

RESEARCH ARTICLE

Feather corticosterone reveals developmental challenges in a long-term study of juvenile northern spotted owls

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Abstract

1. Corticosterone is a steroid hormone integral to a variety of physiological pathways and is strongly associated with the vertebrate stress response. In avian species, circulating corticosterone is sequestered into developing feathers and is used as an indicator of energy allocation during feather growth and widely applied in conservation physiology.
2. The northern spotted owl *Strix occidentalis caurina* is a federally threatened old-growth forest obligate of conservation concern endemic to the Pacific Northwest of the United States and Canada. The effects of landscape characteristics and individual variation on early development in spotted owls remain unstudied despite long recognition of this knowledge gap and its potential importance to species conservation.
3. We quantified corticosterone concentrations in 4,720 feathers from 1,056 juvenile spotted owls across seven study areas between 2001 and 2017. We used an information-theoretic approach to examine the environmental and individual factors related to feather corticosterone in juvenile spotted owls as an indicator of challenges during early development.
4. Feather corticosterone was positively related to temperature and precipitation, and negatively related to juvenile mass at banding. We found strong support for an interaction between mass and precipitation, with greater amounts of precipitation being associated with higher levels of feather corticosterone in lighter juveniles. The temperature and precipitation metric with the strongest relationship with feather corticosterone occurred during the fledging period, suggesting that this period presents an energetic challenge for juvenile spotted owls. Greater juvenile mass decreased the effect of precipitation, suggesting that greater mass was important for juveniles to maintain homeostasis during fledging.
5. Feather corticosterone in juvenile spotted owls provided insights to the challenges faced during early development, adding to our understanding of spotted owl life history and potential for population recovery.

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KEYWORDS

conservation physiology, corticosterone, early life stage physiology, environmental challenges, glucocorticoids, spotted owls

1 | INTRODUCTION

Corticosterone (CORT) is a steroid hormone integral to a variety of physiological functions (e.g. energy intake and regulation, immunity and water balance) and is widely studied due to its secondary actions association with the vertebrate hypothalamic–pituitary–adrenal axis (Romero et al., 2009; Vera et al., 2017; Wingfield & Sapolsky, 2003). While acute increases in CORT are considered adaptive (Angelier et al., 2009; Wingfield, 2013), chronic or prolonged increases in CORT can depress immunity, growth, cognition, reproduction or survival (Romero et al., 2009; Sapolsky et al., 2000; Wingfield & Sapolsky, 2003; Zanette et al., 2011). Using CORT as an indicator of individual or population health has become a useful tool in the field of ecology because CORT mediates resource allocation in the body in response to daily and seasonal energetic needs, as well as stochastic, life-threatening events (Wingfield, 2005; Vera et al., 2017). In avian species, circulating CORT is sequestered into developing feathers (feather CORT) and can be used as a cumulative indicator of the hormone concentrations during feather growth (Bortolotti et al., 2008; Jenni-Eiermann et al., 2015; Romero & Fairhurst, 2016). This is particularly useful to understand how individuals or populations respond to changes in their environment that may have long-term effects on species of conservation concern.

One such species, the northern spotted owl *Strix occidentalis caurina* (spotted owl) is a territorial, old-growth forest obligate endemic to southwest Canada and the Pacific Northwest of the United States (Forsman et al., 1984; Noon & Franklin, 2002). Populations of spotted owls became of conservation concern in the 1970s and 1980s due to widespread logging. The spotted owl is now listed as endangered under the Canadian Species at Risk Act (COSEWIC, 2008), while in the United States, it was listed as threatened in 1990 under the U.S. Endangered Species Act (USFW, 1990) but now warrants reclassification to endangered due to continued population declines (Franklin et al., 2021; USFW, 2020).

