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Year-round molt pattern, body condition and ectoparasitism in the Blue-black Grassquit (*Volatinia jacarina*)

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Understanding how tropical birds organize energetically demanding activities such as molting, breeding, and migration is central to the study of avian life-history strategies. Despite the remarkable diversity of Neotropical species, information on their annual cycles remains scarce. Here, we investigated the temporal pattern of molting and its relationship with body condition and ectoparasite infestation in the Blue-black Grassquit (*Volatinia jacarina*), a socially monogamous, granivorous passerine from central Brazil. Molting was not randomly distributed but exhibited a clear bimodal pattern, with peaks during the dry season and the rainy season. Both body and flight feathers were replaced during the same periods, and no sexual differences in molting timing were detected. Chewing lice infested 47.5% of individuals, with abundance increasing during both the breeding and molting periods, yet without measurable effects on body condition. Individuals molting during the rainy season were in better condition than those molting in the dry season or not molting at all, likely reflecting higher food availability and the influence of environmental seasonality. Our findings reveal that grassquits face overlapping energetic challenges across its annual cycle, suggesting limited flexibility in scheduling molt relative to other life-history events. These results contribute to filling a major gap in our knowledge of annual-cycle dynamics in Neotropical birds and underscore the need for integrative studies linking molt, reproduction, and movement across variable tropical environments.

1. Introduction

Birds experience multiple pressures and costs that vary throughout their annual cycle (Gill 2007). Consequently, decisions about when to molt, migrate, or reproduce affect the adaptive value of individuals (Boukherroub *et al.* 2024). Each of these life-history events entails physiological, energetic, and predation-related costs (Podlaszczuk *et al.* 2017, Oteyza *et al.* 2021). Although all of these life-history events influence fitness, migration can have particularly

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strong carry-over effects on subsequent survival and reproduction (Norris *et al.* 2004). Long-distance migrants may lose up to 33% of their mass-specific body metabolic rate based on lean mass during migration (Battley *et al.* 2001) and expend large amounts of energy at stopover sites due to extensive foraging effort and repair of muscle tissue (Wikelski *et al.* 2003). Because of these high energetic demands, feeding investment must increase, creating a trade-off with other behaviors such as preening, which can lead to higher ectoparasite loads in migratory birds (Rózsa 1997). Thus, the timing of major annual-cycle events may influence not only energetic balance, but also parasite exposure and investment in self-maintenance.

Molting is one of the most critical processes in the avian annual cycle (Gill 2007), influencing survival and reproductive success (de la Hera *et al.* 2010). Feather replacement involves substantial energetic and nutritional costs, including those associated with feather synthesis and tissue growth (Schieltz & Murphy 1997, McQueen *et al.* 2021). Thus, molt can have positive effects when it restores or enhances plumage function (Tomotani & Muijres 2019), but it can also impose short-term costs that may constrain reproduction, migration, or body condition (Lind *et al.* 2004, Alfaro *et al.* 2018). To manage these costs, birds generally schedule molting, migration, and reproduction at different times of the year, as observed in Fork-tailed Flycatchers (*Tyrannus savana*; Jahn *et al.* 2016). Molting may occur for plumage renewal, replacing worn or lost feathers, or for reproductive purposes, when changes in plumage serve functions such as attracting mates or improving crypsis to avoid predation (Jukema *et al.* 2003, Valdez & Benítez-Vieyra 2023). Molt may involve body feathers, flight feathers, or both (Bourgeois & Dromzée 2014, Jahn *et al.* 2017). Similarly to other passerines, in three migratory swallows body molt occurred year-round, but both body and flight feathers were primarily replaced in the wintering grounds (Imlay *et al.* 2017).

Because males and females often differ ecologically and behaviorally, their molting patterns can also differ (Mazur *et al.* 2021). In many species, females use plumage traits to select mates, making male body-feather molt critical for maintaining plumage brightness and chroma (Surmacki *et al.* 2011, Ward *et al.* 2021). Conversely, females often avoid overlapping breeding and molting because reproduction imposes high physiological costs (Echeverry-Galvis & Hau 2012). In a comparative study of 21 tanager species, molt (of both body and flight feathers) was much less frequent among females with brood patches (Penha 2024).

The phenology of avian annual cycles is driven mainly by the onset of spring and summer in temperate regions and by rainfall seasonality in tropical habitats (Araujo *et al.* 2017). In areas with weak climatic seasonality, birds typically exhibit flexible molting and breeding schedules and often show reduced overlap between these activities. In strongly seasonal environments, however, some overlap is expected (Barta *et al.* 2006). Although tropical regions are often assumed to be more stable than temperate ones (Klopfer 1959), environmental seasonality also occurs (Nwaogu *et al.* 2019). Molting is particularly important for migratory species from seasonal environments (Pyle 2022), yet data on molting cycles remain scarce for Neotropical species (*e.g.* Jahn *et al.* 2017, Bonier *et al.* 2018).

Because molt directly replaces the feather substrate used by many ectoparasites and may also alter host investment in self-maintenance, molting can influence ectoparasite abundance, although its effects appear to vary among host–parasite systems (Markov 1940, Baum 1968, Moyer *et al.* 2002, Freed *et al.* 2008). Some studies have reported reduced ectoparasite loads during molt (Blagoveshchensky 1959, Markov 1940, Kettle 1983, Baum 1968, Pérez *et al.* 1996), possibly because parasites and their eggs are shed together with old feathers. However, other studies have found no effect of molt on ectoparasite abundance or even an increase in parasite loads during this period (Hamstra & Badyaev 2009). These contrasting patterns are relevant because ectoparasite infestations generally impose costs on birds (Clayton *et al.* 1999), although the magnitude of these effects may depend on the host's ability to compensate for parasitic stress (Munger & Karasov 1989, Clayton *et al.* 2015). Ectoparasites that consume bodily fluids (Simon *et al.* 2004), transmit

pathogens (Norte *et al.* 2013), or damage feathers (Schreiter *et al.* 2022) can impair host health, increase mortality, and reduce reproductive success (Booth *et al.* 1993, Clayton *et al.* 1999, Møller *et al.* 2004). Their abundance may also fluctuate throughout the year (Galloway & Lamb 2021), often peaking during periods of intense social interaction, such as breeding, when increased contact among hosts can facilitate parasite transmission (Foster 1969, Hamstra & Badyaev 2009, Durkin *et al.* 2015). Accordingly, ectoparasite presence is frequently associated with poorer body condition (Potti & Merino 1995, Norte *et al.* 2013), as reported for Rough-legged buzzards (*Buteo lagopus*), in which infestation by *Craspedorrhynchus* lice was associated with reduced body condition and louse abundance (Maron *et al.* 2024). Conversely, healthier individuals may tolerate, or even harbor, more parasites, as predicted by the Hamilton–Zuk hypothesis (Hamilton & Zuk 1982). In this context, traits that signal resistance to chewing lice may be expressed through ornamental features and contribute to mate choice (Moreno-Rueda & Hoi 2012).

Body condition itself varies seasonally in response to the energetic and physiological challenges imposed by the annual cycle, including molt, reproduction, migration, and parasitism (Borowske *et al.* 2018). Individuals typically improve body condition before migration and breeding (Andersson *et al.* 2018, Aloni *et al.* 2019) as a preparatory strategy. In environments with strong seasonality and unpredictable food availability, greater variability in condition (Danner *et al.* 2013) and higher mortality among poor-condition individuals are expected (Newton 2007).

