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Feather growth rate and hormone deposition vary with elevation but not reproductive costs in resident Mountain Chickadees

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ABSTRACT

Many organisms engage in metabolic tradeoffs to manage costs associated with reproductive output which often leads to these costs carrying over into the future. Compensatory mechanisms vary across life history strategies and are expected to result in near-optimal fitness gains for the investor. Here we investigated whether environmental differences associated with increasing montane elevation and variation in reproductive output of a resident passerine songbird, the Mountain Chickadee (*Poecile gambeli*), were related to physiological conditions during annual molt. Higher elevations are associated with harsher environmental conditions during the winter, which results in later and shorter breeding seasons than at lower elevations. We sampled the outermost tail feathers from adult birds in the fall after their prebasic molt, which initiates closely after reproduction (e.g., after parental care has ceased, ~1–3 weeks). We measured the hormone corticosterone deposited in feathers (fCORT) and feather growth rates for evidence of physiological effort predicted to be driven by several units of reproductive output (e.g., breeding timing, clutch and brood size, and offspring mass). There were no relationships between any measure of reproductive output and feather characteristics between elevations or across years, despite substantial variation in reproductive output in the wider population across this same time. However, birds at the high-elevation site grew their tail feathers significantly faster and had higher fCORT deposition compared to low-elevation birds. These results suggest that although differences in reproductive output and any related signals of associated physiological effort (e.g., fCORT and feather growth rate) may not extend into individual conditions during annual molt, shorter breeding seasons associated with harsher environmental conditions may favor faster feather growth as required by earlier onset of winter.

Keywords: carryover effects, Corticosterone, feather growth, molt, Mountain Chickadee, Paridae, reproductive output

How to Cite

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LAY SUMMARY

- Investigating the drivers of within and between population variation in reproductive output has been of interest for decades. Understanding how animals cope with the costs of reproduction and how these costs impact future life events remain challenging.
- We tracked a population of Mountain Chickadees across three years and two elevations in western North America and tested for the presence of carry over costs during annual molt to levels of reproductive output.
- We used adult chickadee tail feathers to measure fCORT and growth rates in feathers grown immediately after a reproductive bout.
- High elevation dwelling birds grew feathers faster and had higher fCORT compared to their low elevation counterparts.
- Despite variation in feather growth rates and fCORT, there was no relationship between these metrics and reproduction between the montane sites or years of the study.

La tasa de crecimiento de las plumas y la deposición de hormonas, pero no los costos reproductivos, varían con la elevación en residentes de *Poecile gambeli*

RESUMEN

Muchos organismos afrontan compensaciones metabólicas para gestionar los costos asociados con el rendimiento reproductivo, lo que a menudo conduce a que estos costos se arrastren al futuro. Los mecanismos compensatorios varían según las estrategias de la historia de vida y se espera que resulten en ganancias de aptitud casi óptimas para el inversionista. Aquí investigamos si las diferencias ambientales

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asociadas con el aumento de la elevación de la montaña y la variación en el rendimiento reproductivo de un ave canora paserina residente, *Poecile gambeli*, estaban relacionadas con la condición fisiológica durante la muda anual. Las elevaciones más altas están asociadas con condiciones ambientales más duras durante el invierno, lo que resulta en temporadas de cría más tardías y más cortas que a elevaciones más bajas. Muestreamos las plumas de la cola más externas provenientes de aves adultas en el otoño, después de su muda prebásica, que se inicia poco después de la reproducción (e.g., después de que el cuidado parental ha cesado, ~ 1–3 semanas). Medimos la hormona corticosterona depositada en las plumas (pCORT) y las tasas de crecimiento de las plumas en busca de evidencia de un esfuerzo fisiológico previsto a partir de varias unidades de rendimiento reproductivo (e.g., momento de cría, tamaño de la puesta y de la nidada, masa de las crías). No hubo relaciones entre ninguna medida de rendimiento reproductivo y las características de las plumas entre elevaciones o a lo largo de los años, a pesar de la variación sustancial en el rendimiento reproductivo en la población más amplia para este mismo tiempo. Sin embargo, las aves en el sitio de elevación alta presentaron un crecimiento de sus plumas de la cola significativamente más rápido y tuvieron una mayor deposición de pCORT en comparación con las aves de elevación baja. Estos resultados sugieren que, aunque las diferencias en el rendimiento reproductivo y en cualquier señal relacionada del esfuerzo fisiológico asociado (por ejemplo, pCORT y tasa de crecimiento de las plumas) pueden no extenderse a la condición individual durante la muda anual, las temporadas de cría más cortas asociadas con condiciones ambientales más duras pueden favorecer un crecimiento más rápido de las plumas, como se requiere por el comienzo temprano del invierno.

Palabras clave: corticosterona, crecimiento de plumas, efectos de arrastre, muda, Paridae, *Poecile gambeli*

INTRODUCTION

Understanding the drivers of population-level variation in reproductive output is often context-specific and elusive. However, much of this variation can likely be explained by carryover effects, non-lethal costs that alter present and future reproductive investment (Harrison et al. 2011, O'Connor et al. 2014, Moore and Martin 2019). Carryover effects are broadly defined and can include impacts from climatic challenges, reproductive effort, social environment, or a combination of such factors (e.g., Abbey-Lee et al. 2016, Firth and Sheldon 2016, Moore and Martin 2019). These effects have been documented in a wide array of species and oftentimes come with costs that mediate the future fitness of parents and offspring (e.g., Drent and Daan 1980, Moore and Martin 2019). However, accurately quantifying how carryover effects shape the reproductive effort of wild populations remains challenging (Marra et al. 2015).

The study of carryover effects has been the focus of numerous ecological studies for the last several decades (Harrison et al. 2011, O'Connor et al. 2014, Marra et al. 2015, Moore and Martin 2019). Most previous work tests whether high reproductive investment leads to costs that impact future fitness, including survival during the non-breeding period or the ability to find a mate or invest in reproduction in a subsequent season (Rockwell et al., 2012, Saino et al. 2017 and 2018, Sedinger et al., 2011). The transition points between life history stages provide opportunities in which to directly test for carryover effects acting on reproductive and individual investment (e.g., Marra et al. 2015, Western and Ssemakula 1982, Linden and Møller 1989). Thus, species with clearly defined and delineated life history stages, such as migration, have been the focus of much of this work as the conditions on the wintering grounds could have significant impacts on the condition of animals as they travel back to breeding grounds to reproduce (e.g., Marra et al. 1998, Marra et al. 2015, Mauck and Grubb 1995, De La Hera et al. 2009b, Mitchell et al. 2012, Carrete et al. 2013, Catry et al. 2013, Latta et al. 2016, Skrip et al. 2016). For example, winter weather, particularly lack of rainfall, led to male Kirtland's Warblers (*Setophaga kirtlandii*) arriving on breeding grounds later and subsequently fledging fewer young (Rockwell et al. 2012). Climate and overwintering location can predict the probability of reproduction in Brant Geese (*Branta bernicla*; Sedinger et al., 2011). However, similar studies have shown mixed results on the wintering conditions of other avian taxa (e.g., Barn Swallow [*Hirundo rustica*]) and their future reproduction, including little to no impact on arrival date or reproductive output (Bowers et al. 2012, Ockendon et al. 2013, Finch et al. 2014, Saino et al. 2017 and 2018, Broggi et al. 2022).

