($n = 40$): The Southern Yellowthroat is likely to follow a complex basic strategy considering that we did not find any evidence of alternate plumages. The extent of the PF molt was partial ($n = 2$), where all body feathers were replaced along with the inner greater coverts, and was recorded only during January (Fig. 1I). The PB molt was complete ($n = 30$) and occurred from January to March (Fig. 1I).

Sporophila caerulescens ($n = 66$): The Double-collared Seedeater exhibited a complex alternate strategy. The PF molt was the most variable of all 10 species. It ranged from partial to complete (Fig. 2H and 3H). Secondaries one and two (S1,2) were replaced in 90% of the individuals. The tertials, however, were replaced in fewer individuals: from 10 to 40% (Fig. 3H). The appearance of formative-plumaged individuals differed from definitive-plumaged individuals. Formative males had greyish olive body feathers and a greyish diffuse collar. The PF molt ranged from January to March; the PB molt ranged from March to April (Fig. 1J). Individuals that were undergoing their PF molt were replacing body feathers, but none was replacing flight feathers. Even though the PB molt was complete, definitive individuals showed molt limits corresponding to an alternate plumage of limited extent, which suggested a complex alternate molt strategy.

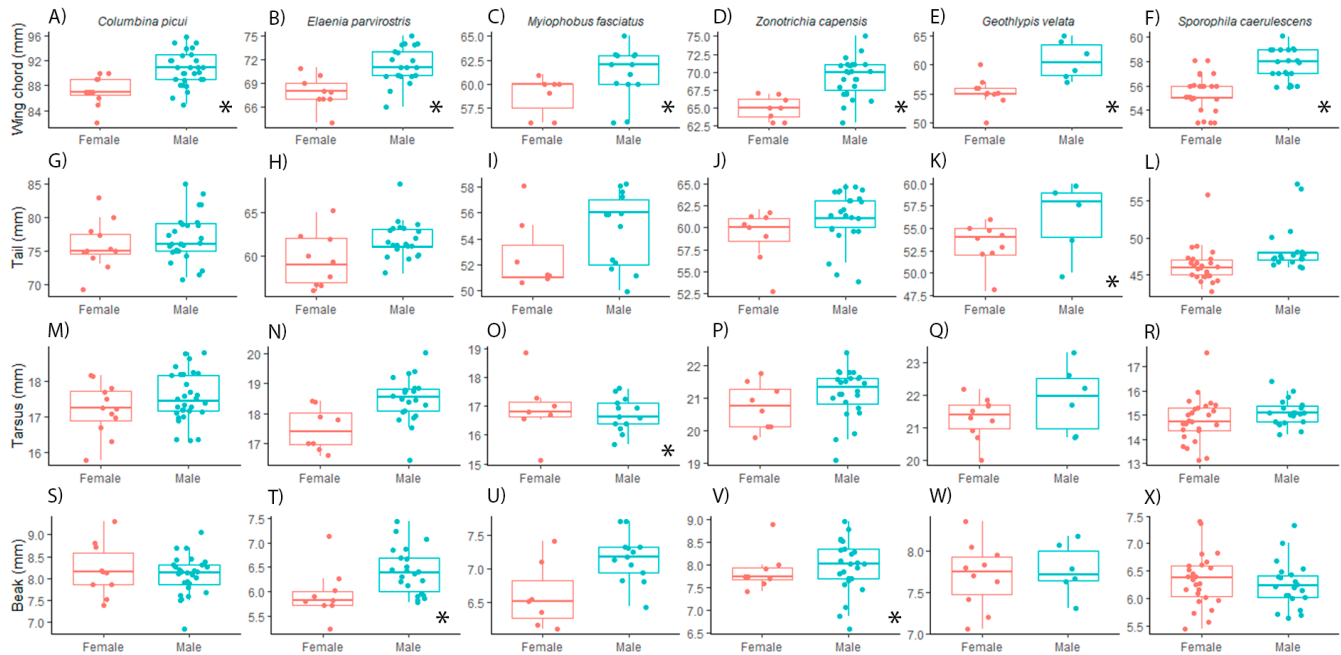
Morphometric analysis

The morphometric measurements were significantly different between the sexes in at least one of the six analyzed species (Fig. 4, Table 2). The wing chord was the most informative measurement: males had a significantly longer wing chord than females in all of the six species (Fig. 4A, B, C, D, E, and F, Table 2). Tail length was significantly different between the sexes only in *S. caerulescens*: males had significantly longer tails than females (Fig. 4L). Tarsus length was significantly different between the sexes only in *E. parvirostris*: males had a significantly longer tarsus than females (Fig. 4N). Beak length was significantly different between the sexes in two species—*E. parvirostris* and *S. caerulescens*: males had significantly longer beaks than females (Fig. 4S and W).