The Blue-black Grassquit (*Volatinia jacarina* Linnaeus, 1766) is a socially monogamous Neotropical passerine (Carvalho *et al.* 2007). This dichromatic species exhibits a male nuptial plumage at the onset of the breeding season (Maia & Macedo 2011), and body condition is correlated with coloration (Doucet 2002). The species migrates to breed in central Brazil during the rainy season (Sick 1997; but movements are not clearly described; Rising 2020), nests mainly between January and April (Aguilar *et al.* 2008, Dias *et al.* 2009) and hosts several ectoparasites, including Philornis flies (Biagolini Jr & Macedo 2021), ticks (Zeringóta *et al.* 2016), and chewing lice (Magalhães *et al.* 2014). Previous research found that the presence of chewing lice (*Phthiraptera*) was negatively associated with nuptial plumage coverage but not with body condition (Magalhães *et al.* 2014). Given this background, the Blue-black Grassquit provides a useful model for examining how molt, reproduction, ectoparasitism, and body condition are linked across the annual cycle in a seasonal Neotropical environment. We aimed to characterize the temporal pattern of molt and to investigate annual variation in body condition and ectoparasite infestation in this species. Specifically, we tested whether: 1) contour- and flight-feather molt occur at different times of the year, predicting temporal separation if these molt types differ in function or energetic cost, following Wright *et al.* 2018; 2) molting patterns differ between sexes (following Mazur *et al.* 2021), predicting that males would show increased body-feather molt before or during the onset of breeding because they acquire nuptial plumage; 3) ectoparasite abundance is lower during months when individuals are molting, as feather replacement may remove parasites and their eggs, following Kettle 1983; 4) ectoparasite abundance is higher during the breeding period, when increased social contact may facilitate transmission, following Foster 1969; 5) body condition declines during molt owing to the energetic costs of feather replacement, following Borowske *et al.* 2018; and 6) ectoparasite abundance is negatively related to individual body condition, as parasitism may impose physiological costs on hosts, following Maron *et al.* 2024.

2. Materials and methods

2.1. Study area

The study was conducted along a 10-km transect parallel to the southern border of the Águas Emendadas Ecological Station (ESECAE; 15°33′17″ S, 47°35′51″ W; Fig. 1), located in the northeastern portion of Distrito Federal, central Brazil. ESECAE is a fully protected conservation unit covering 10,547 ha (Ibram 2025). The

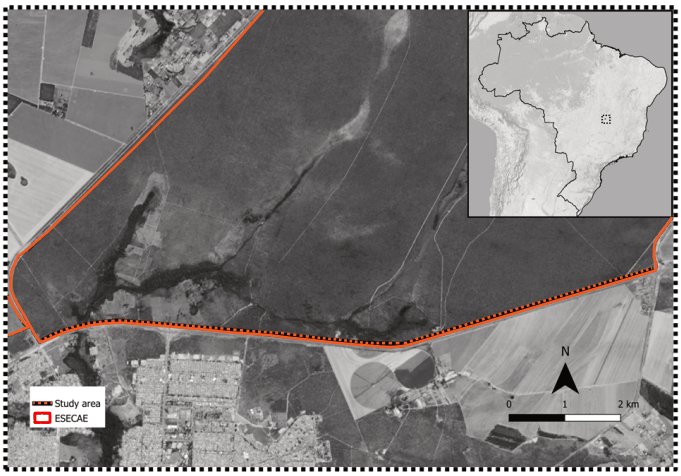

Fig. 1. Study area (10 km transect; shown in dashed red and black) located along the southern border of Águas Emendadas Ecological Station (ESECAE; outlined with a red line), in the Brazilian savanna of central Brazil.

predominant vegetation in the study area is altered open savanna (cerrado ralo), characterized by a high abundance of exotic grasses. The regional climate is tropical wet-and-dry, with a cool-dry season and a hot-wet season. Rainfall is concentrated between November and April, while the dry period extends from May to October, peaking in July and August (Oliveira & Marquis 2002).

2.2. General procedures

From October 2017 to March 2020, birds were captured once per week using a constant effort of six mist nets (9.0 × 2.5 m; 14 × 14 mm mesh) distributed throughout the study area. Captured individuals were marked with a unique combination of three colored plastic bands and one numbered metal band issued by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio). For each individual, we recorded capture date and sex, and measured body mass (to the nearest 0.25 g) using a spring scale and tarsus length (to the nearest 0.02 mm) using a digital caliper. We examined each bird for signs of molt and recorded the body regions involved. Both body and flight feathers were inspected, and body-feather molt and flight-feather molt were recorded separately as presence/absence variables. To assess the temporal dynamics of body-feather molt, we focused on the dorsal regions, including the head, back, and rump, and recorded whether active feather replacement was present in these regions. Flight-feather molt was evaluated by examining the primaries and secondaries of both wings and the rectrices of the tail, and was recorded when active replacement of these feathers was observed. We did not classify molt according to the sequence of feather replacement. Therefore, our classification refers to the presence of active molt in body or flight feathers, regardless of molt origin. Finally, we exposed each wing to ambient light and counted all visible chewing lice on the flight feathers of both wings. The same observer counted all lice (RID). Because chewing lice are small and cryptic, our counts should be interpreted as an index of visible louse abundance rather than an absolute estimate of total parasite load.

2.3. Statistical analyses

We applied the Hermans–Rasson test to the complete molting dataset, as well as separately for contour-feather and flight-feather molt, to determine whether molting occurred randomly throughout the year (Landler *et al.* 2019). The Hermans–Rasson method was chosen because it provides greater sensitivity than other tests for detecting multimodal deviations from uniformity (Landler *et al.* 2018, 2019). Using the function HR_test from the CircMLE package (Fitak & Johnsen 2017), we implemented the updated

version of the test (Landler *et al.* 2019) with 9,999 iterations. Capture dates were converted to radians.

To compare molting patterns between sexes and between contour- and flight-feather molt, we used the activity package (Rowcliffe 2023). Temporal models were fitted using the fitact function, which employs a non-parametric kernel-density approach to estimate temporal patterns of circular data (Linkie & Ridout 2011). Overlap between molting periods was quantified with the overlap index (Dhat4, ovl4 function; Ridout and Linkie 2009), which ranges from $\Delta = 0$ (no overlap) to $\Delta = 1$ (complete overlap). We then tested whether circular distributions differed between groups using Wald tests (compareAct; Rowcliffe 2023).

All statistical models were specified *a priori* based on the biological questions of the study. We fitted relatively simple models to avoid overparameterization, especially because some analyses involved restricted subsets of the data. Model adequacy was assessed by inspecting residual patterns and checking whether model assumptions were met. For count data, we evaluated overdispersion and used a negative binomial error distribution when appropriate. For linear models, we visually inspected residuals to assess normality, homoscedasticity, and the presence of influential observations.

To assess the effects of molt and reproduction on chewing-louse abundance, we fitted a generalized linear model (GLM) with a negative binomial error distribution, due to overdispersion in the data. This analysis included only months when more than 40% of individuals were molting (June–July and November–January). Breeding months (January–April) were defined based on observed nesting activity in the study area. Models were fitted using the glm.nb function from the MASS package (Venables & Ripley 2002). Model adequacy was assessed by checking for overdispersion and inspecting residual patterns. Because the count data were overdispersed, we used a negative binomial error distribution.

We further examined whether body condition was affected by chewing-louse infestation and sex. This analysis included only parasitized individuals for which both body mass and tarsus length were available. Body condition was estimated as the residuals from a linear regression of body mass on tarsus length. Individuals with negative residuals were interpreted as being in poorer condition than those with positive residuals (Jakob *et al.* 1996). Given the debate over condition indices (Green 2001, Schulte-Hostedde *et al.* 2005), we also analyzed body mass alone as an alternative indicator of condition (Labocha & Hayes 2012). We then fitted a linear model with body condition as the response variable and the number of chewing lice and sex as predictors. To improve model fit, the number of chewing lice was transformed using the inverse square-root function.