In addition to this correlational work, field studies that directly manipulate parental condition (e.g., immune challenges or wing clipping) or the resources provided to parents or offspring before and after the reproductive period have become numerous (e.g., Robb et al. 2008, Bowers et al. 2012). Providing supplemental food directly prior to reproduction is a common experimental method thought to boost reproductive output, but these studies rarely follow the same animals over multiple years or multiple reproductive attempts (but see; Boutin 1990, Kaiser et al. 2015, Robb et al. 2008, Murray et al. 2016, Nagy and Holmes 2005). Results of supplemental feeding experiments appear equivocal, as some have shown negative, positive, or negligible consequences for the fitness of the adults and offspring involved (e.g., Boutin 1990, Robb et al. 2008). Studies that directly manipulate the condition of parents by increasing the cost of offspring care have shown that parents in both long-lived and short-lived species reduce the feeding rates of the offspring to increase their own fitness (Mauck and Grubb 1995, Morales et al. 2007), while some shorter-lived species do the opposite (Hemborg and Merilä 1998, Bowers et al. 2012). These results demonstrate that carryover effects may be one of the underlying mechanisms mediating observed life history strategy patterns, but the prevalence and persistence of these effects often remain unclear (e.g., Harrison et al. 2011, Moore and Martin 2019).

Avian species are ideal models to investigate potential carryover effects and their impact either pre- or post-reproduction as they are diverse and ubiquitous, allowing for both short- and long-term studies. They also have several clearly defined life history stages that occur predictably on an annual cycle. These events can be species-specific, such as migratory movements, but there are 2 universal investments shared by all avian species: Molt and reproduction (Barta et al. 2006, Chen et al. 2015, Jenni and Winkler 2020). Molt, or the growth and replacement of plumage, is composed of a variety of strategies, but most temperate breeding avian species undergo an annual complete molt (i.e., replacement of all flight and body feathers) which comes with significant energetic investment (Barta et al., 2006, Jenni and Winkler 2020, Pyle 2022). High-quality feathers influence locomotion, foraging behaviors, mate attraction, and thermoregulation, and a lack of investment can come with severe fitness consequences (Chen et al. 2015, Jenni and Winkler 2020). However, despite its importance, how other life history stages such as reproduction influence molt is still relatively poorly understood (Svensson and Nilsen 1997, Howell 2010, Jenni and Winkler 2020, Pyle 2022).

Here, we tracked the reproductive output of a population of Mountain Chickadees (*Poecile gambeli*) in the northern Sierra Nevada across 3 years at 2 montane elevations to test for the presence of post-reproductive carryover effects during the annual molt. The Mountain Chickadee is a resident and short-lived (ca. 50% of birds die every year and the average life expectancy is just over 1 year) species that breeds and overwinters at the same elevation across years (McCallum et al. 2020). Differences in elevation can affect the onset and duration of winter conditions, and therefore have the potential to influence the relationship between reproductive investment and subsequent carryover effects in the molting period (Kozlovsky et al., 2018, Whitenack et al. 2023). To measure carryover effects, we collected a single tail feather to estimate levels of the physiological burden associated with post-breeding molt (Howell 2010, Pyle 2022). Corticosterone (hereafter CORT when referring generally to the hormone, or fCORT deposited in feathers) is a hormone that is broadly involved in the metabolism of birds and temporal spikes in the levels of this hormone have been linked to acute stress events (Hau et al. 2010, McEwen and Wingfield 2010, Vitousek et al. 2019). Daily feather growth rates have been experimentally shown to reflect nutritional intake and are therefore an indicator of general condition throughout the growth period (Grubb 2006, Jenni and Winkler 2020). Additionally, molt is negatively impacted (e.g., incomplete flight feather molt) by increased reproductive output in some species (Pietiäinen et al. 1984, Rohwer et al. 2011, Jenni and Winkler 2020). There is also past evidence linking slower feather growth rates with larger number of offspring raised prior to molt, showing that this metric is partially reflective of previous energetic expenditure (Gienapp and Merilä 2010). In addition, faster growth rates may contribute to a context-specific shorter overall molt duration (de la Hera et al. 2011, Rohwer and Rohwer 2013, Jenni and Winkler 2020).

We predicted that birds that produced more offspring (e.g., bigger clutches, larger broods, and heavier nestlings) would show higher levels of burden reflected in their feathers (e.g., slower feather growth rates and higher fCORT). In other words, we predicted that the higher levels of energetic investment (assessed by breeding timing, clutch and brood size, and nestling mass) required to lay more eggs and subsequently care for the resulting offspring would elevate circulating CORT (which would then be preserved in feathers) and reduce feather growth rates to a level that would be reflected in feather traits. In addition, birds inhabiting higher elevations experience shorter breeding seasons due to later start of spring and earlier onset of winter conditions; therefore, we also predicted that high-elevation birds would, on average, grow feathers faster and have higher levels of fCORT relative to low elevation birds to compensate for this shorter window while still showing a relationship between reproductive output and feather growth and fCORT.

METHODS

Study Site and Subjects

All data for this study were collected during 2018–2021 at the Sagehen Experimental Forest (Sagehen Creek Field Station, University of California, Berkeley) in the Sierra Nevada, USA. In this long-term study system, we monitored a population of Mountain Chickadees year-round at 2 elevations (Kozlovsky et al. 2018, Sonnenberg et al. 2020). The site sits along a montane elevation gradient in which we compared 2 subsets of the population, 1 at a high elevation site (~2400 m; coord: 39.424020, −120.315015) and one at low elevation site (~1900 m; coord: 39.443500, −120.243248). These sites differed in overwinter conditions, with high elevations being associated with higher snow levels, cooler temperatures, and less predictable winter storms compared to the low elevation site (Kozlovsky et al. 2018, Whitenack et al. 2023). Chickadees at high-elevation commence breeding 2–3 weeks later compared to birds at lower elevations (Kozlovskly et al. 2018, Whitenack et al. 2023). This translates into a shorter breeding season for chickadees at high elevations that leads directly into the fall months when they begin to intensely cache food (Sonnenberg et al. 2020, Whitenack et al. 2023). We captured birds at feeders in the fall and winter months (August–March) using mist nets and at nest boxes by hand during the reproductive season (May–July). Adults were banded with a combination of color band(s) and a colored leg band with an embedded passive integrated transponder tag (Bridge et al. 2019). Adults were sexed via physiological characteristics present at capture (e.g., females with brood patches, males with cloacal protuberances) in spring and summer (June—August) or by wing length (deemed a male with wing length over 74 mm or female if wing length under 67 mm) if captured only during the fall or winter months (September–March; Pyle 2022). Nestlings were banded with a single United States Geological Survey aluminum leg band at day 16 post-hatch and if recaptured were equipped with a color band and a colored leg band with an embedded passive integrated transponder tag. All birds were classified as juveniles (younger than 1 year of age) or adults (older than 1 year of age) at the time of capture based on past capture history or multiple plumage characteristics (Pyle 2022).

