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Short communication

Grooming time parallels molt intensity in wild-caught feral rock pigeons

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Feathers are critical for locomotion, communication, thermoregulation, waterproofing, and protection from UV radiation. To maintain these functions, birds care for their feathers by grooming, which consists of preening with the bill and scratching with the feet. Grooming cleans and arranges feathers, distributes preen oil and powder down, and removes ectoparasites. Birds devote considerable time and energy to grooming, to the exclusion of other activities, such as foraging. All else being equal, birds should aim to minimize their grooming time. Seasonal changes in grooming have been documented, with some species of birds grooming more in summer than winter. The higher rate of summer grooming may be caused by molt; however, the relationship between the dynamics of grooming and molt have been quantified only in captive birds subject to other manipulation, such as induced molt in poultry, or access to mates in zebra finches. We conducted an eight-month study of wild-caught feral rock pigeons *Columba livia* to compare rates of grooming and molt. We found that the intensity of grooming parallels the intensity of molt throughout the molt cycle. Pigeons more than double their grooming time at peak molt, consistent with patterns observed in wild birds. Our results suggest that molt may be more energetically costly than previously realized, given concomitant increases in grooming.

Keywords: behavior, captive, *Columba livia*, feather maintenance, preening, scratching

Introduction

Feathers have a variety of functions, such as locomotion, communication, thermoregulation, waterproofing, and protection from UV radiation (Terrill and Shultz 2023). Over time, feathers are damaged from abrasion, parasitic arthropods, feather-degrading microbes, and exposure to UV radiation (Jenni and Winkler 2020). Feathers must be cared for, or 'maintained', to function effectively (Payne 1972, Merilä and Hemborg 2000). Avian grooming, which consists of preening with the bill and scratching with the feet, is the most common way in which birds maintain their plumage (Cotgreave

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and Clayton 1994). Grooming cleans and arranges feathers, 'zips' barbules of flight feathers back together, distributes preen oil and powder down, and combats ectoparasites (Bush and Clayton 2018).

While necessary, grooming requires time and energy that cannot be devoted to other activities. Most species of birds spend 5–15% of their time grooming, with an energetic cost that is 1.2–2.3 times basal metabolic rate (Goldstein 1988, Croll and McLaren 1993, Cornelius et al. 2011, Viblanc et al. 2011). Grooming also reduces vigilance, which may lead to increased predation and territorial encroachment by conspecifics (Redpath 1988, Beauchamp and Ruxton 2003, Randler 2005). These potential tradeoffs beg the question: how much time should birds devote to grooming? Given the costs associated with grooming, birds should minimize grooming time, all else being equal. However, grooming time is not constant; it varies with factors such as ectoparasite load (Villa et al. 2016), season (Bush et al. 2023) and, perhaps, molt.

Bush et al. (2023) reported that wild American kestrels *Falco sparverius* groom significantly more in summer than winter. Similarly, Verbeek (1972) noted that yellow-billed magpies *Pica nuttalli* groom more in summer than other seasons. The authors of both studies suggested that the higher rate of grooming in summer may be associated with feather molt; however, a comparative analysis of grooming behavior of wild birds found that, among the nine species with available seasonal data, six spent more time grooming in the winter than summer (Cotgreave and Clayton 1994).

Studies of captive birds suggest that grooming increases with molt. For example, laying hens *Gallus gallus* in which molt was artificially induced (Webster 2000, Dunkley et al. 2008) preened substantially more as their new feathers grew. Similarly, Portugal et al. (2007) found that captive barnacle geese *Branta leucopis* nearly doubled their investment in maintenance behavior during the flightless period of their primary molt, although the increase in maintenance behavior may have been influenced by a concomitant decrease in locomotor activity.

A simple explanation for the increase in grooming observed in molting birds is that it helps relieve itching caused by growing new feathers. Grooming also appears to mechanically facilitate the unsheathing of new feathers (Maderson et al. 2009). Given these functions, grooming intensity should parallel molt intensity. However, no study of the dynamics of grooming behavior over the course of a natural molt cycle has been conducted to our knowledge. Here, we quantify how grooming time in captive rock pigeons *Columba livia* changes while birds are molting.

Material and methods

We captured 30 feral rock pigeons with walk-in traps placed on rooftops in Salt Lake City. The birds were housed individually in wire mesh cages (30 × 30 × 56 cm) and provided ad libitum grain (IFA pigeon mix), grit, and water. Handling and housing of birds was performed in accordance with our Institutional Animal Care and Use Committee and Fair et al. (2023).