Finally, to investigate seasonal variation in body condition associated with molting, we fitted a linear model with body condition as the response variable. Based on the annual molt pattern identified in the results, the year was divided into three four-month periods: (1) molt during the rainy season, (2) molt during the dry season, and (3) non-molting period. The molting periods included the months immediately before and after each molt peak. All linear models were implemented using the lm function from the stats package. For linear models, model assumptions were evaluated by inspecting diagnostic plots, including residuals versus fitted values and normal Q–Q plots. Descriptive statistics are presented as mean ± standard deviation. All analyses were performed in R (version 4.4.1, R Core Team, 2024).

3. Results

We captured a total of 493 birds during the study period, representing 480 unique individuals (221 males and 259 females). Only nine individuals were recaptured. The proportion of molting individuals varied considerably throughout the year: more than 80% of birds were molting in June, whereas no molting was recorded in April or May (Table S1 in Supplementary Material).

Molting was not randomly distributed across the year (Hermans–Rasson test: $T = 71.49$, $P < 0.001$). Approximately 34.5% of all individuals ($n = 493$) were undergoing molt at the time of capture. Both males and females showed

a bimodal molting pattern, with peaks during the rainy season (November–December) and the dry season (June–July; Fig. 2). Similar results were obtained for body-feather molt (T = 66.68, $P < 0.001$) and flight-feather molt (T = 72.30, $P < 0.001$). The overlap in molting periods between males and females was relatively high ($\Delta = 0.67$), and the annual distribution of molt did not differ significantly between sexes (W = 0.05; $P = 0.817$). Molting patterns in males and females overlapped and were similarly distributed when considered both body-feather ($\Delta = 0.70$; W = 0.78; $P = 0.376$) and flight-feather molt ($\Delta = 0.61$; W = 1.44; $P = 0.230$) separately. The replacement of contour feathers across body regions appeared to occur randomly within molting periods, suggesting little evidence of a consistent sequence among the head, back, and rump (Table S2).

A total of 226 individuals were infested with chewing lice, corresponding to an overall prevalence of 47.5% (n = 476). The prevalence was slightly higher in males (48.6%) than in females (46.5%). The mean number of chewing lice per bird was 12.41 ± 30.56 (range = 0–237). Louse abundance was higher during the breeding season (16.54 ± 35.83) than during the non-breeding season (9.91 ± 26.62; GLM–NB: z = 3.85, $P < 0.001$), and higher during the molting period (15.07 ± 33.78) than during the non-molting period (10.58 ± 28.03; GLM–NB: z = 3.52, $P < 0.001$). The interaction between breeding and molting periods was also significant, indicating that parasite loads were lowest when individuals were neither molting nor breeding (GLM–NB: z = –2.57, $P = 0.010$; Fig. 3).

The analyzed grassquits (n = 467) had an average body mass of 8.84 ± 0.78 g and a body condition index ranging from –1.84 to 3.25 g. Body condition was higher in individuals molting during the rainy season (0.19 ± 0.81 g) than in those molting during the dry season (–0.18 ± 0.70 g; LM: t = 4.50, $P < 0.001$) and in those not molting (0.02 ± 0.73 g; LM: t = 2.00, $P = 0.047$; Fig. 4). Similar results were obtained when body mass was used as an alternative measure of condition (both analyses: t > 2.09, $P < 0.037$). However, chewing-louse infestation had no significant effect on body condition (LM: t = –0.36, $P = 0.722$), indicating that parasite load did not decrease body condition.

4. Discussion

We found that Blue-black Grassquits molt during two distinct periods of the year, one during the dry season and another during the rainy season,

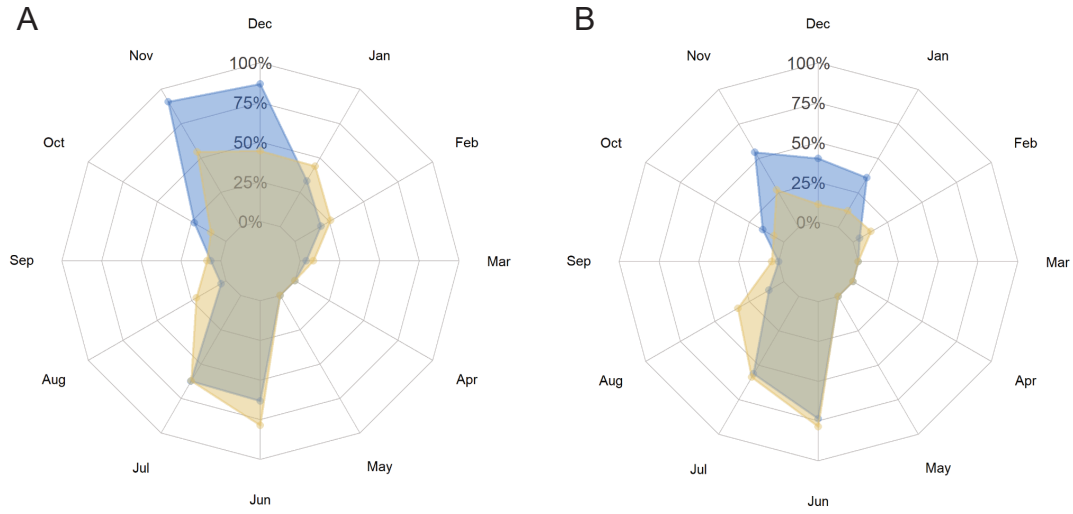

Fig. 2. Annual molting pattern for male (blue) and female (yellow) Blue-black Grassquits (*Volatinia jacarina*), with overlap between sexes shown in brown. A) Body-feather molt and B) Flight-feather molt.

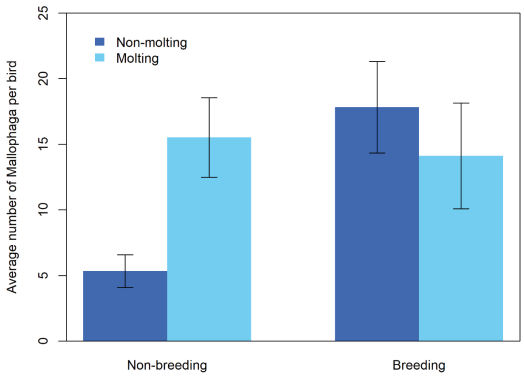

Fig. 3. Effect of breeding and molting behavior on the chewing lice (*Phthiraptera*) infestation on Blue-black Grassquits (*Volatinia jacarina*).

the latter coinciding with the species' reproductive period in the region (Carvalho *et al.* 2007, Aguilar *et al.* 2008). During the rainy season, males transition into their nuptial plumage (Maia & Macedo 2011). Although reproductive costs may differ between sexes (Mazur *et al.* 2021), no sexual differences in molting patterns were detected. The observed bimodal pattern, particularly for flight-feather molt, may have at least two non-mutually exclusive interpretations. First, Blue-black Grassquits may undergo two complete molts per year, corresponding to a prealternate molt (*i.e.* associated with the acquisition of alternate or breeding plumage) before or during the onset of breeding and a post-breeding prebasic molt (*i.e.* associated with the replacement of worn feathers and the acquisition of basic plumage) during the dry season. This interpretation is consistent with the occurrence of two annual molts in several bird species, often corresponding to prebasic and prealternate molts (Moreno-Palacios *et al.* 2013, Wright *et al.* 2018), and may be especially plausible for species inhabiting open grassland-like environments, where feather wear may be high (Renfrew *et al.* 2011). Second, the bimodal pattern may reflect a single complete molt cycle that is initiated during the rainy season, suspended or reduced during breeding, and completed during the dry season. Molt suspension during reproduction has been documented in some bird species and may reduce the temporal overlap between energetically demanding processes (Fernández-Eslava *et al.* 2020). Unfortunately our data do not allow us to discriminate conclusively between these alternatives because detailed information on the sequence of individual flight-feather replacement was not recorded, and only a small number of individuals were recaptured.