For this study, a single fully grown outermost rectrix (tail feather, [r6]) was taken from each bird at time of recapture during the non-breeding months (September–March) of 2018–2020 (Sonnenberg et al., 2022). The feathers originated from the prebasic molt (Humphrey-Parkes H-P-H terminology) which is initiated soon after reproduction (e.g., after parents stop feeding fledged young, which occurs a few weeks after fledging; Howell 2010, Pyle 2022). Feathers store information about individual conditions as they are grown, including glucocorticoid hormone levels (corticosterone was measured for this study) and daily growth rates (Bortolotti et al. 2008 and 2009, McCallum et al. 2020, Pyle 2022). Mountain Chickadees in this study system finish molt in late August–September (pers. obs. of the author) before the onset of winter and before they start caching food. While juveniles disperse during this same time, adults are highly sedentary, and molt is the major life history stage during this period (McCallum et al. 2020).

Measuring Reproductive Output

We monitored nest boxes on a minimum of a semiweekly basis (increasing checks as needed) from the beginning of April through early August (Sonnenberg et al. 2020 and 2022). Nests were checked for signs of nest-building, the laying of the first egg, date of incubation initiation, hatching date, and nest status (success or failure) until nestling processing on day 16 post-hatch. Monitoring visits were increased during critical times such as expected first egg dates (predicted by means of past years in the system) and expected hatch dates (predicted by clutch termination and incubation start dates). After the initiation of incubation was recorded, we monitored for hatching after 12 days and then checked every day until hatching was detected. This allows for precise measures of the first egg dates and hatching dates across years as no chickadees hatch before 12 days of incubation. During monitoring, individual adult birds were identified either via visual identification of leg band combinations or via radio frequency identification (RFID) readers on the nest box (Bridge et al. 2019). We captured unbanded parents at the nest box between days 8 and 12 post-hatch and banded and sexed both adults. Nestlings were collected from the nest box (on day 16 post-hatch) and individually counted (brood size), weighed to the nearest 0.01 g and banded with an aluminum United States Geological Survey band (Sonnenberg et al. 2020 and 2022). We calculated the average nestling mass for each brood within a nest (measure of overall nestling quality) and the coefficient of variation (CV) of within-nest nestling mass (measure of within-nest mass variation). Broods with higher CV of nestling mass may reflect nests that experienced relatively worse conditions during development resulting in significant differences in mass within broods (Sonnenberg et al. 2020 and 2022). Reproductive output metrics used in statistical models for this study were first egg date (day of the year), clutch size, brood size, average nestling mass, and CV of nestling mass.

Feather Size and Growth Rate

Collected feathers were individually stored in labeled coin envelopes in a cool, dry environment until processing. Feathers were measured for overall length using a flat ruler (nearest 0.5 mm) and overall mass to the nearest 0.1 mg using an electronic scale. This process was repeated both before and after the removal of the calamus (the barbless tip of the feather). Removal of the calamus was required by the glucocorticoid extraction protocol (see below).

We measured the feather growth rate via visible growth bars that reflect 24 hours of feather growth (Grubb 2006, Sonnenberg et al., 2022). We secured feathers on 10.16 × 15.24 cm notecards and exposed them to low-angle light to mark growth bar edges (Grubb 2006, Sonnenberg et al., 2022). The beginning and end of each individual growth bar were marked on each notecard, and, after marking, we photographed all notecards. We then used ImageJ software (Schneider et al. 2012) to measure each growth bar to the nearest 0.1 mm. Mean feather growth bar width of individual feathers was used for all analyses. This protocol is based on established ptilochronology methods (Grubb 2006). Though the original methodology was established with the measurement of re-grown feathers after experimental removal, there is no reason to assume that feather growth measured in feathers grown during molt is independent of consumed nutrition and body condition during molt (Grubb 2006).

Feather Corticosterone

We exposed all feathers to a standard corticosterone extraction procedure, which was followed by an enzyme-linked immunosorbent (ELISA) assay using methods established by Bortolotti et al. (2008, 2009 and Bortolotti 2010) and modified following Grant et al. (2020). All feathers, regardless of year of collection, were processed during the fall of 2021. Feather corticosterone (fCORT) is known to remain stable in feathers over long time periods (up to 14 years; Beattie and Romero 2023). We first cut feathers into ~5-mm length pieces (excluding the calamus) and placed these pieces into 20 mL scintillation vials with 7 mL of HPLC grade 100% methanol. Scintillation vials were sonicated in a room temperature water bath for 30 minutes and then placed in a 50°C shaking water bath overnight (16 hours). We removed vials from the bath and separated feather matter from the methanol solution using vacuum filtration and washed the vials twice with 2 mL of methanol in each wash. The methanol was then dried in a FlexiVap station composed of a heat block and a hose system that supplied a constant flow of air over the surface of the methanol to expedite evaporation. We reconstituted dried samples in 300 µL of assay buffer (supplied by the Enzo Life sciences ELISA kit, catalog no. ADI-902-097). All samples were sealed and frozen until assayed. The reconstitution volume and parallelism were determined using previous serial dilution assays of chickadee feathers not used in this experiment. We ran samples diluted by 1:300, 1:600, and 1:900. We generated parallel curves from this assay and the 1:300 dilution had the highest level of parallelism.

We assayed all samples using a corticosterone ELISA kit following the manufacturer's instructions. Feathers from all years (2018–2020) were assayed using the same kit to reduce batch bias. We used a serial dilution of known CORT concentration to create a standard curve and used the CV of known standards (20,000, 4000, 800, 160, and 32 pg/mL) to calculate inter-(9.6%) and intra-assay (plate 1: 10%; plate 2: 10%) variation. Inter-plate CV was calculated from duplicated controls made of pooled fCORT from previous samples and were taken through the entire assay process. Samples were randomized across plates and fCORT values were standardized by feather length (Bortolotti et al. 2008 and 2009). Another study suggested standardizing by mass, but this method did not alter our results in any way and so we followed the original Bortolotti protocol (Lattin et al. 2011). This same protocol was previously used for chickadee feathers from this population (Sonnenberg et al., 2022).

Statistical Analyses

All analyses and associated figures (Wickham 2016) for this study were generated using R Core Team v. 4.2.2 (R Core Team, 2023). We used linear models and generalized linear models ("glmmTMB" package, Brooks et al. 2017) to investigate the relationship between fCORT and feather morphometrics to observe variation in reproductive output of Mountain Chickadees. We tested for significant effects of elevation and year interactions in all models that included elevation and year as fixed effects. If there was no significant interaction detected, the interaction was removed (Engqvist 2005). There were only 3 individual birds that had multiple samples and not across all 3 years. Due to this low sample of repeated individual birds, we did not include any mixed effects models in the analysis. We tested each model for its residual fit using the "DHARMa" package in R (Hartig 2022). R-squared values were calculated using either the "performance" or "rcompanion" packages (Mangiafico 2024, Lüdecke et al. 2021), and post hoc analyses were performed with the "emmeans" package when significant differences between year or elevation were detected (Lenth 2023). Post hoc results including model-corrected means were included within the text of the results.