The 1994 Northwest Forest Plan slowed the rate of old forest loss due to timber harvest on U.S. federal lands but logging on non-federal lands continued and mature forests are damaged on federal lands by forest fires, insects and disease (Davis et al., 2016). Because mature forests are important to spotted owl life history (Forsman et al., 1984), the amount of mature forest within a territory likely contributes to the overall physical condition of juveniles, and habitat degradation is associated with higher CORT concentrations (Cīrule et al., 2017; Suorsa et al., 2003; Wasser et al., 1997).

In addition to shrinking mature forests, the range expansion of the congeneric barred owl *S. varia* also threatens spotted owl persistence—contributing to decreased occupancy, survival,

reproduction and disrupted dispersal dynamics of spotted owls (Franklin et al., 2021; Jenkins et al., 2021; Wiens et al., 2021; Yackulic et al., 2019). Barred owls are a larger, more aggressive generalist species that exist on the landscape at much higher densities than spotted owls (Lesmeister et al., 2018; Singleton et al., 2010). Because the two species have overlapping diets (Lesmeister et al., 2018; Wiens et al., 2014), juvenile spotted owls may experience competitive pressure from barred owls through decreased prey abundance. Competitive pressures through sibling rivalry (Braasch et al., 2014; López-Jiménez et al., 2016; Yosef et al., 2013) or from novel competitors (Anson et al., 2013; Jessop et al., 2015; Narayan et al., 2015) are associated with higher CORT concentrations in other species, and juveniles may feel the effects of extra competitors on the landscape. In other avian species, food declines are associated with nutritional stress and stunted growth (Kitaysky et al., 2005; Lamb et al., 2016; Sears & Hatch, 2008) which can lead to compromised immunity (Saino et al., 2003; Sapolsky et al., 2000; Vera et al., 2017), reduced feather growth and quality (Jenni-Eiermann et al., 2015; Romero & Fairhurst, 2016) and lower survival (Naef-Daenzer et al., 2001; Maness & Anderson, 2013).

Besides competition for shared prey, barred owls displace spotted owls from historical territories and this competitive exclusion from ideal forest stands may be detrimental to juvenile development either directly or indirectly. Forests used by spotted owls for nesting typically have older trees and a closed, complex canopy (Davis et al., 2016; Forsman et al., 1984; Noon & Franklin, 2002). The complex structure of mature forests is important for protection from stochastic weather events (Barrows, 1981). Inclement weather increases energetic demands to maintain homeostasis and results in physiological (Krause et al., 2018; Romero et al., 2000) and behavioural changes such as decreased chick provisioning rates in breeding birds (Dawson & Bortolotti, 2000; Robinson et al., 2017). Various weather metrics are associated with fecundity (i.e. chick survival), adult survival and recruitment of breeding spotted owls (Franklin et al., 2000, 2021), but the mechanism driving these relationships is unknown. For many species, CORT concentrations increase in response to changes in temperature and/or precipitation (Krause et al., 2018; Rogers et al., 1993; Ross et al., 2015). Thus, increasing precipitation can lead to reduced food availability, physiological condition and survival. Protection from stochastic weather provided by the forest canopy may be one of the reasons why mature forest is important to spotted owl fecundity (Dugger et al., 2005, 2016), and might be predicted to impact survival of juveniles either directly through increased exposure or indirectly through influences on food resources or parental behaviour.

However, juvenile development is influenced by more than the physical landscape. Birds with more breeding experience, often measured through number of breeding attempts, tend to produce young in better physiological condition with a higher probability of survival (Maness & Anderson, 2013; Saunders et al., 2012). In addition, breeding experience is related to CORT levels in breeding eiders (*Somateria* spp.; Jaatinen et al., 2013) and may also be related to juvenile CORT through CORT-related differences in adult reproductive effort (Bonier et al., 2009; Schoenle et al., 2017). Breeding experience can be measured either as lifetime reproductive effort or the number of years spent on a given territory. Historically, spotted owls have high mate and site fidelity (Forsman et al., 2002), but breeding dispersal distances and rates have increased with barred owl presence (Jenkins et al., 2019, 2021). Breeding dispersal is costly and typically associated with poor territory quality and low reproductive success (Danchin & Cam, 2002; Jenkins et al., 2019). Therefore, using the number of years on a specific territory rather than overall experience may indicate low overall breeding experience or high turn-over related to undesirable landscape conditions that may manifest in juvenile feather CORT.

