



Differences in molt timing, duration, and intensity between sexes in a Rufous-collared Sparrow population from central Chile

Diferencias en el momento, duración e intensidad de la muda entre sexos en una población de Chincol (*Zonotrichia capensis*) del centro de Chile

[Carlos E. Valeris-Chacin](#)^{1,2} , [Tomás F. Zamorano-Escalona](#)¹, [Katherine R. Chávez-Vásquez](#)^{1,2} , [Guyleine Rios-Robles](#)¹, [Mariana Klesse](#)¹, [Pablo A. Cornejo-Escobar](#)^{1,2} , [Marcela Osorio](#)¹ and [Rodrigo A. Vásquez](#)^{1,2}

ABSTRACT. Molting is a fundamental life history stage for birds and involves the replacement of all (or some) feathers, depending on the molt cycle and strategy, mainly within the annual cycle. Feather replacement is necessary to maintain feathers in good shape, ensuring good flight performance and optimal thermoregulation. The timing, duration, and intensity of molt and feather growth rate are useful variables to evaluate and compare how individuals of different populations, age classes, and sexes organize molt within the annual cycle and its possible evolutionary implications. For this reason, we evaluated how molt differs between sexes in a population of Rufous-collared Sparrows from central Chile. We scored each flight feather to establish molt parameters through the Underhill-Zucchini model I and II to estimate molt timing and duration, and the sum of flight feathers with active molt to evaluate molt intensity. To measure feather growth rate, we applied ptilochronology on photographs taken in the field (photo-ptilochronology). The molt timing, duration, and intensity varied between males and females, with females starting later than males and molting for a shorter period. Females shed more flight feathers simultaneously (ten feathers on average compared to seven feathers in males), but feather growth rate was not statistically different between the sexes. The differences observed could be due to the temporal restriction that females have to initiate the molt, given the higher energy expenditure associated with their reproductive investment, as occurs in many passerine species with different parental roles. The latter could negatively affect the quality of females' flight feathers and overall fitness; it would be important to address this issue in further research.

RESUMEN. La muda es una etapa fundamental en la historia de vida de las aves e implica el reemplazo de todas (o algunas) plumas, dependiendo del ciclo y la estrategia de muda, principalmente dentro del ciclo anual. El recambio de plumas es necesario para mantenerlas en buen estado, asegurando un buen desempeño de vuelo y una termorregulación óptima. El momento, la duración y la intensidad de la muda, y la tasa de crecimiento de las plumas, son variables útiles para evaluar y comparar cómo los individuos de distintas poblaciones, clases de edad y sexos organizan la muda dentro del ciclo anual y sus posibles implicancias evolutivas. Por esta razón, evaluamos cómo difiere la muda entre sexos en una población de chincos del centro de Chile. Calificamos cada pluma de vuelo para establecer los parámetros de muda mediante los modelos I y II de Underhill-Zucchini, para estimar el momento y la duración de la muda, y la suma de las plumas de vuelo con muda activa para evaluar la intensidad de la muda. Para medir la tasa de crecimiento de las plumas, se aplicó ptilocronología en fotografías tomadas en el campo (foto-ptilocronología). El momento, la duración y la intensidad de la muda variaron entre machos y hembras, con las hembras comenzando más tarde que los machos y mudando durante un período más corto. Las hembras mudaron más plumas de vuelo simultáneamente (diez en promedio frente a siete en los machos), pero la tasa de crecimiento de las plumas no fue estadísticamente diferente entre los sexos. Las diferencias observadas podrían deberse a la restricción temporal que tienen las hembras para iniciar la muda, dada la mayor demanda energética asociada a su inversión reproductiva, como ocurre en muchas especies de paseriformes con diferentes roles parentales. Esto podría afectar negativamente la calidad de las plumas de vuelo de las hembras y su condición física general; sería importante abordar este aspecto en futuras investigaciones.