According to the literature, grassquits migrate northward after breeding in central Brazil (Sick 1997). Surprisingly, the dry-season molt coincided with this expected migratory period. One possible explanation is that some individuals may remain in the study area instead of migrating, possibly because they did not molt at

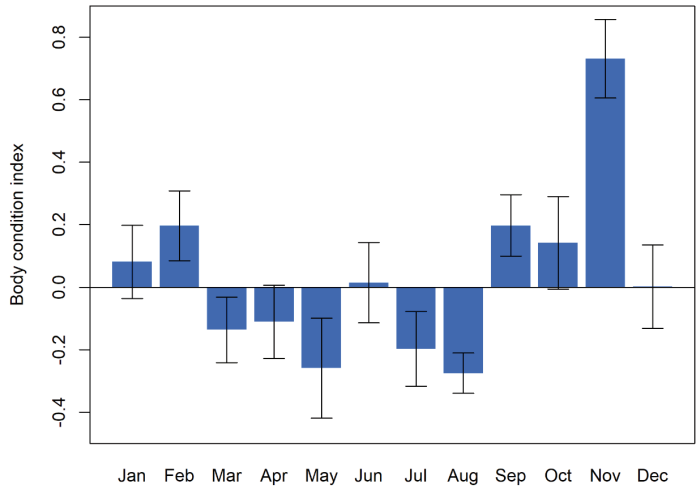

Fig. 4. Monthly variation on the body condition index of Blue-black Grassquits (*Volatinia jacarina*).

the appropriate time or because migratory behavior varies among individuals or populations. Alternatively, some individuals may undergo a prealternate molt prior to migration (Wright *et al.* 2018), whereas others may be completing a suspended molt cycle after breeding. Northern populations, such as those in Colombia, also show two molting peaks, which appear to overlap with both breeding and rainfall peaks in that region (Moreno-Palacios *et al.* 2013). Although flight-feather molt is usually expected to occur before migration (Kiat & Sapir 2017) and body-feather molt before or shortly after reproduction (Jahn *et al.* 2017), we found no clear temporal separation between body and flight-feather molt in Blue-black Grassquits, as both molt types occurred during the same periods.

The prevalence of chewing lice in grassquits was similar to that reported for other Neotropical passerines (Lyra-Neves *et al.* 2005; Enout *et al.* 2009). Host traits are thought to influence lice abundance more strongly than environmental factors (Clayton *et al.* 1992). Interestingly, we found that lice numbers were higher during the breeding season than outside it, consistent with previous studies (Kettle 1983, Hamstra & Badyaev 2009; but see Lamb & Galloway 2016). Lice may exploit the host's energetic constraints during breeding, when immune function and preening activity are reduced, thereby enhancing reproduction and dispersal opportunities (Galloway & Lamb 2021).

Several mechanisms could explain the increased louse abundance during breeding. Vertical transmission between adults and nestlings is well documented (Brooke 2010), while horizontal transmission through social interactions may also facilitate dispersal (Galloway & Lamb 2021). Thus, increased contact among individuals during the breeding season—through territorial disputes, copulation, and courtship chases (Dias *et al.* 2009), may promote parasite transmission. Additionally, phoretic dispersal of lice via hippoboscid flies (Bartlow *et al.* 2016) could be synchronized with the grassquit's breeding period.

Contrary to expectations, louse abundance was higher during molt than during non-molting periods (but see Moyer *et al.* 2002). We expected feather replacement to reduce parasite loads (Galloway & Lamb 2021), as observed in some species in which intense molt is associated with lower louse prevalence (Freed *et al.* 2008). However, a study conducted in the Brazilian savanna found no evidence that molting effectively reduced louse infestation in the Pale-breasted Thrush (*Turdus leucomelas*; Enout *et al.* 2009). Our findings suggest that Blue-black Grassquits may experience the costs of molting and ectoparasitism simultaneously. However, this interpretation should be considered cautiously because differences in parasite detectability between molting and non-molting birds may have influenced our estimates of louse abundance. During molt, changes in plumage structure, feather spacing, or the exposure of growing feathers may make lice more visible during inspection, whereas denser or fully grown plumage may reduce detectability in non-molting individuals. Therefore, the higher louse counts observed during molt may reflect, at least in part, increased detectability rather than only a true increase in parasite abundance. From the lice's perspective, newly grown feathers may provide improved feeding opportunities, potentially enhancing their reproduction (Freed *et al.* 2008). Alternatively, synchronized life cycles between lice and their hosts (Marshall 1981) may facilitate nymph dispersal during molting periods (Galloway & Lamb 2021).

When assessing temporal variation in body condition, we found that grassquits captured during molting periods were in better condition than those captured outside molting periods. This pattern is similar to findings in other tanagers from the Atlantic Forest (Penha 2024). Specifically, individuals captured during the rainy-season molt, which overlaps with the onset of breeding, showed better condition than those captured during the dry-season molt, when breeding does not occur. However, these patterns should be interpreted cautiously because our study did not directly measure the mechanisms that may explain seasonal variation in condition, and the low recapture rate prevents us from distinguishing within-individual changes from differences among individuals sampled at different times of the year. Several non-mutually exclusive explanations are possible. Individuals

in better condition may be more likely to initiate or sustain molt (Moreno-Rueda 2010), as observed in Rufous-collared Sparrows (*Zonotrichia capensis*), in which individuals in better condition replaced more feathers simultaneously (Bonier *et al.* 2018). Alternatively, birds may accumulate energy reserves before molting and reproduction to enhance survival and reproductive success (Merkle & Barclay 1996, Schaub & Jenni 2000), or molting individuals may show better condition because molt occurs during periods of greater resource availability.

Seasonal variation in body condition linked to resource availability has been demonstrated in several bird species (Strong & Sherry 2001). The pronounced seasonality of the Cerrado likely influences grassquit' body condition, the marked decline in rainfall during the dry season results in reduced food resources for granivorous birds (Crowley & Garnett 1999). Studies have shown that seed availability is lower in the dry season than in the wet season in the Brazilian savanna (Ramos *et al.* 2017, Xavier *et al.* 2021). As a granivorous species that feeds mainly on grass seeds, grassquits benefit from exotic grasses such as *Brachiaria spp*. and *Melinis minutiflora* (Aguilar *et al.* 2008). In our study area, seed production of these grasses, and consequently food availability, peaks during the breeding season, aligning with the period of highest body condition.

Contrary to our predictions, chewing lice infestation did not affect body condition. Previous studies have found negative (Maron *et al.* 2024), positive (Rózsa 1997), or neutral (Clayton & Tompkins 1995) relationships between feather lice and host condition. The absence of an effect in our study may be explained by the type of resource exploited by the lice. Members of the suborder *Amblycera* feed on feathers and blood, while those of the *Ischnocera* consume mainly dead material such as feathers and skin debris (Clayton *et al.* 2008). Because we only assessed lice on wing feathers, more severe impacts such as pathogen transmission and anemia (Price & Graham 1997, Prelezov *et al.* 2006) may not apply here. Although chewing lice can damage feathers and impair thermoregulation (Booth *et al.* 1993), condition (Potti & Merino 1995), and migratory performance (Møller *et al.* 2004), infestation of wing feathers alone may not impose significant costs on grassquits.