Exploring patterns in juvenile feather CORT and the factors related to it may reveal sources of energetic demands during development and provide insights into underlying mechanisms driving population declines in northern spotted owls. We measured differences in juvenile spotted owl feather CORT associated with individual and environmental conditions to better understand potential challenges during development. We predicted that juvenile feather CORT would be greater with (1) increased barred owl presence and (2) precipitation and be lower with (1) larger proportions of mature forest within a territory, (2) increased juvenile mass, (3) increased parental experience on a territory and (4) increased temperatures.

2 | MATERIALS AND METHODS

2.1 | Study areas and feather collection

We used feathers collected from seven long-term demographic study areas across the range of spotted owls in the United States (Figure 1; Franklin et al., 2021). Study areas included Cle Elum and Olympic peninsula in Washington, and Coast Range, H.J. Andrews, Tyee, Klamath, and South Cascades in Oregon (Anthony et al., 2006). These study areas were largely representative of the environmental variation across the range of the spotted owl, including land ownership, topography, climate and forest structure (Franklin et al., 2021).

Crews monitored historical spotted owl territories annually between 15 March and 31 August 2001–2017, capturing and banding 1,056 fledged juveniles for individual identification. During banding, observers collected contour feathers from the belly, breast, back, and head of juveniles and stored them in plastic bags at room temperature (19–22°C; Mikkelsen, 2021). Sample collection was opportunistic and to minimize harm to owls, the area of the body

and number of feathers collected varied by natural feather loss, but 4–12 contour feathers was typical. All feathers were fully grown at the time of collection. All relevant state and federal permits were acquired and maintained for all study areas. All protocols for handling owls were approved under animal care and use permits overseen by Oregon State University's Institutional Animal Care and Use Committee.

2.2 | Laboratory methods

Increased circulating CORT decreases feather mass and growth rates (Jenni-Eiermann et al., 2015; Lattin et al., 2011; Patterson et al., 2015), which can distort relationships between feather CORT and environmental variables. To minimize this potential bias, we standardized feather CORT values by total sample mass (picograms CORT per milligram of feather; Freeman & Newman, 2018; Lendvai et al., 2013; Will et al., 2019; Appendix S1). We used radioimmunoassays to estimate corticosterone in feathers between 5 and 90 mg total mass (Appendix S1). We assayed all the feathers in each sample collected for 95% of the samples. Five percent of the samples were greater than 90 mg and were divided into two or three parts of approximately similar mass. Nearly all feathers were entirely or mostly plumulaceous with each sample having a photographic record.

Following the protocol established by Bortolotti et al. (2008), we removed each calamus, measured along the rachis to the nearest mm, and then weighed each feather to the nearest tenth of a milligram. We cut the feather into pieces less than 5 mm² and placed them in 20 ml test tubes with 7 ml of high-performance liquid chromatography grade methanol (VWR International, Radnor, Pennsylvania). We placed samples in a sonicating water bath at room temperature with a cap to limit evaporation for 30 min and then moved them to a shaking water bath at 50°C overnight. We used individual 23 cm disposable glass Pasteur pipettes to transfer each sample extract to 14 ml test tubes and rinsed the original feather sample with an additional 3.0 ml of methanol for 2 hr and that was added to the sample in the 14 ml test tube. We dried each sample under an evaporator rack with pressurized air in a water bath at 40°C. We reconstituted the dried samples in 250 ml of buffer solution, vortexed the samples and then refrigerated them overnight. We then aliquoted the samples into duplicate 5 ml tubes and performed radioimmunoassays following the manufacturer's instructions (MP Biomedicals, LLC; Immunochem™ Double antibody Corticosterone ¹²⁵I RIA Kit, Cat. No. 07-120103), except we used half-volumes. We used a parallelism test of two pool samples sequentially diluted 1:1 (20% binding) to 1:64 (90% binding) to ensure samples fell within the quantitative range of the assay and that our feather mass was adequate to achieve ~50% binding. Both samples were parallel to a standard curve and a 1:4 dilution was adopted. Inter-assay coefficient of variation was 9.2% across seven assays and intra-assay coefficient of variation was 1.9%. For samples that were subset and used to estimate extraction variation, we used the mean feather CORT for subsequent analyses.