Key Words: feather growth rate; molt; molt intensity; sex; photo-ptilochronology

INTRODUCTION

Molt, the replacement of feathers, is one of the most critical life-history stages that birds experience during their annual cycle (Swaddle et al. 1999, Silveira and Marini 2012, Scott 2020). Molt is fundamental because of the importance of feathers for flight, thermoregulation, and, in some species, camouflage and sexual selection (Williams and Swaddle 2003, Romero and Wingfield 2016, Scott 2020). Molt parameters, such as molt timing, duration, and intensity, are relevant life-history traits, with time constraints and trade-offs varying between the sexes in several passerine species (Morton and Morton 1990, Svensson and

Nilsson 1997, Hemborg 1999, Voelker 2000, Newton and Rothery 2005, Oschadleus and Osborne 2005, Bonnevie and Oschadleus 2010).

Feather growth rate, one factor that contributes to variation in the speed of molt, also shows variation between populations (Terrill 2018). Feathers growing at a faster pace have been related to a lower feather quality because they can be asymmetrical, lighter, shorter, less resistant to wear, and have less brightness than those growing at a slower rate (Dawson et al. 2000, Dawson 2004, Griggio et al. 2009, Vágási et al. 2012, Echeverry-Galvis and Hau

¹Instituto de Ecología y Biodiversidad, Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Santiago, Chile, ²Centro Internacional Cabo de Hornos, Universidad de Magallanes, Puerto Williams, Chile

2013). Thus, the speed at which feathers grow can provide insights into the sex differences in molt timing (De La Hera et al. 2011, Kiat and Sapir 2017).

The Rufous-collared Sparrow (*Zonotrichia capensis*) is a socially monogamous and monomorphic neotropical passerine, widespread in the Neotropical region, from southern Mexico (10° N) to the southernmost tip of South America (56° S), occupying a high diversity of habitat types, from sea level up to 4600 m a.s.l. in the Andes Mountain range (Chapman 1940, Cheviron et al. 2008). In central Chile, Rufous-collared Sparrows breed between September and November and molt between December and March (Valeris-Chacín 2023). Females and males have different parental roles, with only females developing a brood patch (Miller and Miller 1968, Class and Moore 2013), suggesting a higher energy investment during breeding than males, as seen in other bird species (see Gow and Stutchbury 2013).

Differences between the reproductive investment of females and males may imply differences in reproduction time and energy expenditures, possibly affecting the time available for females to molt as seen in other passerine species (see Hemborg 1999, Voelker 2000, Newton and Rothery 2005, Oschadleus and Osborne 2005, Bonnevie and Oschadleus 2010, Gow and Stutchbury 2013), including the White-crowned Sparrow (*Zonotrichia leucophrys*) (Morton and Morton 1990), a close relative species (Zink and Blackwell 1996). We hypothesize that females Rufous-collared Sparrows initiate molt later than males because of differences in their reproductive investment, and complete molt faster through more intense molt and faster feather growth rates. Nevertheless, to our knowledge, this is the first time molt timing, duration, and intensity regarding sex have been addressed for a Neotropical bird species.

METHODS

Study area

We evaluated the Rufous-collared Sparrow population in Quebrada de La Plata Nature Sanctuary, Comuna Maipú (33° 29'49" S, 70°54'39" W, altitude between 477 and 683 m a.s.l.), east of the Coastal Range and west of Santiago. The bioclimate corresponds to the semi-arid Mediterranean of the interior, characterized by a high climatic seasonality, with dry and hot summers and rainy and cold winters (di Castri and Hajek 1976). The predominant vegetation comprises a matrix of sclerophyllous and xerophytic arborescent scrub (López-Calleja 1995) surrounding relict sclerophyllous forest restricted to the channels of seasonal streams (Consejo Nacional de Monumentos de Chile 2018).

Data collection

We conducted weekly field trips between September 2018 and January 2020 to capture Rufous-collared Sparrows using mist nets. We marked each captured bird with individually numbered aluminum bird bands and assigned their sex based on the development of a brood patch (females) or cloacal protuberance (males) during the breeding season (see González-Gómez et al. 2013 for details). For individuals with no brood patch or cloacal protuberance (i.e., those captured outside the breeding season), we collected a blood sample through puncture on the brachial vein and microcapillary tubes and stored them in FTA cards. We

used a PCR reaction from FTA card samples (González-Gómez et al. 2013) following the protocol described in Aljanabi and Martinez (1997), and for DNA extraction and bird sexing, the P2/P8 protocol developed by Griffiths et al. (1998) (Mishra et al. 2023).