DISCUSSION

We present the first description of molt patterns for birds in the center of Argentina. We established aging and sexing criteria for 10 bird species using molt patterns and morphometric measurements. In all 10 species, it was possible to identify first year (formative-plumaged) individuals by analyzing their plumage, which ultimately allowed us to separate them into

Fig. 4. Morphometric differences between the sexes for six selected species. Statistical significance is indicated by a bold asterisk.



different cohorts, although some *C. picui* underwent complete PF molts and thereafter could not be aged by plumage. Five species exhibited a partial extent of the PF molt (*Troglodytes aedon*, *Turdus rufiventris*, *Turdus amaurochalinus*, *Z. capensis*, and *G. velata*), the three tyrant species showed an incomplete eccentric pattern (*E. parvirostris*, *E. albiceps*, and *M. fasciatus*), and the two remaining species showed a variable extent (*C. picui* and *S. caeruleascens*). Molting seasons were variable across species, but eight species showed temporally restricted molting seasons toward the end of their reproductive season, a seasonal pattern that is common among passerines at temperate latitudes (Jenni and Winkler 2020, Pyle 2022). We were also able to confirm the study area as the molting grounds for nine species, except for the austral migrant *E. albiceps*. As for the morphometric measurements, the males of *C. picui*, *E. parvirostris*, *M. fasciatus*, *Z. capensis*, *G. velata*, and *S. caeruleascens* had significantly longer wing chord than females, but the ranks for those measurements overlapped.

Molt periods

Given the high energetic cost of molt, it is proposed that it does not overlap other energetically demanding processes, such as migration and reproduction (Hahn et al. 1992). Even though molt–breeding overlap might occur at a population level, it may not at an individual level (Pyle et al. 2016). However, the phenology of molting and breeding overlap is highly variable across species (Johnson et al. 2012). In addition, in highly seasonal environments where resources are temporarily restricted, the timing of molt is constrained (Thomas et al. 2001). We found that even though the timing of molt was variable across species, eight species showed molting seasons that were restricted to the humid season and the end of their reproductive season. This pattern is

consistent with northern hemisphere bird species that inhabit highly seasonal habitats (Pyle 2022). The year-round resident species (*Troglodytes aedon*, *Turdus rufiventris*, *Turdus amaurochalinus*, and *Z. capensis*) showed, at least to some extent, restricted molting seasons. This implies that there might be little breeding–molting overlap at a population level, and therefore, at an individual level.

A restricted molting season was not the case for *C. picui*, which is also a year-round resident, but it exhibited a prolonged season spanning from September to April. Protracted molt periods have also been reported for *C. passerina*, *C. inca*, and *C. talpacoti* in North America (Pyle 2022), and *C. squamata*, *C. talpacoti*, *C. minuta*, and *C. passerina* in the seasonal savannas of Venezuela (Bosque et al. 2004, 2018). In our case, *C. picui* presented molt–breeding overlap at least at a population level.

The short-distance migratory species (*E. parvirostris*, *M. fasciatus*, *G. velata*, and *S. caeruleascens*) also exhibited a marked molting season, at least for their PB molt, toward the end of their breeding season and prior to their northbound migration to the wintering grounds. Interestingly, we did not find any *M. fasciatus* undergoing PF molt. This suggests that its PF molt occurs on its wintering grounds or in a stopover area, but not on its breeding grounds as the PB molt.

E. albiceps, the only long-distance austral migrant analyzed, did not show any signs of molting activity during its southward or northward migration. This suggests that the White-crested Elaenia does not molt in the center of Argentina during its migration, at least within our study area. Pyle et al. (2015) did not report any molting *E. albiceps* on its breeding grounds either, indicating that this species molts entirely on its wintering grounds or in a stopover area.