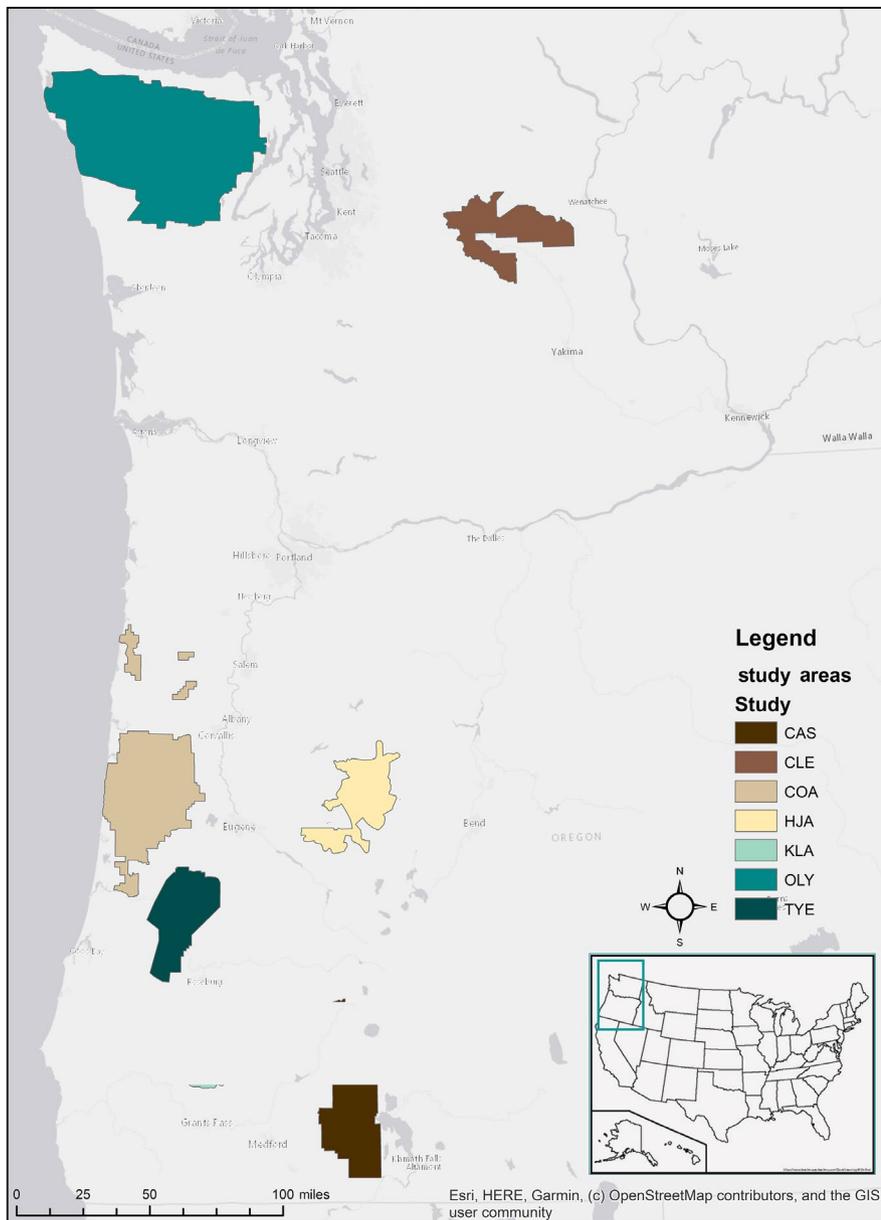


FIGURE 1 Map of the seven study areas across the Pacific Northwest of the United States where spotted owl populations were monitored, and feathers collected during 2001–2017. Study areas included Cle Elum (CLE), Olympic peninsula (OLY), Coast Range (COA), H.J. Andrews (HJA), Tyee (TYE), Klamath (KLA) and South Cascades (CAS)