We evaluated 102 individuals (51 females and 51 males) captured between September 2018 and July 2019 to evaluate molt timing and duration, 43 individuals (22 females and 21 males) captured between December 2018 and February 2019 to determine molt intensity, and 40 individuals (14 females and 26 males) captured and photographed between January 2019 and January 2020 to measure feather growth rate.

Molt timing and duration

We examined the flight feathers (primaries, secondaries, and rectrices) of each bird looking for signs of molt. For birds in active molt, we recorded the molt score for each primary (p1 to p9) and secondary feather (s1 to s6) on both wings, following the scoring system described by Ginn (1975), Ginn and Melville (1983), and Newton (2009). Secondary feathers were included because, in this Rufous-collared Sparrow population, molt concludes with s6 (Valeris-Chacín 2023), providing more accurate estimates of molt timing and duration (see Rodrigues and Marinho de Noronha 2001). For the analysis, we used molt scores from the right wing only and included data from individuals with symmetrical molt (i.e., molting evenly in both wings).

Then we calculated the proportion of feather mass grown (pfmg) using the *ms2pfmg()* function of the Moults package in the R program (Erni et al. 2013, Erni 2018). To carry out the pfmg calculation, we used the weights of the primary and secondary feathers of a Rufous-collared Sparrow with first-cycle formative plumage (FCF) (i.e., the first plumage after juvenal plumage; Pyle et al. 2015, Cueva 2018), taken from a male specimen found lifeless in the net after a predatory attempt. To calculate each primary and secondary feather contribution to the wing area, we extracted each feather from both wings. We weighed them using an analytical balance with a precision of ± 0.1 milligrams and recorded the mass with three decimal digits. We averaged the weight of each feather (i.e., left and right) to calculate the mass proportion of growing feathers. To date, there are no data available on feathers' weights for Rufous-collared Sparrows from central Chile (or elsewhere).

Although the first cycle formative plumage in Rufous-collared Sparrows is incomplete (i.e., retaining juvenal primaries and secondaries feathers; Pyle et al. 2015), the feather proportion, which reflects the contribution of each feather (p1...p9, s1...s6) to the wing area (the most relevant information for the model; Erni et al. 2013, Erni 2018), is similar to those found in adult feathers (i.e., second cycle basic [SCB] and definitive cycle basic [DCB]), and there are no differences between males and females in feather proportion and/or shape (see Pyle et al. 2015).

We estimated molt timing and duration using individual pfmg values for each specimen, based on type I and II models developed by Underhill and Zucchini (1986; hereafter referred to as U-Z models) (Hulley et al. 2004, Oschadleus and Osborne 2005, Bonnevie and Oschadleus 2010). Both U-Z models assume equal capture probabilities for birds that are not molting, actively

molting, or have completed molt. Model I classifies data categorically into three stages: non-molting, molting, and molt completed. In contrast, model II uses individual pfmg values, which quantify molt progress based on the relative contribution of each growing primary (p1-p9) and secondary (s1-s6) feather to the total wing area. These values are calculated by relating each feather's growth stage to its corresponding weight (Underhill and Zucchini 1986, Erni et al. 2013, Erni 2018). Molt analyses were conducted by using the Moults package in R (Erni et al. 2013, Erni 2018, Nwaogu and Cresswell 2021). To evaluate the relationship between molt onset and completion dates and explanatory variables, we applied general linear models (GLMs), with day, sex, and their interaction as predictors (Erni et al. 2013).

Molt intensity

To evaluate molt intensity, we included only adult individuals in active molt (i.e., second prebasic molt [SPB] and definitive prebasic molt [DPB]) captured during the season 2018–2019 (between September 2018 and July 2019). First, we registered the molt score for each feather, including primaries (p1 to p9), secondaries (s1 to s6), and rectrices (r1 to r6) from both sides (i.e., left and right), following the scale described by Ginn (1975) and Ginn and Melville (1983). Then, we summarized the number of flight feathers in active molt as a measure of molt intensity (Echeverry-Galvis and Hau 2012, Mumme et al. 2021). We included only feathers in categories 2 to 4 to represent the active growth of the feather. We excluded feathers in categories 0 (old feather—not molted yet) and 5 (feather with molt completed) for representing the previous and posterior molt categories, and category 1 (absent feather—not started growing yet or in pin—initial growth) because include the feather drop state (i.e., absent feather) (Ginn 1975, Ginn and Melville 1983). We performed a Kruskal-Wallis test to evaluate differences in molt intensity between sexes.