Feather lice and other ectoparasites can cause increases in grooming in captive pigeons (Waite et al. 2012, Villa et al. 2016). Before we began observations of molt and behavior, we eradicated any naturally occurring lice by housing the birds in low-humidity conditions (< 25% relative humidity) for three months, which kills all lice and their eggs by desiccation (Harbison et al. 2008, Villa et. al. 2016). Following this period, the absence of lice and other ectoparasites was confirmed with the visual examination method described by Clayton and Drown (2001). Birds were subsequently maintained at room temperature and > 40% relative humidity for the remainder of the study. We monitored the molt and behavior of birds from April to November 2023.

Molt

Molt is controlled by an endogenous circannual rhythm that is triggered by seasonal changes in photoperiod (Jenni and Winkler 2020). Our birds were exposed to natural changes in photoperiod via windows in our roof-top animal facility. Light from the windows was supplemented with artificial lights on a 12-h photoperiod (07:00–19:00 h). Birds in our study molted on an annual cycle typical of feral pigeons, in which molt occurs between May and October (Johnston and Janiga 1995, Lowther and Johnston 2020).

We quantified molt by examining each bird's plumage six times over the eight-month study. In rock pigeons, molt begins with the loss of the innermost primary 'p1'; additional primary feathers are then replaced in sequence until the most distal primary 'p10' is dropped (Johnston and Janiga 1995, Lowther and Johnston 2020). Molt of the other flight feathers occurs during this time; secondaries and tail feathers typically begin molting about halfway through primary molt (Johnston and Janiga 1995). We tracked the timing of flight feather molt by recording any newly dropped or emerging primary feathers during each examination.

Like secondaries and tail feathers, core body feathers also molt during the latter half of primary feather molt (Johnston and Janiga 1995). Unlike the synchronous molt of some birds, which lose all (or nearly all) of their feathers in a particular region at the same time, body molt in pigeons is quite gradual. Consequently, we tracked the intensity of body molt by recording the number of body regions that were molting each month. We examined eight major body regions: crown, nape, back, rump, neck/breast, keel, flank, and vent (Fig. 1). We considered a given region to be molting if approximately 10% or more of the feathers in that region were emerging pinfeathers.

All birds were examined the same day and given at least 24 h to acclimate from handling before any grooming data were collected. The study was concluded at the end of November when very few new pinfeathers were observed on any region of the body.

Behavior

The relative frequencies of five common behaviors were estimated by 'instantaneous scan sampling', a standard

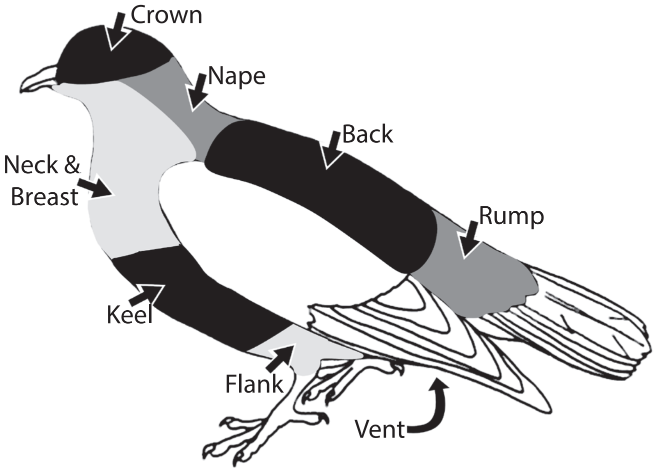

Figure 1. Eight body regions visually examined for molt. Redrawn from Booth et al. (1993).

methodology for quantifying behavior (Altmann 1974, Lehner 1992). Briefly, the method involves recording which of several mutually exclusive behaviors is occurring during each of many instantaneous observations of less than one second in duration each. This sampling design allows the exact calculation of the relative amount of time that individuals spend performing each behavior. The method does not require continuous observation (i.e. focal sampling) of each individual; indeed, it is the method of choice for the simultaneous collection of behavioral data from many individuals (Altmann 1974). Using this method, we recorded when birds were preening, scratching, feeding/drinking, engaged in other movement (e.g. walking or flapping), or motionless (e.g. standing or sitting). Preening was defined as touching the plumage with the bill; scratching was defined as touching the plumage with a foot (Clayton and Cotgreave 1994, Goodman et al. 2020). Behaviors were recorded using the Animal Behaviour Pro ver. 1.6 app for iPhone (Newton-Fisher 2021, van der Marel et al. 2021).

Over the course of the study, behavioral data were collected during six observation periods, each lasting four weeks. An observation period included 12 scan sampling sessions, which were divided about equally between morning (07:00–12:00 h) and afternoon (12:00–19:00 h). Each session began with a 15-min acclimation period during which the observer sat motionless within full view of all birds. After this acclimation period, birds were observed sequentially, with the behavior of a different bird being noted every 10 s. Each bird was observed roughly 25 times per session.