2.3 | Development of covariates

To link feather CORT concentrations of juvenile spotted owls to environmental covariates, we delineated spotted owl territory boundaries by generating Thiessen polygons based on geographical points of annual nest locations, activity centres or owl locations (Franklin et al., 2021). Thiessen polygons define an area that is closest to each point categorized as a specific territory, relative to all other points categorized within surrounding territories (Franklin et al., 2021). In some cases, juvenile feathers were collected outside of historical study areas or did not have a Thiessen polygon associated with it. In these cases, we used ArcMap 10.5.1 to create a buffer of 901 hectares around the banding location, which was the average Thiessen polygon size.

During the banding process, observers weighed juveniles to the nearest gram which we used as the MASS covariate (Table 1),

but approximately 13% of juveniles were released prior to weighing. We used mean mass for the study area a juvenile was banded to represent MASS for these individuals. We checked our model with the full dataset against a subset without the populated MASS records and determined that it was appropriate to retain the samples missing MASS for analysis (Appendix S2, Table S1). MASS was positively correlated with the day of year on which a juvenile was banded ($r = 0.49$), which may indicate that MASS does not represent body condition but is confounded with juvenile age. We compared data between siblings to control for differences in age, genetics and resource availability and determined that MASS was indicative of overall body condition, which may include structural size, but MASS was not completely confounded by juvenile age (Appendix S2, Figure S1).

We calculated the amount of forest cover within each territory with 2018 LandSat data, Google Earth Engine and LandTrendr to

TABLE 1 Landscape and individual covariate descriptions and predicted effects on variation in northern spotted owl juvenile feather corticosterone from seven study areas in the Pacific Northwest of the United States during 2001–2017

Covariate	Description	Expected Relationship with feather CORT
PPT ₁ –PPT ₈	Annual study area specific mean of daily precipitation (mm) in 8 different 2-week periods: 1: April 10–April 23; 2: April 24–May 7; 3: May 8–May 21; 4: May 22–June 4; 5: June 5–June 18; 6: June 19–July 2; 7: July 3–July 17; 8: July 18–July 31	+
TEMP ₁ –TEMP ₈	Study area specific mean of daily mean temperatures (°C) in 8 different 2-week periods: 1: April 10–April 23; 2: April 24–May 7; 3: May 8–May 21; 4: May 22–June 4; 5: June 5–June 18; 6: June 19–July 2; 7: July 3–July 17; 8: July 18–July 31	+ (early spring) – (summer)
MASS	Net mass of juvenile in grams at time of first banding	–
BO	Study area specific cumulative proportion of spotted owl territories occupied by barred owls in given year	+
N/R FOREST	The proportion of 30 × 30 m pixels in a juvenile's natal territory covered in forest designated as suitable for nesting/roosting in the year they hatched	–
EAS	The number of known years a juvenile's parents had occupied a territory, considered their number of breeding seasons of experience at a site	–

generate a year-specific proportion of 30 m × 30 m pixels that were classified as suitable forest for nesting and roosting within each territory in a juvenile's hatch year (N/R FOREST; Table 1; Davis et al., 2016; Mikkelsen, 2021).

More years spent at one of these sites by spotted owls indicates an increasing number of breeding attempts and success should improve with years of experience (Dugger et al., 2005). We used data from confirmed detections and identification of spotted owls to build capture histories and determine the number of years each adult had spent on the territory prior to and including the juvenile's hatch year to represent known parental experience on a territory (EAS; Table 1).