Feather growth rate

To determine the feather growth rate, we applied photopitochronology (Valeris et al. 2020) to individuals who completed their molt between March and October 2019. In the field, we captured digital images of the extended rectrices (ventral view) placed on a flat surface with a millimetric scale as a length reference. For each photograph, we marked two points between three to six growth bars (at the junction of the growth bars with the rachis) and measured the distance between them three times using ImageJ software calibrated with the millimetric scale, following Terrill (2018). The final feather growth rate was calculated as the average distance in millimeters (to three decimal places) (see Valeris et al. 2020). We performed a Kruskal-Wallis test to evaluate differences in feather growth rates between sexes.

Differences in wing and tail length between sexes

To explore sex differences in wing (chord) and tail length that could potentially contribute to differences in molt timing and duration between males and females, we performed a post hoc analysis on the same individuals previously sexed via PCR. The measurements were taken from the same researcher, following Pyle (1997). We used Welch's t-tests and linear models to compare wing chord and tail length between males and females (Leys and Grieses 2023). All analyses were conducted in R version 4.4.2 (R Core Team 2024).

RESULTS

Molt timing and duration

Based on U-Z model type I, male Rufous-collared Sparrows started molting on average on 22 November 2018 (day 114 from 1 August, S.E. = 15.02 d), with an average duration of 94 d (S.E. = 15.89 d), whereas females started molting on average on 4 December 2018 (day 126 from 1 August, S.E. = 6.98 d), with an average duration of 79 d (S.E. = 8.67 d), which means that males started molting on average 12 d earlier and molted 15 d longer than females (Table 1). U-Z model type II also showed differences in molt timing and duration between sexes, with males starting earlier and having a more extended molt schedule than females, with males molting on average 7 d longer, and starting 12 d earlier than females (Table 1, Fig. 1).

Table 1. Molt parameters of male and female Rufous-collared Sparrows at Quebrada de La Plata. Duration and standard errors (S.E.) represent the number of days. The mean start-day corresponds to days after 1 August 2018. Days were rounded to the nearest whole day.

Sex	U-Z model	Duration (days)	S.E. duration (days)	Mean start-day	S.E. mean start-day
Males	I	94	16	114	15
	II	91	11	107	8
Females	I	79	9	126	7
	II	84	7	119	5

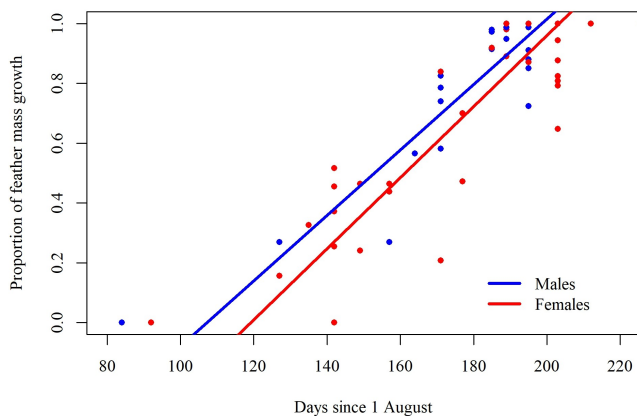
Models assessing the effect of date on the timing of molt initiation and completion showed positive and significant results (estimate = 0.072, S.E. = 0.023, $z = 3.20$, $P = 0.001$) meaning that the probability of initiating and completing molt increases as days progress after 1 August, reflecting the natural progression of molt through the annual cycle.