We predicted that the individuals who initiated breeding earlier in the season would show lower indicators of physiological burden. This is based on past evidence from this system that older, more experienced pairs breed earlier (Pitera et al. 2021) and this earlier timing may allow for a recouperation of bodily resources before molt initiation (Tarwater and Arcese 2017). We predicted that within seasons adults that had higher reproductive outputs (i.e., had nests with more eggs, more nestlings, and nestlings of higher mass) would display signs of physiological burden during the immediate post-breeding prebasic molt (Svensson and Nilsen 1997). Eggs cost energy to produce and we predict that larger clutches cost more energy to produce and maintain than smaller clutches (Burlacu and Baltac 1971, Haftorn and Reinertsen 1985, Monaghan et al. 1998, Nager and Houston 2000, Clifford and Anderson 2001, Nilsson and Råberg 2001, Visser and Lessells 2001, Vézina et al. 2003 and 2006, te Marvelde et al. 2012, Hodges et al. 2015, Pick et al. 2016, Skrip et al. 2016, Romano et al. 2022), which may then be reflected in feathers. Larger broods compound the costs of egg production, incubation, and the amount of feeding required by both adults (Haftorn and Reinertsen 1985, Monaghan et al. 1998, Visser and Lessells 2001, Hodges et al. 2015, Guindre-Parker and Rubenstein 2018). Thus, parents with larger broods are expected to expend more energy throughout the reproductive period compared to those with smaller broods (Haftorn and Reinertsen 1985, Hemborg and Merilä 1998, Visser and Lessells 2001, Santos and Nakagawa 2012, Hodges et al. 2015). Lastly, broods that display a larger mean mass or lower coefficients of variation in nestling mass may be reflective of higher feeding rates or higher quality parental foraging efforts, and so broods of these larger and more consistent masses may indicate more energetic investment (Hemborg and Merilä 1998, Hodges et al. 2015, Guindre-Parker and Rubenstein 2018).

To examine the reproductive output of the entire adult population of chickadees across elevations and years of the study, we used our long-term, population-wide dataset. Including these data helped identify yearly trends in the reproductive output and investment of the population that are likely environmentally driven and help inform the outcomes of this study. Assuming yearly variation in reproductive output is associated with variation in environmental conditions, we can directly test if such yearly variation was associated with differences in both metabolic processes as measured by fCORT and in feather growth rates during molt. Mountain Chickadees are a short-lived species with an average life expectancy of just 1 year (McCallum et al., 2020, this population's age class mode is 1, median of 2, and shows a range of 1–10 years of age, reflecting 10 years of data). As such, every reproductive event may be an individual's last and so it can be expected that chickadees should invest maximally in reproduction rather than reduce reproductive investment during years with poor environmental conditions by shifting towards self-investment (Bowers et al. 2012). Therefore, we may also expect overall higher costs associated with reproduction in years with low, on average, reproductive output for the broader population (in contrast to the relationship between reproductive output and costs with each given year). So, while within each year, larger clutches, broods, or nestlings are likely associated with higher parental investment, across years, years with on average lower reproductive output are likely associated with higher parental costs. We have monitored the reproductive output of this population for the last 10 years (2013–2022) and all birds with sampled feathers came from this population during the years 2018–2021. For this study, we only used a targeted subset of the long-term data set from the same years in which feathers were also collected. All breeding pairs from the 3 years of the study were used to estimate population-level differences in reproductive performance across years and elevation. These sample sizes were much larger than those of individuals with feather and breeding data as not all breeding individuals were recaptured after the completion of breeding and molt. We used reproductive parameters including date of first egg, clutch size, brood size, mean nestling mass, and the CV of nestling mass as response variables and elevation and year as fixed effects to examine population-wide trends and identify high-quality or poor-quality years. Models were first run including an interaction between elevation and year, but this interaction was removed if nonsignificant. Pair ID (unique male and female combination) was initially included as a random effect but explained so little of the variation that it was removed. We compared overall population variation to that of the smaller sample (individuals with breeding and feather data) using the same reproductive parameters as noted above as response variables and complete feather sample, elevation, and year as fixed effects. This was performed to rule out whether a biased sample of high- or low-quality individuals were encountered in this subset of the data.

We quantified corticosterone in each feather in picograms per millimeter of feather (fCORT; Bortolloti et al. 2008 and 2009, Sonnenberg et al. 2022). This metric was used in all models except for those that included feather length or mass as the response variable; in these cases, we used the total picogram values of each sample (CORT). We fit models to test for variation across time and location using year and elevation as fixed effects and fCORT, feather length, feather mass, and feather growth rate (mm per 24-hour period) as response variables. Due to right-skewed distributions for both mean feather growth and fCORT, generalized linear models were fit with gamma distributions. We also tested for differences between sexes using sex as a fixed effect and fCORT, feather mass, feather length, and feather growth rate as response variables. To test for relationships between feather morphological characteristics and corticosterone deposition, we fit models with total CORT (in pg) as the response variable and feather length, feather mass, and feather growth rate as fixed effects. These models included all adult individuals in which a viable feather was collected and sampled including those which were not detected breeding.

To test the relationships between reproductive output and its associated physiological burden, we fit models using first egg date (day of the year), clutch size, brood size, nestling mean mass (g), and CV of nestling mass (g) as fixed effects and fCORT and feather growth rate as response variables. Separate analyses investigating each predictor variable were performed for pooled adults (i.e., males and females), males only, and females only. Analyses involving fCORT as a response variable were fitted with gamma distributions to account for right-skewed data while feather growth rate models were fit with Gaussian distributions.

RESULTS

Variation in Feather Metrics Across Years and Elevations

fCORT did not vary across years or between sexes but chickadees at high elevations had higher fCORT levels compared to birds at low elevations (post hoc: $N = 138$, estimate = −0.04 ± 0.02, $t = -2.1$, $P = 0.03$; high elevation: $N = 95$, 8.90 ± 0.91 pg/mm; low elevation: $N = 43$, 6.32 ± 0.79 pg/mm; Table 1; Figure 1A). These data included all adult birds sampled in the study regardless of whether they were detected breeding or had confirmed sex.