Overall, our results bring a new perspective into the temporal relationships among key events in the grassquit's annual cycle and contribute to the still limited knowledge of molt strategies in tropical birds. The overlap between molting, migration, and breeding suggests that hidden physiological or ecological costs may constrain the timing of these activities. Although molting did not reduce lice numbers, increased parasite loads during breeding appear to have little measurable impact on body condition, suggesting that the consequences of ectoparasitism may depend on host tolerance, seasonal context, or parasite detectability. Future studies should investigate how individual birds respond to these overlapping demands over time, assess whether molting differs between migratory and resident individuals, and examine how annual variation in plumage coloration relates to ectoparasite presence. A broader understanding of how tropical birds balance the timing of energetically costly events will shed light on the trade-offs shaping avian molt strategies, host–parasite interactions, and life-history evolution.

Samettisirkkusen (*Volatinia jacarina*) ympärivuotinen sulkasadon ajoitus, linnun kunto ja ulkoloisten esiintyminen

Keskeinen osa lintujen elinkiertostrategioiden tutkimusta on ymmärtää, miten trooppiset linnut ajoittavat paljon energiaa vaativat toiminnot, kuten sulkasadon, lisääntymisen ja muuton. Huolimatta neotrooppisten lintulajien huomattavasta monimuotoisuudesta niiden vuotuisista elinkierroista on edelleen niukasti tietoa. Tässä tutkimuksessa selvitettiin sulkasadon ajoitusta sekä sen yhteyttä linnun kuntoon ja ulkoloisten määrään samettisirkkusella (*Volatinia jacarina*), joka on Keski-Brasiliassa elävä yksiavioinen ja siemeniä ravinnokseen käyttävä varpuslintu.

Sulkasato ei jakautunut satunnaisesti vuoden aikana, vaan sen ajoitus oli selkeästi kaksihuippuinen: sulkasadon huippujaksot sijoittuivat kuivaan kauteen ja sadekauteen. Sekä ruumiinhöyhenet että siipisulat uusiutuivat

samoina ajanjaksoina, eikä sukupuolten välillä havaittu eroja sulkasadon ajoittumisessa.

Väiveitä esiintyi 47,5 prosentilla tutkituista yksilöistä. Loisten määrä kasvoi sekä lisääntymis- että sulkasatokauden aikana, mutta niillä ei havaittu mitattavaa vaikutusta lintujen kuntoon. Sadekautena sulkivat yksilöt olivat paremmassa kunnossa kuin kuivana kautena sulkivat tai ne yksilöt, jotka eivät sulkineet lainkaan. Tämä johtunee suuremmasta ravinnon saatavuudesta sekä ympäristön vuodenaikaisvaihtelun vaikutuksista.

Tulokset osoittavat, että samettisirkkuset kohtaavat vuotuisen elinkiertonsa aikana useita samanaikaisia energiataloudellisia haasteita. Tämä viittaa siihen, että sulkasadon ajoittuminen on jäykempää kuin muiden elinkiertotapahtumien. Tutkimus auttaa paikkaamaan merkittävää tiedonpuutetta neotrooppisten lintujen vuotuisen elinkierron dynamiikasta ja korostaa tarvetta kokonaisvaltaisille tutkimuksille, joissa tarkastellaan sulkasadon, lisääntymisen ja liikkumisen välisiä yhteyksiä vaihtelevissa trooppisissa ympäristöissä.

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Author contributions. GCC: Conceptualization, Investigation, Writing – original draft. RID: Investigation, Formal analysis, Writing – original draft, Writing – review & editing, Supervision.

Ethics statement. All animal procedure (capture, handling, banding) were approved by the Brazilian authority: Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio number: SISBIO 58743-1 and CEUB Ethical Committee for Animal Research number: 006/17.

Data availability. The data supporting the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.22920873.

References

Aguilar, T.M., Dias, R.I., Oliveira, A.C. & Macedo, R.H. 2008: Nest-site selection by blue-black grassquits in a Neotropical savanna: do choices influence nest success? — Journal of Field Ornithology 79: 24–31. https://doi.org/10.1111/j.1557-9263.2008.00142.x

Alfaro, M., Sandercock, B.K., Liguori, L. & Arim, M. 2018: Body condition and feather molt of a migratory shorebird during the non-breeding season. — Journal of Avian Biology 49: e01480. https://doi.org/10.1111/jav.01480

Aloni, I., Markman, S. & Ziv, Y. 2019: Autumn temperatures at African wintering grounds affect body condition of two passerine species during spring migration. — PLoS One 14: e0217619. https://doi.org/10.1371/journal.pone.0217619

Andersson, N., Piha, M., Meller, K., Välimäki, K. & Lehikoinen, A. 2018: Variation in body condition of songbirds during breeding season in relation to sex, migration strategy and weather. — Ornis Fennica 95: 70–81. https://doi.org/10.51812/of.133931

Araujo, H.F.P., Vieira-Filho, A.H., de Barbosa, M.R.V., Diniz-Filho, J.A.F. & da Silva, J.M.C. 2017: Passerine phenology in the largest tropical dry forest of South America: effects of climate and resource availability. — Emu – Austral Ornithology 117: 78–91. https://doi.org/10.1080/01584197.2016.1265430

Barta, Z.A., Houston, A.I., McNamara, J.M., Welham, R.K., Hedenström, A., Weber, T.P. & Feró, O. 2006: Annual routines of non-migratory birds: optimal moult strategies. — Oikos 112: 580–593. https://doi.org/10.1111/j.0030-1299.2006.14240.x

Bartlow, A.W., Villa, S.M., Thompson, M.W. & Bush, S.E. 2016: Walk or ride? Phoretic behaviour of amblyceran and ischnoceran lice. — International Journal for Parasitology 46: 221–227. https://doi.org/10.1016/j.ijpara.2016.01.003

Baum, H. 1968: Biology and ecology of the feather lice of blackbirds. — Angewandte Parasitologie 9: 129–175.

Battley, P.F., Dekinga, A., Dietz, M.W., Piersma, T., Tang, S. & Hulsman, K. 2001: Basal metabolic rate declines during long-distance migratory flight in great knots. — The Condor 103: 838–845. https://doi.org/10.1093/condor/103.4.838

Biagolini Jr, C. & Macedo, R.H. 2021: *Philornis* infection in blue-black grassquits: impact on nestlings and risk factors involved. — Journal of Avian Biology 52: e02592. https://doi.org/10.1111/jav.02592

Blagoveshchensky, D.I. 1959: Mallophaga. Part 1. Introduction (English translation). — Nasekomye pukhoedy, Fauna SSSR: Insecta, Mallophaga, 1: 1–202.