The effect of sex (female vs. male) was not significant when considered independently (estimate = 0.90, S.E. = 1.60, $P = 0.57$), which is expected. However, sex was significant in interaction with date ($\sim$ day:sex), with both males (estimate = 0.083, $P = 0.011$) and females (estimate = 0.093, $P = 0.033$) showing differing slope patterns. This suggests that the probability of starting and completing molt changes over time in slightly different ways for males and females (Fig. 1).

Molt intensity

Molt intensity averaged 10 feathers molting simultaneously in females (S.D. = 4), and 7.1 in males (S.D. = 3.4). Molt intensity between females and males was statistically different (Kruskal-Wallis $X^2_{(2-1)} = 5.4452$, $P = 0.01$). Females simultaneously molted more flight feathers tracks with 50% of individuals molting primaries, secondaries, and rectrices in the same period. Most males molted simultaneously one or two feather tracks, with few individuals showing active molt in all flight feather tracks, like females. Both sexes started molting with primary feathers, with females overlapping rectrices and secondaries but males overlapping only one of those feather tracks (rectrices or secondaries, but not both).

Fig. 1. Molt trajectories of male and female Rufous-collared Sparrows (*Zonotrichia capensis*) from Quebrada de La Plata during the 2018–2019 molt season. Each point represents the proportion of feather mass grown (pfmg) for an individual relative to the day of capture. Males and females are shown in blue and red, respectively. The trajectories depict the average temporal pattern of feather growth during molt, with sex-specific differences in timing and progression estimated using the Underhill–Zucchini (U-Z) Type II model based on pfmg data.



Feather growth rate

The feather growth rate in females averaged 3.288 mm/day (max. = 3.941 mm/day; min. = 3.045 mm/day, S.D. = 0.250 mm/d), whereas males averaged 3.195 mm/day (max. = 3.730 mm/day; min. = 2.774 mm/day, S.D. = 0.237 mm/day). There were no significant differences between the feather growth rate of females and males (Kruskal-Wallis $X^2_{(2-1)} = 0.5435$, $P = 0.461$), although males showed higher variability within the values.

Differences in wing and tail length between sexes

We found significant differences in both wing and tail length between sexes. Males had longer wing chords than females (males = 74.99, S.D. = 1.90 mm, females = 71.33, S.D. = 1.78 mm; Welch's $t = -8.86$, $df = 75.35$, $P < 0.001$) and longer tails (males = 62.44, S.D. = 2.11 mm, females = 59.50, S.D. = 1.77 mm; Welch's $t = -6.78$, $df = 77.54$, $P < 0.001$). Linear models confirmed these results, with sex having a significant effect on wing chord (estimate = 3.66, S.E. = 0.42 mm, $t = 8.78$, $P < 0.001$, $R^2 = 0.497$) and tail length (estimate = 2.94, S.E. = 0.44 mm, $t = 6.63$, $P < 0.001$, $R^2 = 0.360$).

DISCUSSION

As observed in the Rufous-collared Sparrow population at Quebrada de La Plata, differences in molt timing and duration between sexes align with findings in other monomorphic bird species (e.g., Hemborg 1999). Models showed that sex is an important variable for both the beginning and end of molt, which implies that males and females follow distinct molt schedules, as reflected in molt trajectories (see Fig. 1). Females initiated molt later than males but completed the process more quickly by

replacing more feathers simultaneously than males, including primaries, secondaries, and rectrices. Conversely, males began molt earlier than females, typically replacing fewer feathers simultaneously, from fewer tracks at once.

Contrary to our initial hypothesis, feather growth rates did not differ between sexes, which implies that differences in molt duration between males and females are not a consequence of the feather growth rate. De La Hera et al. (2011) found that feather growth rates are negatively correlated with molt duration, but its contribution, when molt intensity was considered, was very low, suggesting that molt intensity plays a more important role in molt duration.

The differences in molt traits observed between sexes could also result from varying selective forces, environmental constraints, and ecological or evolutionary pressures (Svensson and Nilsson 1997, Broggi et al. 2011, Borrás et al. 2004, Romero and Wingfield 2016, Kiat et al. 2019). These factors may shape molt schedules and intensity differently in males and females (see Avery 1985). Such sex-based differences in molt timing and strategy have been reported in various passerine species (Avery 1985, Morton and Morton 1990, Hemborg, 1999, Voelker 2000, Newton and Rothery 2005, Oschadleus and Osborne 2005, Bonnevie and Oschadleus 2010), supporting the idea that these patterns are widespread among passerines (Hemborg 1999).