Feather growth rate showed no relationship with year or sex (post hoc: $N = 125$, estimate = 0.01 ± 0.07, $t = 0.1$, $P = 0.99$) but chickadees at high elevation grew their feathers at a higher rate compared to birds at low elevation (post hoc: $N = 125$, estimate = 0.09 ± 0.04, $t = 2.3$, df = 116, $P = 0.02$; high elevation: $N = 84$, 2.41 ± 0.03 mm/24 hours; low elevation: $N = 41$, 2.32 ± 0.03 mm/24 hour; Table 1; Figure 1B, Figure 2C). Feather length and mass were not different across years or elevations, but males had significantly longer (post hoc: $N = 140$, [females = 32, males = 59], estimate = −3.05 ± 0.41, $t = -7.5$, $P < 0.01$) and heavier ($N = 141$, estimate = −0.74 ± 0.09, $t = -8.3$, $P < 0.01$) feathers compared to females (Figure 2A, B). Feather length ($N = 140$, estimate = $1.20e^{-4} \pm 2.80e^{-4}$, $t = 0.4$, $P = 0.67$) and feather growth rate ($N = 125$, estimate = $-5.33e^{-5} \pm 2.74e^{-5}$, $t = -1.9$, $P = 0.05$, $R^2 = 0.04$) were not related to overall corticosterone (the total detected CORT within the feather before controlling for feather length), and we did not investigate feather mass because feather length and mass were highly correlated ($N = 140$, estimate = 2.99 ± 0.27, $t = 11.2$, $P < 0.01$, $R^2 = 0.48$). These results show that larger or faster-growing feathers did not contain more or less corticosterone than smaller or slower-growing feathers.

Reproductive Metrics Across Years and Elevations

There was substantial variation in reproductive timing and output across the 3 years of the study (2018 – 2020). Egg-laying initiation timing was associated with differences between elevation and year (Table 2). Multiple post hoc analyses showed that egg laying was always later at high elevation compared to low elevation (Supplementary Material Table S1: Marginal means from post hoc model: Low elevation: 139 ± 0.42 day of year; high elevation: 153 ± 0.50 day of year) but that low elevation was very consistent across years (low elevation average range: 138–140 day of year) while high elevation showed more varying start times (high elevation average range: 149–158; Supplementary Material Table S1). This variability at the higher elevation site is related to high variability in overwinter snow depth in this system (Whitenack et al. 2021).

Chickadee clutch size was associated with an interaction between elevation and year (Table 2) and a post hoc analysis revealed differences among years at high elevation, with chickadees having smaller clutch sizes in 2020 (mean clutch size: 6.22 ± 0.14 eggs) compared to both 2018 ($N = 332$, estimate = 1.10 ± 0.04, z ratio = 3.03, $P = 0.03$; mean clutch size: 6.86 ± 0.16 eggs) and 2019 ($N = 332$, estimate = 1.10 ± 0.03, z ratio = 2.95, $P = 0.04$; mean clutch size: 6.82 ± 0.16 eggs). Birds at the low elevation (mean clutch size: 7.27 ± 0.14 eggs) site had larger clutch sizes compared to high elevation (mean clutch size: 6.22 ± 0.14 eggs) but only in 2020 ($N = 332$, estimate = 0.86 ± 0.02, z ratio = −5.27, $P < 0.01$).

Brood size varied between years and elevations (Table 2) and post hoc analyses showed that 2018 (mean brood size: 6.29 ± 0.15 chicks) was associated with larger brood sizes than 2020 (mean brood size: 5.72 ± 0.14 chicks, $N = 278$, estimate = 1.10 ± 0.04, z ratio = 2.90, $P = 0.01$) but there were no differences in brood size between 2018 and 2019 (mean brood size 2019: 5.85 ± 0.14, $N = 278$, estimate = 1.08 ± 0.03, z ratio = 2.21, $P = 0.07$) or 2019 and 2020 ($N = 278$, estimate = 1.02 ± 0.03, z ratio = 0.68, $P = 0.78$). Chickadees at low elevation (mean brood size: 6.16 ± 0.11 nestlings) produced larger broods on average compared to high elevation (mean brood size: 5.74 ± 0.13 nestlings, $N = 278$, estimate = 0.93 ± 0.03, z ratio = −2.52, $P = 0.01$) in the same model.

Mean nestling mass was consistently higher at the high elevation site (mean nestling mass: 12.2 ± 0.08 g) compared to the low elevation site (mean nestling mass: 11.9 ± 0.07 g;

TABLE 1. Variation in feather Cort (fCORT), length, mass, and growth rate.

Response variable	N	Fixed effect	Output	P	Pseudo R^2
Cort_f (pg mm^{-1})	138	Elevation	**$X^2 = 4.99$**	**$P = 0.025$**	Full model:
		Year	$X^2 = 0.86$	$P = 0.650$	$R^2 = 0.14$
		Sex	$X^2 = 0.45$	$P = 0.799$	
		Wing length	$X^2 = 0.44$	$P = 504$	
Feather growth rate (mm 24 hr^{-1})	125	Elevation	**$X^2 = 5.42$**	**$P = 0.012$**	Full model:
		Year	$X^2 = 2.87$	$P = 0.238$	$R^2 = 0.08$
		Sex	$X^2 = 2.49$	$P = 0.287$	
		Wing length	$X^2 = 0.07$	$P = 0.793$	
Feather length (mm)	140	Elevation	$X^2 = 0.05$	$P = 0.828$	Full model:
		Year	$X^2 = 0.27$	$P = 0.871$	$R^2 = 0.31$
		Sex	**$X^2 = 56.29$**	**$P < 0.001$**	
Feather mass (mg)	141	Elevation	$X^2 = 0.23$	$P = 0.634$	Full model:
		Year	$X^2 = 1.21$	$P = 0.545$	$R^2 = 0.35$
		Sex	**$X^2 = 68.71$**	**$P < 0.001$**	

Linear models comparing the variation across years, elevations, and sexes in feather metrics for all adults sampled for the study. These sample sizes are large as all samples are included and not just samples from adults who also have reproductive data. Bolded values indicate significance.