During spotted owl surveys, field crews documented barred owl detections (Dugger et al., 2016), but barred owls were not targeted specifically. The probability of incidentally detecting a barred owl if it is present on the territory at least once when ≥3 surveys per season were conducted was relatively high (e.g. ~0.86; Wiens et al., 2011). Thus, we used this index of annual barred owl presence to calculate the cumulative proportion of surveyed spotted owl territories in a study area where a barred owl was detected ≥1 time per season, in or before an owl's hatch year (BO; Table 1).

To model the relationship between weather and juvenile feather CORT, we used data from Oregon State University's Parameter-elevation Regressions on Independent Slopes Model (PRISM) Climate Group (<http://prism.oregonstate.edu>) to generate annual study area specific covariates (Table 1). Within each study area, we selected five 4 km² PRISM cells spaced throughout study areas and obtained the annual daily mean temperature (°C; TEMP) and daily precipitation (mm; PPT) from 10 April, which captured the mean

clutch initiation and hatch date, to July 31, when subadult plumage is fully grown (Forsman, 1981; Forsman et al., 1984). Because of the wide variation in temperature and precipitation within the juvenile rearing period, we binned April 10 through July 31 into eight, 2-week periods and calculated average mean daily temperature (TEMP) and average precipitation (PPT) for each of those 2-week periods. In other words, the average of mean daily temperatures during 10–24 April was named TEMP₁, the average of mean daily temperatures during 25 April–9 May was named TEMP₂ and so on.

2.4 | Statistical analysis

We natural log transformed the extracted feather CORT values to normalize the distribution of the data. We standardized all covariates with a z-transformation, then used general mixed-effects linear regression models in R version 4.0.3 (R Core Team, 2020) using the `LME4` package to examine relationships between juvenile spotted owl feather CORT concentrations and environmental and individual covariates (Bates et al., 2015; Zuur et al., 2009). We began the modeling process by determining the best random effects structure by comparing intercept-only models containing the additive effect of study area, year (as a categorical variable), nest number, all combinations of these additive effects, and an interaction between year and study area on the intercept. The interaction allowed feather CORT to vary among study areas and among years within study areas. Retaining the best random effects structure, we then modelled fixed effects.

2.5 | Model set development

We used an information-theoretic approach and Akaike's information-theoretic criterion for small sample sizes (AIC_c) to determine the most supported model from an a priori model set using a combination of build-up modelling and secondary-candidate modelling strategies

(Burnham et al., 2002; Morin et al., 2020). To determine the most supported 2-week period for PPT and TEMP, we used AIC_c scores, model weights and model deviances for each period, and used the most supported weather covariates in subsequent modelling steps (Mikkelsen, 2021). We fit univariate models of each covariate and retained all models within seven AIC_c units in the next stage of

TABLE 2 Most supported models explaining variation in juvenile spotted owl feather corticosterone from seven study areas across Washington and Oregon collected between 2001 and 2017. The structure of the top four models is provided with the AIC_c weight (w_i), AIC_c scores, the difference in AIC_c score from the top model (ΔAIC_c), model deviance, the number of estimated parameters, the beta estimate ($\hat{\beta}$) and the 95% confidence intervals of the beta estimate (LCI, UCI)