At the end of the study, all birds were euthanized, and the sex of each bird was determined by necropsy and visual examination of the gonads. Each bird was also re-examined for ectoparasites using the post mortem ruffling procedure described by Clayton and Drown (2001), which is more thorough than visual examination of live birds. Three birds were found to be infested with lice during this examination (1–11 lice were recovered from each of these birds). The three birds were excluded from the analyses. In addition, two birds died of natural causes before the study ended. Thus, the final sample size for analysis was 25 birds, 16 of which were male and 9 were female.

Data analysis

We determined the amount of time each bird spent grooming by dividing the number of grooming observations (preening and scratching) by the total number of observations for that bird during each four-week observation period. The intensity of body molt was scored at the end of each of the six observation periods. Although molt was only measured once per observation period, pigeons molt their body feathers slowly; consequently, this strategy allowed us to accurately assess molt status for the period in which behavior was observed.

We used three linear mixed-effects models (LMM) to analyze the relationship between body molt and grooming using maximum likelihood methods (Murphy et al. 2022). We included bird ID as a random intercept in both models to account for the non-independence of behavioral observations taken from the same individual over time. The null model predicted grooming time by individual bird ID and did not account for molt. The molt model predicted grooming time as a function of body molt intensity and individual bird ID. The sex model predicted grooming time as a function of body molt intensity, sex, the interaction between sex and body molt intensity, and individual bird ID. Akaike information criterion (AICc) scores were used to evaluate model fit. The best model was determined to be the one with the lowest corrected AICc score (Burnham and Anderson 2002). To determine if molt or sex significantly improved model fit, we performed likelihood ratio tests (LRT) between our null molt and sex models (Magezi 2015). All analyses were conducted in R (ver. 4.4.0, www.r-project.org) using the 'nlme' and 'MuMln' packages (Pinheiro et al. 2024 (ver. 3.1-166), Bartoń 2025 (ver. 1.48.11)). In addition, we used a two-way ANOVA to test for a difference in the timing and intensity of molt between sexes. The ANOVA predicted molt intensity by sex, observation period, and the interaction between sex and observation period.

Results

Molt

On average, birds molted their first primary feather (mean ± SE) on 29 July (± 5.3 days) and their last primary on 21 November (± 3.7 days) (Fig. 2a, Supporting information). The number of body regions that were molting varied over time (Fig. 2b). The intensity of body molt (mean number of body regions molting ± SE) increased dramatically from April (0.88 ± 0.09) to its peak in early September (4.68 ± 0.41), followed by a sharp decrease in November. There was no significant difference between male and female birds in the timing ($p = 0.82$) or intensity of molt ($p = 0.71$).