Bonier, F., Martin, P.R., Small, T.W., Danner, J.E., Danner, R.M., Nelson, W.A. & Moore, I.T. 2018: Energetic costs and strategies of post-juvenal molt in an equatorial bird, the rufous-collared sparrow (*Zonotrichia capensis*). — Ornitología Neotropical 29: S19–S28. https://doi.org/10.58843/ornneo.v29i2.190

Booth, D.T., Clayton, D.H. & Block, B.A. 1993: Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. — Proceedings of the Royal Society of London B 253: 125–129. https://doi.org/10.1098/rspb.1993.0091

Borowske, A., Field, C.R., Ruskin, K.J. & Elphick, C.S. 2018: Consequences of breeding system for body condition and survival throughout the annual cycle of tidal marsh sparrows. — Journal of Avian Biology 49: e01529. https://doi.org/10.1111/jav.01529

Boukherroub, S., Desrochers, A. & Tremblay, J.A. 2024: Nesting phenology of migratory songbirds in an eastern Canadian boreal forest, 1996–2020. — Avian Conservation and Ecology 19: 2. https://doi.org/10.5751/ACE-02565-190102

Bourgeois, K. & Dromzée, S. 2014: Moulting strategies of the Yelkouan Shearwater *Puffinus yelkouan* during the breeding season. — Journal of Ornithology 155: 265–271. https://doi.org/10.1007/s10336-013-1011-y

Brooke, M.D.L. 2010: Vertical transmission of feather lice between adult blackbirds *Turdus merula* and their nestlings: a lousy perspective. — Journal of Parasitology 96: 1076–1080. https://doi.org/10.1645/GE-2513.1

Carvalho, C.B., Macedo, R.H. & Graves, J.A. 2007: Breeding strategies of a socially monogamous Neotropical passerine: extra-pair fertilizations, behavior, and morphology. — The Condor 108: 579–590. https://doi.org/10.1093/condor/108.3.579

Clayton, D.H., Adams, R.J. & Bush, S.E. 2008: Phthiraptera, the chewing lice. — In Atkinson, C.T., Thomas, N.J., Hunter, D.B. (Eds.), Parasitic Diseases of Wild Birds. Wiley-Blackwell, Ames, Iowa, USA, pp. 515–526.

Clayton, D.H., Bush, S.E. & Johnson, K.P. 2015: Coevolution of life on hosts: integrating ecology and history. — University of Chicago Press, Chicago, Illinois.

Clayton, D.H., Gregory, R.D. & Price, R.D. 1992: Comparative ecology of Neotropical bird lice (Insecta: Phthiraptera). — Journal of Animal Ecology 61: 781–795. https://doi.org/10.2307/5631

Clayton, D.H., Lee, P.L.M., Tompkins, D.M. & Brodie, E.D. 1999: Reciprocal natural selection on host–parasite phenotypes. — The American Naturalist 154: 261–270. https://doi.org/10.1086/303237

Clayton, D.H. & Tompkins, D.M. 1995: Comparative effects of mites and lice on the reproductive success of rock doves (*Columba livia*). — Parasitology 110: 195–206. https://doi.org/10.1017/s0031182000063964

Crowley, G. & Garnett, S. 1999: Seeds of the annual grasses *Schizachyrium* spp. as a food resource for tropical granivorous birds. — Austral Ecology 24: 208–220. https://doi.org/10.1046/j.1442-9993.1999.00964.x

Danner, R.M., Greenberg, R.S., Danner, J.E., Kirkpatrick, L.T. & Walters, J.R. 2013: Experimental support for food limitation of a short-distance migratory bird wintering in the temperate zone. — Ecology 94: 2803–2816. https://doi.org/10.1890/13-0337.1

de la Hera, I., Hedenström, A., Pérez-Tris, J. & Tellería, J.L. 2010: Variation in the mechanical properties of flight feathers of the blackcap *Sylvia atricapilla* in relation to migration. — Journal of Avian Biology 41: 342–347. https://doi.org/10.1111/j.1600-048X.2009.04835.x

Dias, R.I., Kuhlmann, M., Lourenço, L.R. & Macedo, R.H. 2009: Territorial clustering in the blue-black grassquit: reproductive strategy in response to habitat and food requirements? — The Condor 111: 706–714. https://doi.org/10.1525/cond.2009.090142

Doucet, S.M. 2002: Structural plumage coloration, male body size, and condition in the blue-black grassquit. — The Condor 104: 30–38. https://doi.org/10.1093/condor/104.1.30

Durkin, E.S., Luong, L.T. & Bird, J. 2015: Mechanisms underlying parasite infection: influence of host body mass and age on chewing louse distribution among brown-headed cowbirds. — Parasitology Research 114: 4169–4174. https://doi.org/10.1007/s00436-

015-4648-z

Echeverry-Galvis, M.A. & Hau, M. 2012: Moult–breeding overlap alters moult dynamics and behavior in zebra finches, *Taeniopygia guttata castanotis*. — Journal of Experimental Biology 215: 1957–1964. https://doi.org/10.1242/jeb.065474

Enout, A.M., Lobato, D.N., Azevedo, C.S., Antonini, Y. 2009: Parasitism of chewing lice (Insecta) and feather mites (Acari) on *Turdus leucomelas* (Aves) during reproductive and molt seasons at the State Park of Rio Preto, Minas Gerais, Brazil. — Zoologia (Curitiba) 26: 534–540. https://doi.org/10.1590/S1984-46702009000300017

Fernández-Eslava, B., Alonso, D., Galicia, D., Arizaga, J. 2020: Estimation of moult duration in birds with suspended moults: the case of the Red Crossbill and its relation to reproduction. — Journal of Ornithology 161: 481–490. https://doi.org/10.1007/s10336-019-01739-7

Fitak, R.R. & Johnsen, S. 2017: Bringing the analysis of animal orientation data full circle: model-based approaches with maximum likelihood. — Journal of Experimental Biology 220: 3878–3882. https://doi.org/10.1242/jeb.167056

Foster, M.S. 1969: Synchronized life cycles in the orange-crowned warbler and its mallophagan parasites. — Ecology 50: 315–323. https://doi.org/10.2307/1934858

Freed, L.A., Medeiros, M.C. & Bodner, G.R. 2008: Explosive increase in ectoparasites in Hawaiian forest birds. — Journal of Parasitology 94: 1009–1021. https://doi.org/10.1645/GE-1378.1

Galloway, T.D. & Lamb, R.J. 2021: Population dynamics of chewing lice (Phthiraptera) infesting birds (Aves). — Annual Review of Entomology 66: 209–224. https://doi.org/10.1146/annurev-ento-041420-075608

Gill, F.B. 2007: Ornithology. — W. H. Freeman and Company, New York.

Green, A.J. 2001: Mass/length residuals: measures of body condition or generators of spurious results? — Ecology 82: 1473–1483. https://doi.org/10.1890/0012-9658(2001)082[1473:MLRMOB]2.0.CO;2

Hamilton, W.D. & Zuk, M. 1982: Heritable true fitness and bright birds: a role for parasites? — Science 218: 384–387. https://doi.org/10.1126/science.7123238

Hamstra, T.L. & Badyaev, A.V. 2009: Comprehensive investigation of ectoparasite community and abundance across life history stages of avian host. — Journal of Zoology 278: 91–99. https://doi.org/10.1111/j.1469-7998.2008.00547.x

Ibram. 2025: Unidades de Conservação e Parques. https://www.ibram.df.gov.br/. Accessed 01 July 2025

Imlay, T.L., Steenweg, R.J., Garcia-Perez, B., Hobson, K.A. & Rohwer, S. 2017: Temporal and spatial patterns of flight and body feather molt of Bank, Barn, and Cliff swallows in North and South America. — Journal of Field Ornithology 88: 405–415. https://doi.org/10.1111/jofo.12235

Jahn, A.E., Bejarano, V., Guzmán, M.B., Brown, L.M., Provinciato, I.C., Cereghetti, J., Cueto, V.R., Giraldo, J.I., Gómez-Bahamón, V., Husak, M.S., LePage, H.K., MacPherson, M., Marini, M.A., Pizo, M.A., Quickle, A., Roeder, D.V., Sarasola, J.H. & Tuero, D.T. 2017: Molting while breeding? Lessons from New World *Tyrannus* flycatchers. — Journal of Ornithology 158: 1061–1072. https://doi.org/10.1007/s10336-017-1464-5