Model	w_i	AIC_c	ΔAIC_c	Deviance	k	Parameters	$\hat{\beta}$	LCI	UCI
MASS*PPT4+TEMP3	0.56	1841.2	0	1823.0	5	INTERCEPT	4.851	4.740	4.953
						MASS	-0.522	-0.560	-0.485
						PPT4	0.074	0.015	0.134
						TEMP3	0.074	0.013	0.135
						MASS*PPT4	-0.041	-0.075	-0.008
MASS*PPT	0.26	1842.7	1.5	1826.6	4	INTERCEPT	4.816	4.693	4.938
						MASS	-0.053	-0.091	-0.016
						PPT4	0.081	0.025	0.137
						MASS*PPT4	0.042	0.008	0.075
MASS+PPT+TEMP	0.08	1845.0	3.8	1828.8	4	INTERCEPT	4.853	4.750	4.957
						MASS	-0.056	-0.094	-0.018
						PPT4	0.087	0.029	0.146
						TEMP3	0.077	0.016	0.139
MASS+PPT	0.04	1846.7	5.5	1832.6	3	INTERCEPT	4.815	4.688	4.941
						MASS	-0.057	-0.094	-0.019
						PPT4	0.095	0.040	0.150
MASS*TEMP+PPT	0.03	1847.0	5.8	1828.8	5	INTERCEPT	4.854	4.723	4.99
						MASS	-0.057	-0.084	-0.029
						TEMP3	0.077	0.015	0.139
						PPT4	0.087	0.029	0.146
						MASS*TEMP3	0.004	-0.044	0.051
GENERAL	0.03	1847.3	6.1	1818.9	10	INTERCEPT	4.876	4.790	4.961
						MASS	-0.054	-0.092	-0.015
						PPT4	0.075	0.018	0.132
						TEMP3	0.093	0.039	0.147
						xBO	-0.059	-0.116	-0.002
						EASm	0.008	-0.030	0.046
						EASf	-0.012	-0.050	0.027
						N/R FOREST	0.008	-0.031	0.047
INTERCEPT	0.00	1862.9	21.7	1852.8	1	INTERCEPT	4.833	4.70	4.965

modelling. We also included the intercept-only model and a general model, which included all a priori hypotheses in a single model (Table 2). Covariates with a Pearson correlation coefficient ≥ 0.50 were not included in the same model. In addition to AIC_c weights, we assessed the strength of specific relationships with beta coefficient estimates (β) and the extent to which 95% confidence intervals for those estimates overlapped zero (Burnham et al., 2002). Those that did not contain zero indicated strong support, with ~10% of the interval overlapping zero indicated moderate support, and intervals widely overlapping zero indicated weak support (Forsman et al., 2011).

3 | RESULTS

3.1 | Responses of juvenile feather CORT to weather and individual mass

We used 4,720 feathers from 1,056 spotted owl juveniles with samples consisting of an average of 3.8 feathers with a mean mass of 41.8 mg. The geometric mean juvenile feather CORT was 131.6 pgmg^{-1} . The best random effect structure included the additive effects of study area, year and nest number. Univariate models within seven AIC_c were precipitation in the 4th period (PPT₄; May 22–June 4), temperatures during the 3rd period (TEMP₃; May 8–May 21) and MASS. The final model set contained four models within seven AIC_c units that comprised 0.99 of cumulative model weight. Other models had very little support, with model weights

≤ 0.01 (Table 2; Table S2). The top model contained a negative relationship between feather CORT and MASS, positive relationships with PPT₄ and TEMP₃, and an interaction between MASS and PPT₄, in which the positive relationship between feather CORT and PPT₄ became weaker as MASS increased (Table 2). We found weak or no support for an effect of BO, N/R FOREST or EAS on feather CORT (Table S2).

PPT₄ was the most supported univariate model, with 1.5 times more support in the data than the second-best univariate model (MASS; Table S2). Coefficients from models with PPT₄ (no interaction) were consistently positive and when MASS and TEMP₃ in the top model were held at their means, a 1 mm increase in precipitation corresponded to a 3.9% increase in feather CORT (Table 2; Figure 2b). The highest ranked model without PPT₄ was 9.0 AIC_c units from the top model and had a model weight of 0.006 (Table S2).

MASS was present in all competitive models and, in models without interaction terms, coefficients were consistently negative (Table 2; Figure 2a). In the top model, when all other coefficients were held at their means, an increase in mass of 50 g corresponded to a 3.3% decrease in feather CORT. Based on demographic analysis of the same dataset, birds below the mean weight of 546 g, each increase of 50 g corresponds to ~0.07 increase in survival probability and a 0.03–0.05 increase in recruitment probability (Mikkelsen, 2021).