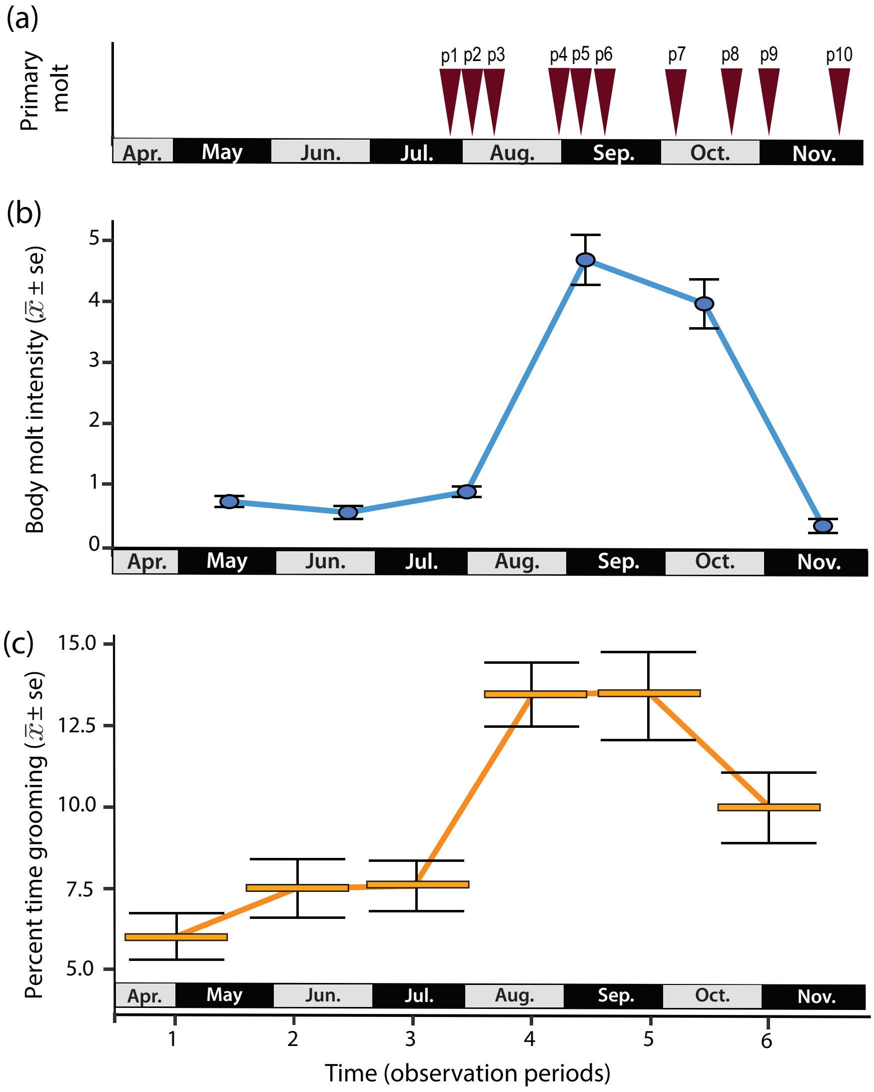

Figure 2. Timing of molt in relation to the grooming behavior of rock pigeons (n = 25). (a) Mean date that each of the 10 primary feathers (p1 to p10) had dropped or had begun emerging (n = 25 birds). (b) Number of body regions molting ('molt intensity'). Molt intensity was noted at the end of each 4-week observation period. (c) Time spent grooming during each four-week observation period. Body molt intensity is significantly correlated with percent time spent grooming (linear mixed-effects models, LMM, $p < 0.001$).

Behavior

Over the course of the study, we observed each bird at least 2600 times, with a mean (± SE) of 310 ± 3.27 observations per bird during each of the six observation periods. The percent of time birds spent grooming varied dramatically over the course of the study (Fig. 2c). In late April to early May, before the onset of molt, birds spent a mean (± SE) of 6.10 ± 0.71% of their time grooming. Birds groomed the most from August to early October (13.52 ± 0.98%, and 13.67 ± 1.35% for observation periods 4 and 5, respectively; Fig. 2c).

Grooming time was best predicted by the model that included molt intensity as a fixed effect (ΔAICc = 36.5, LMM, $p < 0.001$, Table 1). The addition of molt intensity as a fixed effect significantly improved model fit (LRT, $X^2_1 = 38.7$, $p < 0.001$), indicating that grooming time is significantly correlated with molt. Neither sex, nor the interaction between sex

Table 1. Maximum likelihood parameter estimates (± SE) of linear mixed models investigating the relationship between body molt, bird ID, and grooming (*p < 0.001).

Model	Intercept	Body molt intensity	Sex	Interaction of sex and body molt intensity	Bird ID (σ of intercept)	AICc
Null	9.77 ± 0.78*	–	–	–	3.41	918.8
Molt	7.81 ± 0.83*	1.05 ± 0.15*	–	–	3.55	882.3
Sex	6.30 ± 1.36*	1.18 ± 0.23*	2.37 ± 1.70	−0.11 ± 0.31	3.48	882.4

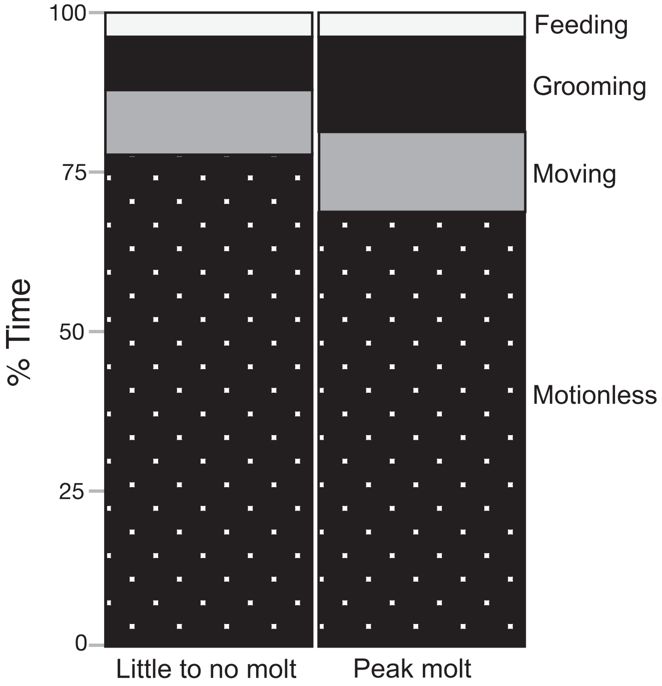

Figure 3. Pigeon behavior in observation periods with little to no molt (periods 1, 2, 3, and 6) compared to observation periods during peak molt (periods 4 and 5). The percent time birds allocated to each behavior differed significantly with molting status ($n=46\,522$ observations, $X^2_3=594.4$, $p < 0.0001$; Supporting information). During peak molt, the increased time spent grooming was associated with a concomitant decrease in the time birds spent motionless.