Table 2. Statistical analysis comparing mean morphometric measurements between the sexes for six selected species using a *t* test comparison. Numbers in brackets indicate the measurement range (highest and lowest value recorded). Only species with at least five captures of each sex were taken into account for the statistical analysis. *P* values in bold and with an asterisk are statistically significant. *P* values in italic indicate traits analyzed using Wilcoxon test instead of the *t* test.

| Species | | Morphometric measurements (mm) | | df | <i>t</i> test | |
|---------------------------------|------------|--------------------------------|--------------------------|--------|---------------|------------------------------|
| | | Male Mean ± SD | Female Mean ± SD | | Statistic | <i>P</i> value |
| Picui Ground Dove | Wing chord | 90.7 ± 3.5 (96–85) | 87.2 ± 24.3 (90–82) | 20.968 | -4.0544 | 5 × 10⁻⁴* |
| <i>Columbina picui</i> | Tail | 76.8 ± 3.5 (85–71) | 75.8 ± 3.6 (83–69) | 17.693 | -0.82575 | 0.42 |
| (Male = 31; Female = 12) | Tarsus | 17.5 ± 0.7 (18.8–16.0) | 17.2 ± 0.7 (18.2–15.8) | 19.679 | -1.3938 | 0.18 |
| | Beak | 8.1 ± 0.4 (9.06–6.80) | 8.2 ± 0.6 (9.3–7.4) | 12.665 | 0.55088 | 0.59 |
| Small-billed Elaenia | Wing chord | 71.20 ± 2.24 (75–66) | 67.9 ± 2.0 (71–64) | 16.461 | -4.0308 | 9 × 10⁻⁴* |
| <i>Elaenia parvirostris</i> | Tail | 61.8 ± 2.1 (68–58) | 59.6 ± 3.0 (65–56) | 11.533 | -2.1175 | 0.055 |
| (Male = 23; Female = 9) | Tarsus | 18.5 ± 0.7 (20.1–16.4) | 17.5 ± 0.7 (18.4–16.6) | 12.779 | -3.2834 | 6 × 10⁻³* |
| | Beak | 6.4 ± 0.5 (7.4–5.8) | 5.9 ± 0.5 (7.4–5.2) | 13.681 | -2.2719 | 0.034* |
| White-crested Elaenia | Wing chord | 74.3 ± 2.8 (80–69) | – | – | – | – |
| <i>Elaenia albiceps</i> | Tail | 62.1 ± 3.3 (69–55) | – | – | – | – |
| (Male = 30; Female = 0) | Tarsus | 18.8 ± 0.7 (20.3–17.5) | – | – | – | – |
| | Beak | 6.8 ± 0.5 (8.03–5.50) | – | – | – | – |
| Bran-colored Flycatcher | Wing chord | 61.1 ± 2.7 (65–56) | 58.8 ± 2.1 (61–56) | 15.671 | -2.0708 | 0.055 |
| <i>Myiophobus fasciatus</i> | Tail | 54.7 ± 2.9 (58–50) | 52.7 ± 2.7 (58–51) | – | 26.5 | <i>0.1358</i> |
| (Male = 14; Female = 7) | Tarsus | 16.7 ± 0.6 (17.6–15.7) | 16.9 ± 1.1 (18.9–15.1) | 7.8195 | 0.43334 | 0.68 |
| | Beak | 7.1 ± 0.3 (7.7–6.4) | 6.6 ± 0.5 (7.4–6.1) | 9.5036 | -2.6498 | 0.025* |
| House Wren | Wing chord | 51.1 ± 1.8 (55–48) | 54.0 ± 6.1 (61–50) | – | – | – |
| <i>Troglodytes aedon</i> | Tail | 45.1 ± 3.6 (57–41) | 44 ± 1 (45–43) | – | – | – |
| (Male = 20; Female = 4) | Tarsus | 17.6 ± 0.8 (18.8–14.6) | 18.4 ± 0.5 (18.9–18.5) | – | – | – |
| | Beak | 8.7 ± 0.5 (9.7–7.8) | 8.5 ± 0.1 (8.6–8.4) | – | – | – |
| Rufous-bellied Thrush | Wing chord | 117.8 ± 6.3 (124–101) | 113 | – | – | – |
| <i>Turdus rufiventris</i> | Tail | 105.3 ± 4.6 (110–96) | – | – | – | – |
| (Male = 14; Female = 1) | Tarsus | 36.4 ± 1.2 (38.2–33.7) | 36.9 | – | – | – |
| | Beak | 15.1 ± 1.2 (17.1–12.3) | 15.1 | – | – | – |
| Creamy-bellied Trush | Wing chord | 115.5 ± 0.8 (120–110) | 113 ± 2 (115–111) | – | – | – |
| <i>Turdus amaurochalinus</i> | Tail | 98.3 ± 4.9 (110–88) | 96.3 ± 1.5 (98–95) | – | – | – |
| (Male = 23; Female = 3) | Tarsus | 33.6 ± 1.3 (36.4–31.6) | 31.9 ± 0.2 (32.1–31.2) | – | – | – |
| | Beak | 13.3 ± 0.7 (14.8–11.9) | 13.9 ± 0.4 (14.4–13.6) | – | – | – |
| Rufous-collared Sparrow | Wing chord | 69.3 ± 2.6 (75–63) | 65.0 ± 1.6 (67–63) | 19.186 | -5.7147 | 1.5 × 10⁻⁵ |
| <i>Zonotrichia capensis</i> | Tail | 61.2 ± 2.9 (65–54) | 59.1 ± 2.9 (62–53) | – | 53.5 | <i>0.051</i> |
| (Male = 29; Female = 9) | Tarsus | 21.1 ± 0.8 (22.4–19.1) | 20.7 ± 0.7 (21.8–19.8) | 12.787 | -1.3037 | 0.21 |
| | Beak | 7.9 ± 0.6 (9.0–6.6) | 7.9 ± 0.5 (8.9–7.4) | 15.344 | -0.4469 | 0.66 |
| Southern Yellowthroat | Wing chord | 60.8 ± 3.3 (65–57) | 55.3 ± 2.5 (60–50) | 8.4461 | -3.5343 | 7 × 10⁻³* |
| <i>Geothlypis velata</i> | Tail | 56.2 ± 4.1 (60–50) | 53.2 ± 2.4 (56–48) | 5.5135 | -1.4755 | 0.19 |
| (Male = 7; Female = 10) | Tarsus | 21.9 ± 1.0 (23.3–20.7) | 21.3 ± 0.6 (22.2–20.2) | 7.2725 | -1.2316 | 0.26 |
| | Beak | 7.8 ± 0.3 (8.2–7.3) | 7.7 ± 0.4 (8.4–7.1) | 12.577 | -0.38793 | 0.7 |
| Double-collared Seedeater | Wing chord | 57.4 ± 1.9 (60–56) | 55.5 ± 1.6 (58–53) | 43.932 | -5.6951 | 9 × 10⁻⁷* |
| <i>Sporophila caeruleascens</i> | Tail | 48.4 ± 3.1 (57–46) | 46.3 ± 2.5 (56–43) | – | 113 | 5 × 10⁻⁴* |
| (Male = 22; Female = 27) | Tarsus | 15.1 ± 0.5 (16.4–14.2) | 14.70 ± 0.93 (17.6–13.1) | – | 212.5 | 0.13 |
| | Beak | 6.2 ± 0.4 (7.3–5.6) | 6.3 ± 0.5 (7.4–5.4) | 45.96 | 0.65763 | 0.5141 |