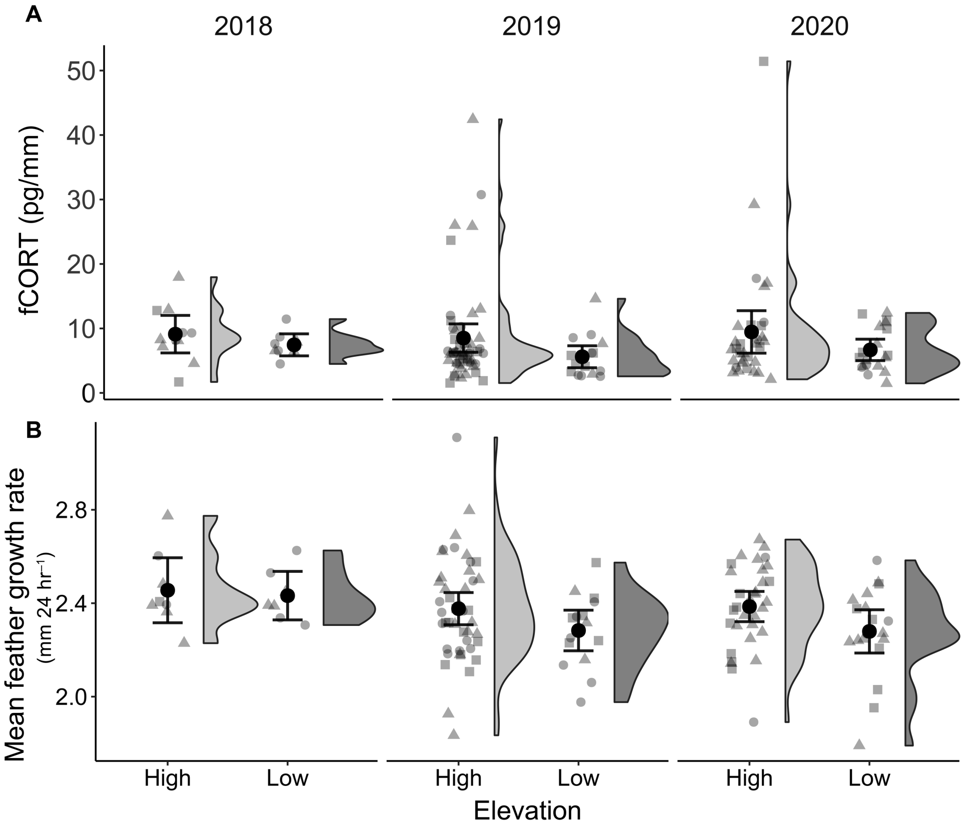

FIGURE 1. Variation of fCORT (**A**) and mean feather growth rate (**B**) across years and elevations with males designated by squares, females by circles, and unknown sex by triangles. Error bars represent 95% confidence intervals.

Table 2; post hoc analysis: $N = 276$, estimate = 0.31 ± 0.11, t ratio: 2.78, $P < 0.01$). Differences across years were more variable with 2020 (mean nestling mass: 11.4 ± 0.09 g) being associated with nestling smaller masses by nearly a gram compared to both 2019 (mean nestling mass: 12.5 ± 0.09 g, $N = 276$, estimate = 1.1 ± 0.13, t ratio = 8.44, $P < 0.01$) and 2018 (mean nestling mass: 12.2 ± 0.09 g, $N = 276$, estimate = 0.77 ± 0.13, t ratio = 5.86, $P < 0.01$). In addition, in 2019, nestlings had larger mean mass compared to 2018 ($N = 276$, estimate = −0.33 ± 0.13, t ratio = −2.55, $P = 0.03$).

The CV of nestling mass showed differences among years but not between elevations (Table 2). This measure indicates the level of developmental stress within a nest, with larger measures indicating a broader range of nestling masses which suggests worse conditions (Palmer and Strobeck 1986, Eeva et al. 2000, Sillanpää et al. 2010, Sonnenberg et al. 2020). In 2020, we observed the largest CV of nestling mass (mean CV: 0.07 ± 0.004), and it was larger than the CV in both 2018 (mean CV: 0.05 ± 0.004, $N = 275$, estimate = −0.02 ± 0.005, t ratio = −3.42, $P < 0.01$) and 2019 (mean CV: 0.06 ± 0.004, $N = 275$, estimate = −0.02 ± 0.005, t ratio = −3.08, $P < 0.01$). There were no differences in CV between 2018 and 2019 ($N = 275$, estimate = −0.002 ± 0.005, t ratio = −0.35, $P = 0.93$).

Lastly, there were no differences between any reproductive parameters of the adults that were successfully sampled for feathers post-reproduction and the overall population (Supplementary Material Table S2). This suggests that the subset of individuals from which we collected feathers were representative of our broader sampled population. In further support of this, the ranges of the 2 data sets are also quite similar across all reproductive parameters (date of first egg [day number counted from January 1st]): All breeders (128–169), breeders with feather data (128–164); clutch size (total egg number): All breeders (2–11), breeders with feather data (4–9); brood size (total number of living offspring on day 16 post-hatch): All breeders (1–9), breeders with feather data (4–8); mean nestling mass (grams): All breeders (8.04–13.97), breeders with feather data (9.81–13.46); CV of nestling mass (grams): All breeders (0.01–0.27), breeders with feather data (0.01–0.20; Figures A1–A5).

Reproductive Output and Physiological Burden Measures

Despite natural variation in both fCORT and feather growth rate, no reproductive predictor variable including the date of the first egg (Supplementary Material Table S3), clutch size (Supplementary Material Table S4), brood size (Supplementary Material Table S5), mean nestling mass (Supplementary Material Table S6), or CV of nestling mass (Supplementary Material Table S7) was related to either measure of physiological burden while controlling for elevation. This was the case for all models including those that tested all individuals, males only, and females only and which used a much smaller sample size of individuals that had feathers collected in the fall or winter months directly after a confirmed breeding attempt in the previous summer.

DISCUSSION

Overall, we found no evidence of reproductive carryover effects impacting fCORT or feather growth rates across 3 years

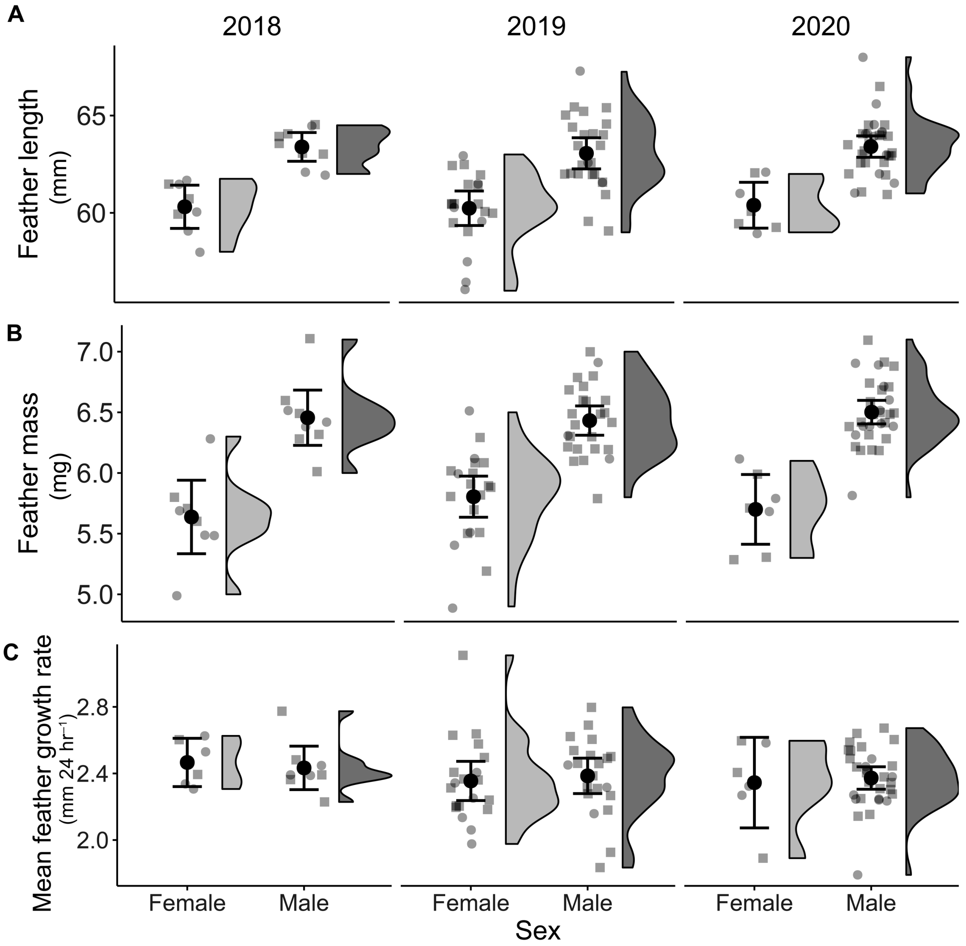

FIGURE 2. Mean differences in feather length (**A**), feather mass (**B**) and mean feather growth rate (**C**) between males and females with circles designating high elevation and squares low elevation individuals.