and molt intensity, predicted grooming time ($p > 0.05$, Table 1). Nor did the sex model significantly improve model fit compared to the molt model (LRT, $X^2_1=4.208$, $p=0.12$). The increase in grooming time during peak molt (observation periods 4 and 5) was offset by a significant decrease in the amount of time birds were motionless (Fig. 3).

Discussion

Prior studies have suggested that grooming behavior increases during molt (Verbeek 1972, Delius 1988, Portugal et al. 2007, Bush et al. 2023). It is assumed that this is driven by itching, or that grooming facilitates the unsheathing of new pin feathers. To our knowledge, however, no study has quantified grooming dynamics over the course of a natural molt cycle for any species of bird. We therefore investigated the relationship between molt and grooming behavior in wild-caught rock pigeons over an eight-month period.

In our study, pigeons molted their primary feathers between July and November, and the body molt was most intense in September and October, decreasing into November (Fig. 2b). This pattern is consistent with the timing of molt observed in free-ranging rock pigeons (Johnston and Janiga 1995). Molt timing and intensity did not differ between the sexes. Sex-based differences in molt have been documented in other species of birds, particularly when there is unequal investment in reproduction (Siikamäki et al. 1994, Svensson and Nilsson 1997, Serra et al. 2010, Gow and Stutchbury 2013). In contrast, among pigeons and doves, both parents incubate and feed the young. The prolonged molt typical of columbiform species is thought to facilitate this overlap between molt and reproduction (Cornelius et al. 2011, Braun et al. 2015, Rohwer and Rohwer 2018).

Overall, the birds in our study spent 9.8% of their time grooming, most of which was preening (98.8%), with the remainder scratching (1.2%). Another study of 12 bird species found that the grooming times of wild and captive individuals were highly correlated, with captive birds grooming about twice as much as their wild counterparts, presumably because captive birds have ad libitum food and are released from competition, predation, and other natural pressures (Walther and Clayton 2005). Birds in our study actually groomed somewhat less than their wild counterparts: a study of wild feral rock pigeons in Singapore reported that they spent 14–16% of their time preening (Soh et al. 2021). It is possible that the captive birds in our study groomed less than the wild birds in the study by Soh et al. because our birds were cleared of ectoparasites. By comparison, birds in a study of captive feral rock pigeons infested with lice preened 19.5% of the time (Villa et al. 2016). The infection status of birds in the Soh et al. (2021) study was unknown.

The amount of time the pigeons in our study groomed is broadly similar to the amount of time other bird species spend grooming. In a comparative analysis of the grooming behavior of 62 species of birds, Cotgreave and Clayton (1994) found that most species ($n=37$) devoted between 5 and 15% of their time to maintenance behaviors, most of which is preening. The molt status of individual birds included in Cotgreave and Clayton's (1994) review was unknown.

In our study, birds groomed the least in April (6.1%), before molt began (Fig. 2). During molt, birds more than doubled the amount of time spent grooming. Birds groomed the most from August to early October (13.5–13.7%), when molt was most intense (Fig. 2). As the intensity of body molt decreased from late October to November, grooming time also decreased (Fig. 2). Over the course of the study, grooming time was significantly correlated with molt intensity (Table 1). Neither sex nor the interaction between sex and molt predicted grooming time. This is not surprising, as there was no significant difference in timing of molt between the sexes.