Jahn, A.E., Giraldo, J.I., MacPherson, M., Tuero, D.T., Sarasola, J.H., Cereghetti, J., Masson, D.A. & Morales, M.V. 2016: Demographic variation in timing and intensity of feather molt in migratory Fork-tailed Flycatchers (*Tyrannus s. savana*). — Journal of Field Ornithology 87: 143–154. https://doi.org/10.1111/jofo.12147

Jakob, E.M., Marshall, S.D. & Uetz, G.W. 1996: Estimating fitness: a comparison of body condition indices. — Oikos 77: 61–67. https://doi.org/10.2307/3545585

Jukema, J., Tulp, I. & Bruinzeel, L. 2003: Differential moult patterns in relation to antipredator behaviour during incubation in four tundra plovers. — Ibis 145: 270–276. https://doi.org/10.1046/j.1474-919X.2003.00147.x

Kettle, P.R. 1983: The seasonal incidence of parasitism by Phthiraptera on starlings (*Sturnus vulgaris*) in England. — New Zealand Entomologist 7: 403–408. https://doi.org/10.1080/00779962.1983.9722430

Kiat, Y. & Sapir, N. 2017: Age-dependent modulation of songbird summer feather molt by temporal and functional constraints. — The American Naturalist 189: 184–195. https://doi.org/10.1086/690031

Klopfer, P.H. 1959: Environmental determinants of faunal diversity. — The American Naturalist 93: 337–342. https://doi.org/10.1086/282092

Labocha, M.K. & Hayes, J.P. 2012: Morphometric indices of body condition in birds: a review. — Journal of Ornithology 153: 1–22. https://doi.org/10.1007/s10336-011-0706-1

Lamb, R.J. & Galloway, T.D. 2016: Seasonal population

dynamics of chewing lice (Phthiraptera: Amblycera and Ischnocera) infesting three species of woodpeckers (Aves: Piciformes: Picidae) in Manitoba, Canada. — The Canadian Entomologist 148: 683–692.

Landler, L., Ruxton, G.D. & Malkemper, E.P. 2018: Circular data in biology: advice for effectively implementing statistical procedures. — Behavioral Ecology and Sociobiology 72: 1–10. https://doi.org/10.1007/s00265-018-2538-y

Landler, L., Ruxton, G.D. & Malkemper, E.P. 2019: The Hermans–Rasson test as a powerful alternative to the Rayleigh test for circular statistics in biology. — BMC Ecology 19: 1–8. https://doi.org/10.1186/s12898-019-0246-8

Lind, J., Gustin, M. & Sorace, A. 2004: Compensatory bodily changes during moult in Tree Sparrows *Passer montanus* in Italy. — Ornis Fennica 81: 75–83.

Linkie, M. & Ridout, M.S. 2011: Assessing tiger–prey interactions in Sumatran rainforests. — Journal of Zoology 284: 224–229. https://doi.org/10.1111/j.1469-7998.2011.00801.x

Lyra-Neves, R.M., Farias, A.M. & Telino-Júnior, W.R. 2005: Interações entre Phthiraptera (Insecta) e aves (Emberizidae) de Mata Atlântica, Pernambuco, Brasil. — Revista Ornithologia 1: 43–47.

Magalhães, R.B., Diniz, P. & Macedo, R.H. 2014: Plumage coverage is related to body condition and ectoparasitism in blue-black grassquits. — The Wilson Journal of Ornithology 126: 581–584. https://doi.org/10.1676/13-197.1

Maia, R. & Macedo, R.H. 2011: Achieving luster: prenuptial molt pattern predicts iridescent structural coloration in blue-black grassquits. — Journal of Ornithology 152: 243–252. https://doi.org/10.1007/s10336-010-0576-y

Markov, G.C. 1940: Seasonal and annual variations in parasito-fauna of starlings in connection with changes in meteorological factors. — Zoologicheskii Zhurnal 19: 741–749.

Maron, M.W., Paprocki, N., Owen, J.P. & Conway, C.J. 2024: Differential effects of chewing lice on body condition across host age and sex in rough-legged hawks (*Buteo lagopus*). — Journal of Wildlife Diseases 60: 991–995. https://doi.org/10.7589/JWD-D-24-00013

Marshall, A.G. 1981: The ecology of ectoparasitic insects. — Academic Press, London.

Mazur, A.E., Remisiewicz, M. & Underhill, L.G. 2021: Sex-specific patterns of fuelling and pre-breeding body moult of little stints *Calidris minuta* in South Africa. — Ibis 163: 99–112. https://doi.org/10.1111/ibi.12840

McQueen, A., Delhey, K., Szecsenyi, B., Crino, O.L., Roast, M.J. & Peters, A. 2021: Physiological costs and age constraints of a sexual ornament: an experimental study in a wild bird. — Behavioral Ecology 32: 327–338. https://doi.org/10.1093/beheco/araa143

Merkle, M.S. & Barclay, R.M. 1996: Body mass variation in breeding mountain bluebirds *Sialia currucoides*: evidence of stress or adaptation for flight? — Journal of Animal Ecology 65: 401–413. https://doi.org/10.2307/5776

Møller, A.P., De Lope, F. & Saino, N. 2004: Parasitism, immunity, and arrival date in a migratory bird, the barn swallow. — Ecology 85: 206–219. https://doi.org/10.1890/02-0451

Moreno-Palacios, M., Losada-Prado, S. & Echeverry-Galvis, M.Á. 2013: Ciclos de reproducción y muda del Volatinero Negro (*Volatinia jacarina*) y el Semillero Gris (*Sporophila intermedia*) en un matorral secundario al norte del Tolima, Colombia. — Ornitología Neotropical 24: 421–431.

Moreno-Rueda, G. 2010: Experimental test of a trade-off between moult and immune response in house sparrows *Passer domesticus*. — Journal of Evolutionary Biology 23: 2229–2237. https://doi.org/10.1111/j.1420-9101.2010.02090.x

Moreno-Rueda, G. & Hoi, H. 2012: Female house sparrows prefer big males with a large white wing bar and fewer feather holes caused by chewing lice. — Behavioral Ecology 23: 271–277. https://doi.org/10.1093/beheco/arr182

Moyer, B.R., Gardiner, D.W. & Clayton, D.H. 2002: Impact of feather molt on ectoparasites: looks can be deceiving. — Oecologia 131: 203–210. https://doi.org/10.1007/s00442-002-0877-9

Munger, J.C. & Karasov, K.W. 1989: Sublethal parasites and host energy budgets: tapeworm infection and white-footed mice. — Ecology 70: 904–921.

Newton, I. 2007: Weather-related mass-mortality events in migrants. — Ibis 149: 453–467. https://doi.org/10.1111/j.1474-919X.2007.00704.x

Norris, D.R., Marra, P.P., Kyser, T.K., Sherry, T.W. & Ratcliffe, L.M. 2004: Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. — Proceedings of the Royal Society B 271: 59–64. https://doi.org/10.1098/

rspb.2003.2569

Norte, A.C., Lobato, D.N.C., Braga, E.M., Antonini, Y., Lacorte, G., Gonçalves. M, Lopes de Carvalho, I., Gern, L., Núncio, M.S. & Ramos, J.A. 2013: Do ticks and *Borrelia burgdorferi* s.l. constitute a burden to birds? — Parasitology Research 112: 1903–1912. https://doi.org/10.1007/s00436-013-3343-1

Nwaogu, C.J., Tieleman, B.I. & Cresswell, W. 2019: Weak breeding seasonality of a songbird in a seasonally arid tropical environment arises from individual flexibility and strongly seasonal moult. — Ibis 161: 533–545. https://doi.org/10.1111/ibi.12661

Oliveira, P.S. & Marquis RJ (eds). 2002: The cerrados of Brazil: ecology and natural history of a Neotropical savanna. — Columbia University Press.