TABLE 2. Variation in the reproductive output of the total long-term study population during the years of the study (2018–2019).

Response variable	*N*	Fixed effect	Output	*P*	marginal R^2
First egg date (day of year)	345	Elevation	**$X^2 = 59.0$**	**$P < 0.01$**	Full model:
		Year	**$X^2 = 54.6$**	**$P < 0.01$**	$R^2 = 0.61$
		Year * Elevation	**$X^2 = 33.1$**	**$P < 0.01$**	
Clutch size (egg number)	332	Elevation	$X^2 = 1.7$	$P = 0.19$	Full model:
		Year	**$X^2 = 12.2$**	**$P < 0.01$**	$R^2 = 0.02$
		Year * Elevation	**$X^2 = 16.8$**	**$P < 0.01$**	
Brood size (nestling number)	278	Elevation	**$X^2 = 6.4$**	**$P = 0.01$**	Full model:
		Year	**$X^2 = 9.2$**	**$P = 0.01$**	$R^2 = 0.02$
Mean nestling mass (g)	276	Elevation	**$X^2 = 7.7$**	**$P < 0.01$**	Full model:
		Year	**$X^2 = 74.7$**	**$P < 0.01$**	$R^2 = 0.18$
Coefficient of variation (CV) in nestling mass (g)	275	Elevation	$X^2 = 0.3$	$P = 0.58$	Full model:
		Year	**$X^2 = 14.2$**	**$P < 0.01$**	$R^2 = 0.01$

Linear models test for variation across years and elevations in the reproductive metrics of the total long-term study population within the years of the study. Post hoc analyses were conducted for each significant result and results from these analyses are included in the main text of the results. Bold values indicate significance.

and 2 elevations despite large annual variations in reproductive output of the larger population. However, we did find differences in both fCORT and feather growth rates between elevations, with birds at high elevations having more fCORT deposition and faster feather growth rates compared to low-elevation individuals. These results were consistent with our predictions, as individuals inhabiting high elevations experience a relatively condensed breeding season compared to their low elevation counterparts, resulting in less time to complete molt (Kozlovsky et al. 2018, Whitenack et al. 2023). Growing feathers faster should allow high-elevation birds to be prepared for the more adverse fall and winter conditions experienced at higher montane elevations in the Sierra Nevada. Despite faster growth, high-elevation birds did not appear to compromise feather quality which has also been reported in a close relative (De La Hera et al. 2011) as there were no differences in feather mass or length between elevations or years of the study. The feathers of high-elevation birds contained more fCORT but this likely reflects the higher metabolic expense required to acquire resources in the short time window before winter and to grow these feathers more quickly or at higher elevations (Dawson et al. 2000, DesRochers et al. 2009, Addis et al. 2011). This result could also suggest that the same level of reproductive investment at this higher elevation results in higher fCORT compared to lower elevation birds. Overall, these results support the idea that seasonal variation in environmental conditions may have a strong effect on timing and energy investment in annual molt of resident passerine bird species (Hall and Fransson 2000, Barta et al. 2006, De La Hera et al. 2009a and b, Harms et al. 2015, Treen et al. 2015, Vágási et al. 2012).

There is mixed evidence in the current literature for the presence of carryover effects from reproduction in wild populations and the extent and methods of these studies are highly variable (Evans Ogden and Stutchbury 1996, Gienapp and Merilä 2010, Harrison et al. 2011, Santos and Nakagawa 2012, O'Connor et al. 2014, Harms et al. 2015, Fokkema et al. 2016). This variability is in part due to the broad definition of carryover effects (Stearns 2000, Harrison et al. 2011, Moore and Martin 2019). Much of the work on wild avian populations has focused on species with biannual migratory movements or on the impacts of supplemental feeding prior to reproduction (Carrete et al. 2013, Catry et al. 2013, De La Hera et al. 2009a and b, Finch et al. 2014, Gunnarsson et al. 2005a and b, Latta et al. 2016, Marra et al. 1998, Mauck and Grubb 1995, Mitchell et al. 2012, Robb et al. 2008, Rockwell et al. 2012, Sedinger et al. 2011). Very few studies have examined how carryover effects post-reproduction may impact one of the largest annual individual investments, the prebasic molt (Evans Ogden and Stutchbury 1996, Hemborg and Merilä 1998, Hemborg and Lundberg 2001, Gienapp and Merilä 2010, Jenni and Winkler 2020). Feathers are ideal candidates for examining carryover effects as they store information across the period in which they are grown (Bortolotti et al. 2008 and 2009, Chen et al. 2015). However, previous studies have shown that during molt periods birds downregulate fCORT, likely because high levels of CORT can directly impair protein synthesis required for optimal feather structure and growth (Romero et al. 2005, Chen et al. 2015). Thus, individuals may display low levels and limited variation in CORT feather deposition regardless of post-reproductive condition (Hau et al. 2010, Fairhurst et al. 2012, Legagneux et al. 2013, Harms et al. 2015). This seems to be the case in our study as the total levels of fCORT detected in adults were much lower than those observed in a previous study measuring fCORT in juvenile birds of the same species and population (using the same methodology and laboratory space; Hau et al. 2010, Sonnenberg et al. 2022). This higher level in juveniles likely reflects the higher metabolic demands of development compared to molt alone but could also reflect a suite of other pressures (e.g., predation; Chen et al. 2015, Sonnenberg et al. 2022). Another reason for these observed differences in fCORT between age classes is that juvenile feathers are grown simultaneously in the nest while adult birds symmetrically and sequentially grow pairs of feathers in their wings and tails (Jenni and Winkler 2020). This means that feathers likely reflect different levels of CORT depending on their growth sequence and that the 2 outermost feathers sampled for this study may have lower fCORT compared to inner tail feathers that were the first to grow (Jenni and Winkler 2020). The collection of these outer tail feathers for this study could have led to a lack of detected relationship between fCORT and reproductive output.

Despite the sampling of the outermost tail feather and the expected downregulation in metabolic hormones during molt, one could still expect to observe hormonal variation indicative of individual differences in reproduction (Mauck and Grubb 1995, Romero et al. 2005, Hau et al. 2010, Harms et al. 2015), but this was not the case for this study. This lack of variation associated with reproductive output measures suggests that fCORT may not be an ideal means for detecting potential carryover effects from experiences prior to molt (Romero et al. 2005, Bortollotti 2010). However, feather growth rates in this study did not vary based on differences in reproductive output either, suggesting that carryover effects may not have been detectable via these methods in this system (Legagneux et al. 2013, Chen et al. 2015). This may be system or method-specific as past work on Siberian Jays (Gienapp and Merilä 2010) did show that feather growth rates during molt were slower in individual parents that raised more offspring in the proceeding breeding attempt. We did not detect similar effects in our study even though we used exactly the same measures of reproductive output-brood size.