Bush et al. (2023) hypothesized that seasonal changes in the grooming time of wild American kestrels were caused by molt; our results are consistent with this hypothesis. Bush et al. (2023) noted a 2.5-fold increase in the summer grooming of American kestrels in the Bahamas, and a 3.6-fold increase in the summer grooming of kestrels in Utah. Similarly, Verbeek (1972) noted a 3.5-fold increase in the summer grooming of yellow-billed magpies in California. Both yellow-billed magpies and American kestrels molt their plumage quickly, whereas rock pigeons experience a protracted molt (Lowther and Johnston 2020, Smallwood and

Bird 2020, Koenig et al. 2022). Cotgreave and Clayton (1994) found no correlation between molt duration (number of days per year that a given species of bird spends in molt) and mean grooming time across 37 bird species, but they suggested that grooming might vary with molt strategy. Specifically, they suggested that birds with short, intense molt patterns (e.g. perching birds and raptors) may have brief, intense spikes in time devoted to grooming, while birds with slow, less intense molts (e.g. pigeons and doves) may increase grooming only a little, but for a longer period of time. Our observation that the increase in grooming time of pigeons during peak molt is less than what was noted in American kestrels (Bush et al. 2023) and yellow-billed magpies (Verbeek 1972) is consistent with this hypothesis; however, more research is needed to better understand the relationship between variation in molt strategy and grooming behavior among birds of the world.

Molt is a physiologically demanding process that can be energetically costly (Cornelius et al. 2011, Jenni and Winkler 2020). Molting European starlings *Sturnus vulgaris*, for example, expend 32% more energy than non-molting starlings (Cyr et al. 2008). These costs may be why molt is often offset from other demanding activities, such as reproduction and migration (Holmgren and Hedenström 1995, Hemborg and Lundberg 1998, Pageau et al. 2020). Indeed, a study of molt in zebra finches *Taeniopygia guttata* found that non-breeding individuals molted faster than breeding birds (Echeverry-Galvis and Hau 2012). The energetic demands of molt may also contribute to the tendency of birds to be quiescent during feather replacement (Ben-Hamo et al. 2016), but see Mumme et al. (2021) and Hedenström (2023), who suggest that reduced flight performance during molt contributes to a reduction in activity. Given that other studies have shown that grooming behaviors elevate metabolic rate (Goldstein 1988, Croll and McLaren 1993, Cornelius et al. 2011, Viblanc et al. 2011), our data suggest that molt may be more costly than previously thought. In conclusion, we suggest that future studies estimating the cost of molt should consider the potential energetic cost of increased grooming, in addition to the physiological costs of producing new feathers.

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Permits – The work was performed in accordance with University of Utah Institutional Animal Care and Use Committee protocol no. 20-09012, and according to standard guidelines for the use of wild birds in research (Fair et al. 2023).

Author contributions

Parker E. Guzman: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Nicole A. Amedee**: Investigation (equal); Writing – review and editing (equal). **Hannah M. Warr**: Investigation (equal); Writing – review and editing (equal). **Ruby J. Linnell**: Investigation (equal); Writing – review and editing (equal). **Matthew M. Waller**: Formal analysis (equal); Writing – review and editing (equal). **Dale H. Clayton**: Conceptualization (equal); Funding acquisition (equal); Project administration (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Sarah E. Bush**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.73n5tb38g (Guzman et al. 2025).

References

Altmann, J. 1974. Observational study of behavior: sampling methods. – Behav. 49: 227–267.

Bartoń, K. 2025. Mumin: multi-model inference. – R package ver. 1.48.11, https://CRAN.R-project.org/package=MuMIn.

Beauchamp, G. and Ruxton, G. D. 2003. Changes in vigilance with group size under scramble competition. – Am. Nat. 161: 672–675.

Ben-Hamo, M., Burns, D. J., Bauchinger, U., Mukherjee, S., Embar, K. and Pinshow, B. 2016. Behavioural responses during feather replacement in house sparrows. – J. Avian Biol. 47: 103–108.

Booth, D. T., Clayton, D. H. and Block, B. A. 1993. Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. – Proc. R. Soc. B 253: 125–129.

Braun, C. E., Tomlinson, R. E. and Wann, G. T. 2015. Seasonal dynamics of mourning dove (*Zenaida macroura*) body mass and primary molt. – Wilson J. Ornithol. 127: 630–638.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multi-model inference: a practical information-theoretic approach. – Springer.

Bush, S. E. and Clayton, D. H. 2018. Anti-parasite behaviour of birds. – Philos. Trans. R. Soc. B 373: 20170196.

Bush, S. E., Waller, M. M., Herman, J. M., Hobbs, K. S., Clayton, A. R., Watson, J. L., Oleyar, M. D. and Clayton, D. H. 2023. Birds groom more in regions with higher parasite pressure: a comparison of temperate and subtropical American kestrels. – Anim. Behav. 201: 125–135.

Clayton, D. H. and Cotgreave, P. 1994. Relationship of bill morphology to grooming behavior in birds. – Anim. Behav. 47: 195–201.

Clayton, D. H. and Drown, D. M. 2001. Critical evaluation of five methods for quantifying chewing lice (Insecta: Phthiraptera). – J. Parasitol. 87: 1291–1300.