Preformative molt extent

The three tyrant species analyzed in this study (*E. parvirostris*, *E. albiceps*, and *M. fasciatus*) exhibited differences in the extent of their PF molt. *E. albiceps* usually replaced more inner primaries and secondaries than did *E. parvirostris* and *M. fasciatus*. The retained outer primary coverts during the incomplete PF molt in *E. albiceps* is consistent with previous reports on its breeding grounds in southern Argentina and Chile (Pyle et al. 2015, Gorosito et al. 2020). Our findings are also consistent with the general pattern of incomplete PF molt extent within the Tyrannidae family, with an eccentric replacement pattern (Pyle 1997, 1998, Johnson and Wolfe 2017, Guallar et al. 2018, Díaz et al. 2022). The extent of feather molt can be variable among species and populations due to different factors (Hemborg et al. 2001, Remisiewicz et al. 2019). For example, in Nearctic flycatcher

species (*Empidonax* genus), it has been proposed that differences in PF molt extent might be related to wintering latitude and habitat (Carnes et al. 2021). Our three species differ in breeding latitude and habitat (Capllonch and Lobo 2005). *E. parvirostris* and *M. fasciatus* nest in semi-arid forests (Chaco and Espinal), whereas *E. albiceps* breeds in Patagonian forests (Capllonch and Lobo 2005, Capllonch et al. 2011, Jiménez et al. 2016). Additionally, longer migrating distance might result in higher feather exposure and wear, thereby promoting feather replacement (Terrill et al. 2020). Both differences in habitats and migrating distance might influence the time available for molt and, therefore, molt extent (Butler et al. 2013, Pérez-Granados et al. 2021). Altogether, these factors might explain the higher wing feather replacement percentage during the PF molt that we found in *E. albiceps* in comparison with *E. parvirostris* and *M. fasciatus*.