Chickadees exhibit a complex basic molt strategy, as adult individuals only have a single molt per annual cycle (Howell 2010, McCallum et al. 2020), during which birds replace all flight and body feathers (Chen et al. 2015, Pyle 2022). Due to the importance of feathers to the general survival and function of individual birds, this large energetic investment likely has mechanisms that shield molt from harmful perturbations (Romero et al. 2005, Chen et al. 2015, Jenni and Winkler 2020). As discussed above, the downregulation of metabolic hormones could be part of such a mechanism (Romero et al. 2005). Feathers can give indications of extreme stress events through the presence of stress bars or depigmented and structurally weakened areas of the feather, but we did not observe these features in any of the feathers that were included in this study (Jovani and Rohwer 2017, Jenni and Winkler 2020, Pyle 2022). The logistics of this study did require that a bird was detected reproducing in a given year and then was recaptured and sampled within 4–5 mo. This limited our sample size considerably, which could be another reason for a lack of detected carryover effects. For example, our sampling method may have only allowed us to sample individuals in good condition that survived reproduction and the following molt period. However, we saw no significant differences in the variation of any reproductive parameter between the sampled birds and the larger population, suggesting that we captured a reasonable amount of variation in our sample. However, this does not rule out that the individuals that were sampled were still of higher quality (Wilson and Nussey 2010), or simply had enough resources for a healthy molt, as we did not directly measure parental quality before or during reproduction. Another explanation is that individuals in poor condition may forego reproduction completely, as a compromised molt increases the likelihood of death (McCallum et al., 2020).

It is also possible that each individual adjusted reproductive investment according to their local environmental conditions and their own internal condition (Kristensen et al. 2018). In fact, our methods of using clutch sizes and brood sizes may not be ideal for measuring all components of direct parental investment in this species. For example, Tree Swallows (*Tachycineta bicolor*) have been shown to lay enormous clutches of eggs if manipulated with very low observed fitness consequences (Murphy et al. 2000). In fact, another study found that a direct measure of metabolic traits were better predictors of energetic output in swallows (Jimeno et al. 2020). This suggests that for some species clutch size alone may not be an ideal measure for predicting energetic investment during reproduction (Charnov and Krebs 1974). However, the production of more eggs requires more energy regardless of whether such additional energy comes with or without a detected fitness cost (Burlacu and Baltac 1971, Haftorn and Reinertsen 1985, Monaghan et al. 1998, Nager and Houston 2000, Nilsson and Råberg 2001, Visser and Lessells 2001, Vézina et al. 2003 and 2006, te Marvelde et al. 2012, Hodges et al. 2015, Pick et al. 2016, Skrip et al. 2016, Romano et al. 2022). In species much more closely related to Mountain Chickadees, Great Tits (*Parus major*) and Blue Tits (*Cyanistes caeruleus*), there have been clear indications that larger clutch and brood sizes come with both energetic and fitness costs (Haftorn and Reinertsen 1985, Visser and Lessells 2001, Fokkema et al 2016). Despite this, Mountain Chickadees may be able to adjust their reproductive output to their present condition and local environments in such a way that prevents or minimizes future costs associated with fitness. This alternative is supported by a recent meta-analysis (Winder et al. 2023). Nonetheless, our results are important as they show that variation in reproductive output (clutch size, brood size, and fledgling quality) both within and across years is not associated with differences in fCORT or feather growth.

Chickadees in this population have been monitored for their reproductive output for the past ten years. While only 3 years of data were used in this study, 2020 was one of the poorest reproductive years on record (Sonnenberg et al. 2022, Whitenack et al. 2023). These poor reproductive years are identified primarily by tracking the mean nestling mass and the CV of nestling mass across years (Sonnenberg et al. 2022). In 2020 we saw the lowest mean masses our population has ever recorded, as well as some of the highest CV's, indicating that 2020 may have been a poor resource year. However, we did not detect the same patterns across any of the sampled feather metrics. In fact, there were no differences among fCORT and mean feather growth rates between any years of the study which contrasts variation observed in other taxa (Hau et al. 2010, Legagneux et al. 2013, Treen et al. 2015).

The differences that we did observe in feathers were indicative of dimorphism in size between males and females. Sexual dimorphism, with males generally being slightly larger than females, has been previously documented in this species (McCallum et al. 2020). Males had larger and heavier feathers compared to females, but there was no difference in feather growth rates between sexes. We predicted that high-elevation birds would have faster feather growth rates and higher fCORT as they may have a shorter period in which to molt, which was supported by the data (Kozlovsky et al. 2018, Hall and Fransson 2000). High-elevation birds begin breeding later in the year given climatic constraints such as higher snow levels and cooler temperatures (Whitenack et al. 2023). Past evidence has shown that other species with similar differences in reproductive timing have faster molt compared to unconstrained species; however, we did not directly measure molt duration in this study, and differences in length are predicted by multiple factors including environmental conditions (Dawson et al. 2000, Hall and Fransson 2000, De La Hera et al. 2009a, Legagneux et al. 2013, Jenni and Winkler 2020). The higher levels of fCORT in high-elevation birds are likely related to greater metabolic demands of higher elevations (e.g., unpredictable weather events, cooler temperatures) including faster feather growth (Addis et al. 2011). Experimentally increasing the rate of molt or increasing fCORT have resulted in reduced feather quality (Dawson et al. 2000, Hall and Fransson 2000, De La Hera et al. 2009b, Jenni-Eiermann et al. 2015, Romero et al. 2005). However, in our field study, neither variation in feather growth rate nor fCORT affected feather length or mass.

Overall, our study did not detect any significant carryover effects from reproductive effort in a long-term study system, despite including years with significantly lower reproductive outputs. However, we did show a strong effect of environment (e.g., elevation) on both feather growth rate and fCORT across a small spatial area and within the same species. Our results add to previous evidence that molt likely has mechanisms to preserve feather quality from potential carryover effects or current detrimental environmental conditions but is still shaped by local conditions (Romero et al. 2005, Legagneux et al. 2013). It is also possible that individual parents adjust their reproductive decisions to the local conditions which would significantly reduce any consequences of individual variation in reproductive output. Additional studies are needed to determine whether feathers collected after the post-reproduction prebasic molt is an accurate method for detecting carryover effects from previous life history stages.

Supplementary material

Supplementary material is available at *Ornithology* online.

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Ethics Statement

All fieldwork and laboratory work were conducted in accordance with University of Nevada, Reno Institutional

Animal Care and Use Committee (Protocol 00818, 00046 and 00603) and California Department of Fish and Wildlife permit: D-0011776516-4.

Conflict of interest statement

The authors declare that they have no competing interests.

Data availability

Analyses reported in this article can be reproduced using the data provided by Sonnenberg et al. (2024).

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