Cornelius, J. M., Perfito, N., Zann, R., Breuner, C. W. and Hahn, T. P. 2011. Physiological trade-offs in self-maintenance: plumage molt and stress physiology in birds. – J. Exp. Biol. 214: 2768–2777.

Cotgreave, P. and Clayton, D. H. 1994. Comparative analysis of time spent grooming by birds in relation to parasite load. – Behaviour 131: 171–187.

Croll, D. A. and McLaren, E. 1993. Diving metabolism and thermoregulation in common and thick-billed murres. – J. Comp. Physiol. B 163: 160–166.

Cyr, N. E., Wikelski, M. and Romero, L. M. 2008. Increased energy expenditure but decreased stress responsiveness during molt. – Physiol. Biochem. Zool. 81: 452–462.

Delius, J. 1988. Preening and associated comfort behavior in birds. – Ann. N. Y. Acad. Sci. 525: 40–55.

Dunkley, C. S., Friend, T. H., McReynolds, J. L., Kim, W. K., Dunkley, K. D. , Kubena, L. F., Nisbet, D. J. and Ricke, S. C. 2008. Behavior of laying hens on alfalfa crumble molt diets. – Poult. Sci. 87: 815–822.

Echeverry-Galvis, M. A. and Hau, M. 2012. Molt-breeding overlap alters molt dynamics and behavior in zebra finches, *Taeniopygia guttata castanotis*. – J. Exp. Biol. 215:1957–1964.

Fair, J., Paul, E., Jones, J. and Bies, L. (eds) 2023. Guidelines to the use of wild birds in research. – Ornithological Council.

Goldstein, D. L. 1988. Estimates of daily energy expenditure in birds: the time–energy budget as an integrator of laboratory and field studies. – Am. Zool. 28: 829–844.

Goodman, G. B., Klingensmith, M. C., Bush, S. E. and Clayton, D. H. 2020. The role of scratching in the control of ectoparasites on birds. – Auk Ornith. Adv. 137: 1–9.

Gow, E. A. and Stutchbury, B. J. 2013. Understanding sex differences in parental effort in a migratory songbird: examining a sex-specific trade-off between reproduction and molt. – Condor 115: 640–649.

Guzman, P. E., Amedee, N., Warr, H. M., Linnell, R., Waller, M. M., Clayton, D. H. and Bush, S. E. 2025. Data from: Grooming time parallels molt intensity in wild-caught feral rock pigeons. – Dryad Digital Repository, https://doi.org/10.5061/dryad.73n5tb38g.

Harbison, C. W., Bush, S. E., Malenke, J. R. and Clayton, D. H. 2008. Comparative transmission dynamics of competing parasite species. – Ecology 89: 3186–3194.

Hedenström, A. 2023. Effects of wing damage and moult gaps on vertebrate flight performance. – J. Exp. Biol. 226: jeb227355.

Hemborg, C. and Lundberg, A. 1998. Costs of overlapping reproduction and moult in passerine birds: an experiment with the pied flycatcher. – Behav. Ecol. Sociobiol. 43: 19–23.

Holmgren, N. and Hedenström, A. 1995. The scheduling of molt in migratory birds. – Evol. Ecol. 9: 354–368.

Jenni, L. and Winkler, R. 2020. The biology of moult in birds. – Bloomsbury Publishing.

Johnston, R. F. and Janiga, M. 1995. Feral pigeons. – Oxford Univ. Press.

Koenig, W. D., Reynolds, M. D. and Airola, D. A. 2022. Yellow-billed magpie (*Pica nuttalli*), ver. 2.0. – In: Kirwan, G. M. and Keeney, B. K. (eds), Birds of the world. Cornell Lab of Ornithology, https://doi.org/10.2173/bow.yebmag.02.

Lehner, P. N. 1992. Sampling methods in behavior research. – Poult. Sci. 71: 643–649.

Lowther, P. E. and Johnston, R. F. 2020. Rock pigeon (*Columba livia*), ver. 1.0. – In: Billerman, S. M. (ed.), Birds of the world. Cornell Lab of Ornithology, https://doi.org/10.2173/bow.rocpig.01.

Maderson, P. F. A., Hillenius, W. J., Hiller, U. and Dove, C. C. 2009. Towards a comprehensive model of feather regeneration. – J. Morphol. 270: 1166–1208.

Magezi, D. A. 2015. Linear mixed-effects models for within-participant psychology experiments: an introductory tutorial and free, graphical user interface (LMMgui). – Front. Psychol. 6: 2.

Merilä, J. and Hemborg, C. 2000. Fitness and feather wear in collared flycatcher (*Ficedula albicollis*). – J. Avian Biol. 31: 504–510.