The flexibility of molt intensity may play an adaptive mechanism to compensate for a late onset of molt, by reducing the feather gap during molt, but may impose survival and fitness consequences, through a detrimental feather quality (Guallar and Quesada 2023). Given that molt is one of the most energy-demanding life-history stages in birds (Svensson and Nilsson 1997, Dawson 2008, Echeverry-Galvis and Hau 2012), and because of its photoperiodic control (Dawson et al. 2001, Dawson 2004), the limited time available for molting for temperate bird species underscores the importance of these compensatory mechanisms.

Because Rufous-collared Sparrows are monomorphic, it is not likely that molt differences are associated with variations in feather shape, size, or coloration, as observed in dimorphic species (see Kiat and Sapir 2022). However, the Rufous-collared Sparrow has differences in the wing length (see Ridgway and Friedmann 1901), with wings of males being longer than those of females, which may at least partially compensate the female's later onset of molt. Although morphological differences in wing and tail length were statistically significant in Rufous-collared Sparrows from Quebrada de La Plata, the average difference in feather length (+3.66 mm wing length and +2.94 mm tail length in males) corresponds to approximately one day of feather growth in both sexes (based on the mean feather growth rate in the same population), suggesting that wing and tail size differences explain only a small portion of the molt timing and duration differences observed.

Nevertheless, feather quality between sexes may vary, as reported in other passerine species (Dawson et al. 2000, Echeverry-Galvis and Hau 2013). Notably, we observed that females generally exhibited greater wear on their primaries and rectrices than males, but we could not analyze this further because of the low number of recaptures in the subsequent season.

From an ecological and physiological perspective, the differences in molt timing and duration between males and females may also reflect behavioral and energetic constraints. Male Rufous-collared Sparrow are more active during the breeding season, engaging in singing and territorial defense (Miller and Miller 1968), which may increase their vulnerability to predation. In contrast, females exhibit quieter and less conspicuous behavior particularly during incubation, potentially reducing their exposure to predators. However, during molt behavioral differences among sexes could be less important. At a physiological level, egg production and incubation represent significant energetic costs, imposing additional energy demands on females. As a result, females may require more time to recover after the breeding season to initiate molt (Williams 2012).

Physiological differences, such as variation in fat reserves and muscle composition across the annual cycle, may further explain females' capacity to exhibit a more intense molt (see Woodburn and Perrins 1997). Although it is known that Rufous-collared Sparrows from Quebrada de la Plata change their thermal conductance and metabolic rate during winter and summer (Novoa et al. 1994, Novoa and Rosenmann 1996), and their diet (Novoa et al. 1996), there are no studies about physiological differences between sexes in populations of this species. Although our results offer insights into metabolic differences associated with sex and help explain sex-related variation in molt schedules and strategies, future studies should evaluate sex-based differences in fat reserves and muscle profiles before, during, and after molt to better understand these associations. Additionally, assessing whether similar sex-specific molting patterns occur across different habitats would further clarify the ecological and physiological drivers underlying these patterns.

In sum, molt timing, duration, and intensity differ between male and female Rufous-collared Sparrows. Although females start molting later than males, they complete the process more quickly, primarily because of differences in molt intensity rather than feather growth rate or differences in feather size. This suggests that molt intensity may be the key mechanism enabling females to finish molt within a shorter time window in the annual cycle.

Author Contributions:

CEV-C: Conceived the idea, designed methods, collected and analyzed data, and wrote the paper. TZ-E: Analyzed the data and review the paper. KC: Collected, analyzed data, and review the paper. GR: Collected, analyzed data, and review the paper. MK: Collected, analyzed data, and review the paper. PC: Collected, analyzed data, and review the paper. MT: Analyzed data and review the paper. RAV: Collected data, analyzed data, contributed substantial materials, resources and funding, and edited the paper.

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Data Availability:

The datasets generated and analyzed during the current study are available in Zenodo at <https://zenodo.org/records/17477826>.

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