Oteyza, J.C., Mouton, J.C. & Martin, T.E. 2021: Adult survival probability and body size affect parental risk-taking across latitudes. — Ecology Letters 24: 20–26. https://doi.org/10.1111/ele.13615

Penha, V.A.S. 2024: Sex, moulting dynamics, and reproductive status in Atlantic Forest tanagers and their collective impact on body condition. — Emu – Austral Ornithology 124: 177–186. https://doi.org/10.1080/01584197.2024.2328675

Pérez, J.M., Ruiz-Martínez, I. & Cooper, J.E. 1996: Occurrence of chewing lice on Spanish raptors. — Ardeola 43: 129–138.

Podlaszczuk, P., Wlodarczyk, R., Janiszewski, T., Kaczmarek, K. & Minias, P. 2017: When moult overlaps migration: moult-related changes in plasma biochemistry of migrating common snipe. — PeerJ 5: e3057. https://doi.org/10.7717/peerj.3057. eCollection 2017

Potti, J. & Merino, S. 1995: Louse loads of pied flycatchers: effects of host's sex, age, condition and relatedness. — Journal of Avian Biology 26: 203–208. https://doi.org/10.2307/3677320

Prelezov, P.N., Groseva, N.I. & Goudaheva, D.I. 2006: Pathomorphological changes in the tissues of chickens experimentally infected with biting lice (Insecta: Phthiraptera). — Veterinarski Archiv 76: 207–215.

Price, M.A. & Graham, O.H. 1997: Chewing and sucking lice as parasites of mammals and birds. — US Department of Agriculture, Technical Bulletin No. 849.

Pyle, P. 2022: Defining moults in migratory birds: a sequence-based approach. — Journal of Avian Biology 2022: e02958. https://doi.org/10.1111/jav.02958

R Core Team. 2024: R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ramos, D.M., Diniz, P., Ooi, M.K., Borghetti, F. & Valls, J.F. 2017: Avoiding the dry season: dispersal time and syndrome mediate seed dormancy in grasses in Neotropical savanna and wet grasslands. — Journal of Vegetation Science 28: 798–807. https://doi.org/10.1111/jvs.12531

Renfrew, R.B., Frey, S.J. & Klavins, J. 2011: Phenology and sequence of the complete prealternate molt of Bobolinks in South America. — Journal of Field Ornithology 82: 101–113. https://doi.org/10.1111/j.1557-9263.2010.00312.x

Ridout, M.S. & Linkie, M. 2009: Estimating overlap of daily activity patterns from camera trap data. — Journal of Agricultural, Biological, and Environmental Statistics 14: 322–337. https://doi.org/10.1198/jabes.2009.08038

Rising, J.D. 2020: Blue-black Grassquit (*Volatinia jacarina*), version 1.0. — In Birds of the World (eds. J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana). — Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.blbgra1.01

Rowcliffe, M. 2023: activity: Animal Activity Statistics. R package version 1.3.4. https://CRAN.R-project.org/package=activity

Rózsa, L. 1997: Patterns in the abundance of avian lice (Phthiraptera: Amblycera, Ischnocera). — Journal of Avian Biology 28: 249–254.

Schaub, M. & Jenni, L. 2000: Body mass of six long-distance migrant passerine species along the autumn migration route. — Journal für Ornithologie 141: 441–460. https://doi.org/10.1046/j.1439-0361.2000.00037.x

Schieltz, P.C. & Murphy, M.E. 1997: The contribution of insulation changes to the energy cost of avian molt. — Canadian Journal of Zoology 75: 396–400. https://doi.org/10.1139/z97-049

Schreiter, R., Herzog, M. & Freick, M. 2022: Effects of the poultry red mite (*Dermanyssus gallinae*) load on the plumage condition in commercial laying hen farms. — PLoS One 17: e0277513. https://doi.org/10.1371/journal.pone.0277513

Schulte-Hostedde, A.I., Zinner, B., Millar, J.S. & Hickling, G.J. 2005: Restitution of mass–size residuals: validating body condition indices. — Ecology 86: 155–163. https://doi.org/10.1890/04-0232

Sick, H. 1997: Ornitologia brasileira. — Nova Fronteira,

Rio de Janeiro.

Simon, A., Thomas, D., Blondel, J., Perret, P. & Lambrechts, M.M. 2004: Physiological ecology of Mediterranean blue tits (*Parus caeruleus* L.): effects of ectoparasites (*Protocalliphora* spp.) and food abundance on metabolic capacity of nestlings. — Physiological and Biochemical Zoology 77: 492–501. https://doi.org/10.1086/383512

Strong, A.M. & Sherry, T.W. 2001: Body condition of Swainson's warblers wintering in Jamaica and the conservation value of Caribbean dry forests. — The Wilson Bulletin 113: 410–418.

Surmacki, A., Liu, M., Mercadante, A. & Hill, G.E. 2011: Effect of feather abrasion on structural coloration in male eastern bluebirds *Sialia sialis*. — Journal of Avian Biology 42: 514–521. https://doi.org/10.1111/j.1600-048X.2011.05503.x

Tomotani, B.M. & Muijres, F.T. 2019: A songbird compensates for wing molt during escape flights by reducing the molt gap and increasing angle of attack. — Journal of Experimental Biology 222: jeb195396. https://doi.org/10.1242/jeb.195396

Valdez, D.J. & Benitez-Vieyra, S.M. 2023: Annual molt period and seasonal color variation in the Eared Dove's crown. — PLoS One 18: e0280819. https://doi.org/10.1371/journal.pone.0280819

Venables, W.N. & Ripley, B.D. 2002: Modern applied statistics with S. 4th edn. — Springer, New York. https://www.stats.ox.ac.uk/pub/MASS4/

Ward, G.M., Mahoney, S.M., Joly, S. & Reudink, M.W. 2021: Effects of age and weather during moult on mountain bluebird *Sialia currucoides* structural colouration. — Journal of Avian Biology 52: e02524. https://doi.org/10.1111/jav.02616

Wikelski, M., Tarlow, E.M., Raim, A., Diehl, R.H., Larkin, R.P. & Visser, G.H. 2003: Costs of migration in free-flying songbirds. — Nature 423: 704–704. https://doi.org/10.1038/423704a

Wright, J.R., Tonra, C.M. & Powell, L.L. 2018: Prealternate molt-migration in rusty blackbirds and its implications for stopover biology. — The Condor 120: 507–516. https://doi.org/10.1650/CONDOR-17-177.1

Xavier, R.O., Christianini, A.V., Pegler, G., Leite, M.B. & Silva-Matos, D.M. 2021: Distinctive seed dispersal and seed bank patterns of invasive African grasses favour their invasion in a Neotropical savanna. — Oecologia 196: 155–169. https://doi.org/10.1007/s00442-021-04904-z

Zeringóta, V., Maturano, R., Santolin, Í.D.A.C., McIntosh, D., Famadas, K.M., Daemon, E. & Faccini, J.L.H. 2016: New host records of *Haemaphysalis leporispalustris* (Acari: Ixodidae) on birds in Brazil. — Parasitology Research 115: 2107–2110. https://doi.org/10.1007/s00436-016-4978-5

Online supplementary material

Supplementary material available in the online version of the article includes Tables S1–S2.