Mumme, R. L., Mulvihill, R. S. and Norman, D. 2021. High-intensity flight feather molt and comparative molt ecology of warblers of eastern North America. – Ornithol. 138: 1–16.

Murphy, J. I., Weaver, N. E. and Hendricks, A. E. 2022. Accessible analysis of longitudinal data with linear mixed effects models. – Dis. Model. Mech. 15: dmm048025.

Newton-Fisher, N. E. 2021. Animal behaviour pro mobile app, ver. 1.6. – https://apps.apple.com/us/app/animal-behaviour-pro/id579588319.

Pageau, C., Tonra, C. M., Shaikh, M., Flood, N. J. and Reudink, M. W. 2020. Evolution of moult-migration is directly linked to aridity of the breeding grounds in North American passerines. – Biol. Lett. 16: 20200155.

Payne, R. 1972. Mechanisms and control of molt. – In: Farmer, D. S. and King, J. R. (eds), Avian biology, vol. II. Academic Press, pp. 103–155.

Pinheiro, J., Bates, D. and R Core Team 2024. *nlme*: linear and nonlinear mixed effects models. – R package ver. 3.1-166, https://cran.r-project.org/web/packages/nlme/nlme.pdf.

Portugal, S. J., Green, J. A. and Butler, P. J. 2007. Annual changes in body mass and resting metabolism in captive barnacle geese (*Branta leucopsis*): the importance of wing moult. – J. Exp. Biol. 210: 1391–1397.

Randler, C. 2005. Coots *Fulica atra* reduce their vigilance under increased competition. – Behav. Proc. 68: 173–178.

Redpath, S. 1988. Vigilance levels in preening dunlin *Calidris alpina*. – Ibis 130: 555–557.

Rohwer, S. and Rohwer, V. G. 2018. Breeding and multiple waves of primary molt in common ground doves of coastal Sinaloa. – PeerJ 6: e4243.

Serra, L., Pirrello, S., Licheri, D., Griggio, M. and Pilastro, A. 2010. Sex-dependent response of primary moult to simulated time constraints in the rock sparrow *Petronia petronia*. – J. Avian Biol. 41: 327–335.

Siikamäki, P., Hovi, M. and Rätti, O. 1994. A trade-off between current reproduction and moult in the pied flycatcher – an experiment. – Funct. Ecol. 8: 587–593.

Smallwood, J. A. and Bird, D. M. 2020. American kestrel (*Falco sparverius*), ver. 1.0. – In: Poole, A. F. and Gill, F. B. (eds), Birds of the world. Cornell Lab of Ornithology, https://doi.org/10.2173/bow.amekes.01.

Soh, M. C., Pang, R. Y., Ng, B. X., Lee, B. P. H., Loo, A. H. and Er, K. B. 2021. Restricted human activities shift the foraging strategies of feral pigeons (*Columba livia*) and three other commensal bird species. – Biol. Conserv. 253: 108927.

Svensson, E. and Nilsson, J. A. 1997. The trade-off between molt and parental care: a sexual conflict in the blue tit? – Behav. Ecol. 8: 92–98.

Terrill, R. S. and Shultz, A. J. 2023. Feather function and the evolution of birds. – Biol. Rev. 98: 540–566.

van der Marel, A., O'Connell, C. L., Prasher, S., Carminito, F., C. X. and Hobson, E. A. 2021. A comparison of low-cost behavioral observation software applications for handheld computers and recommendations for use. – Ethol. 128: 275–284.

Verbeek, N. A. M. 1972. Daily and annual time budget of the yellow-billed magpie. – Auk 89: 567–582.

Viblanc, V. A., Mathien, A., Saraux, C., Viera, V. M. and Groscolas, R. 2011. It costs to be clean and fit: energetics of comfort behavior in breeding-fasting penguins. – PLoS One 6: e21110.

Villa, S. M., Campbell, H. E., Bush, S. E. and Clayton, D. H. 2016. Does antiparasite behavior improve with experience? An experimental test of the priming hypothesis. – Behav. Ecol. 27: 1167–1171.

Waite, J. L., Henry, A. R. and Clayton, D. H. 2012. How effective is preening for controlling mobile ectoparasites? An experimental test with pigeons and hippoboscid flies. – Int. J. Parasitol. 42: 463–467.

Walther, B. A. and Clayton, D. H. 2005. Elaborate ornaments are costly to maintain: evidence for high maintenance handicaps. – Behav. Ecol. 16: 89–95.

Webster, A. B. 2000. Behavior of white leghorn laying hens after withdrawal of feed. – Poult. Sci. 79: 192–200.