The non-migratory species (*Troglodytes aedon*, *Turdus rufiventris*, *Turdus amaurochalinus*, and *Z. capensis*) exhibited, in general, less variability in wing feather replacement during PF molt extent than migratory species. The *Turdus* genus presents, in general, a partial extent of the PF molt (Pyle et al. 2004, Guallar et al. 2009, Ryder and Wolfe 2009, Johnson and Wolfe 2017, Pyle 2022), a stable molt pattern consistent with what we found in *T. rufiventris* and *T. amaurochalinus*. The PF partial extent for *Troglodytes aedon* resembles the species PF description for México (Guallar et al. 2009), North America (Pyle 2022), and central Chile (Pyle et al. 2015). But we did not record any excentric replacement pattern as some North American individuals (Pyle 2022). For *Z. capensis*, the partial extent of the PF molt was also reported in Chile (Pyle et al. 2015) and Colombia (Miller 1961, Cueva 2018). A previous study in the north of Argentina (King 1972) also reported a partial PF molt that occurred approximately during the same period of the year that we found. Even though both species, *Troglodytes aedon* and *Z. capensis*, are widely distributed across the continent, the extent of their PF molt seems to remain partial, at least in temperate seasonal areas. However, near tropical areas, differences in molt patterns appear, such as two complete molts per year (Miller 1961). Even within Argentina, King (1972) did not report any signs of a PA molt.

The most variable extent of the PF molt was exhibited by *S. caerulescens*. The feather tract that showed the lowest percentage of replacement was the tertials (T1 and 3). This is not an expected pattern, given that tertials remain exposed to the sun when the wing is closed and deteriorate more. However, retention of tertials during the PF molt has also been reported in *S. lineola* (Ferreira et al. 2023), and even secondaries and outer primaries in *S. corvina* (Wolfe et al. 2009). Additionally, the aspect of formative-plumaged individuals differs from definitive-plumage adults. This suggests a delayed plumage maturation, a common pattern documented for other *Sporophila* species (Repenning and Fontana 2013, Ferreira et al. 2023).

Morphometric analysis

Morphometric differences between the sexes provide a useful non-invasive method for sex determination, especially for monochromatic species (Leys and Grieves 2023), such as the Northern Waterthrush (*Parkesia noveboracensis*) and Swainson's Thrush (*Catharus ustulatus*) (Covino 2015), and the Neotropical Grey-breasted Wood-Wren (*Henicorhina leucophrys*) (Machado-Stredel and Pérez-Emán 2017). In all six species we analyzed, the males had a significantly longer wing chord than females. However, wing chord measurements showed, at least to some extent, an overlap between the sexes. For that reason, these measurements are not entirely reliable as sexing criteria but can be useful for species in which larger male wing chords do not overlap females, such as in *C. picui*, *E. parivrostris*, *M. fasciatus*, and *Z. capensis*.

The difference in tail length between the sexes in *S. caerulescens* and *E. parivrostris*, and in beak length in *M. fasciatus* was statistically significant. However, the overlap in the range of measurements was considerable; therefore, these measurements are not reliable sexing criteria. It is worth noting that we did not include other factors that have to be taken into account when building confidence intervals to age birds using morphometric measurements (i.e., separating first cycle individuals from definitive ones). Thus, such studies are still necessary to produce robust sexing models.

CONCLUSION

Our study provides an important resource to address the gap in knowledge about the natural history of southern hemisphere bird species. We believe that the patterns we describe will facilitate aging and sexing birds in the field, and therefore, will enhance bird monitoring programs and surveys. We also hope to encourage other long-term initiatives of banding stations and monitoring programs, as well as molt pattern-oriented studies in southern South America.

Author Contributions:

All authors conceived of the project and contributed to analysis and writing. All authors carried out the fieldwork, and MP took the lead in statistical analysis and the writing of the manuscript.

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Data Availability:

Data/code sharing is not applicable to this article because no data/code were analyzed in this study.

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