The interaction term between MASS and PPT₄ had over 6.8 times more support in the data than the additive only model (Table 2). The effect of PPT₄ on feather CORT was ameliorated by juvenile mass as

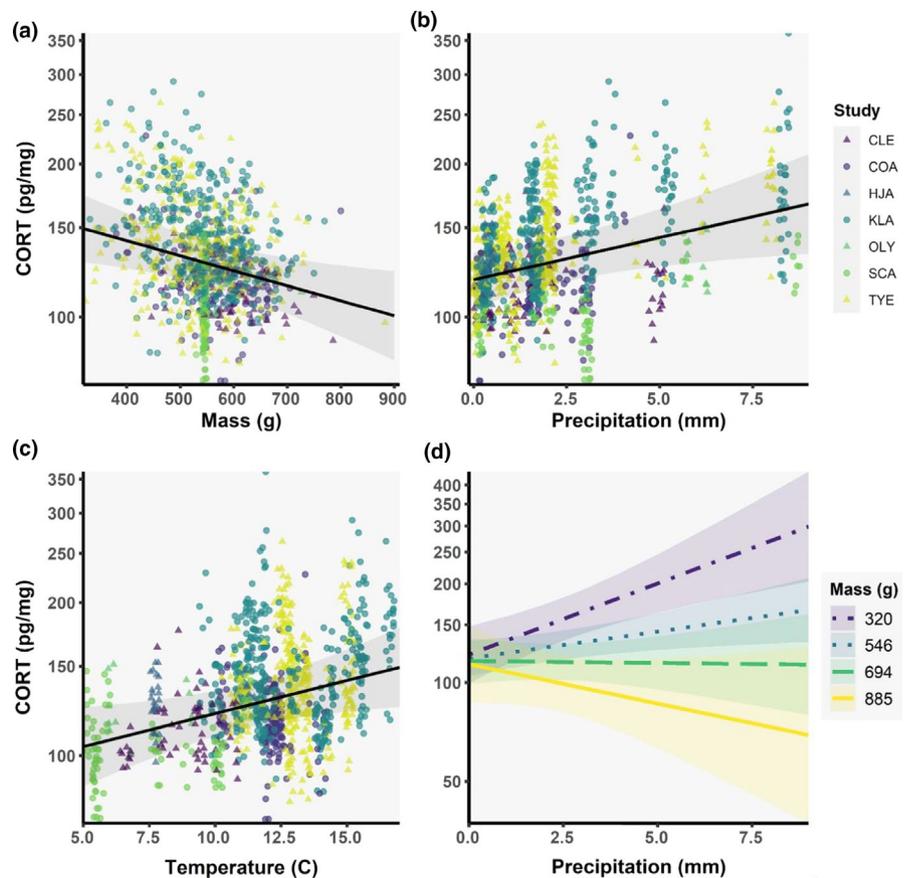


FIGURE 2 Partial residual plots of fitted northern spotted owl juvenile feather corticosterone (feather CORT) and covariates from the most supported model (MASS*PPT₄+TEMP₃) with all y-axes on the natural log scale. The lines represent the fitted regressions for juvenile mass (g) at banding (a), annual average precipitation (mm) for May 22–June 4 (b), annual mean temperature (°C) for the 2-week period from May 8 to May 21 (c), and the interaction between mass and precipitation (d). Shaded areas represent 95% confidence intervals, with the fitted estimates of feather CORT represented by points that vary in symbol and colour related to the study area from which they were collected (a–c). Estimates were derived by holding all other variables in the model at their means

the effect of precipitation on feather CORT decreased as MASS increased (Figure 2d). In the top model, a 400 g juvenile would have an 8.1% increase in feather CORT with 1 mm increase in precipitation, whereas a 450 g juvenile would have only a 6.6% increase in feather CORT, which is a difference of 1.5%. The effect of increased precipitation on feather CORT decreased as chick mass increased to ~694 g, at which point increasing precipitation no longer influenced feather CORT and for juveniles >694 g, the relationship became negative (Figure 2d).

The final model set also indicated support for a positive relationship between juvenile feather CORT and $TEMP_3$, with four of the six competitive models containing $TEMP_3$ (Table 2). The coefficients for $TEMP_3$ were consistently positive, and based on the most supported model, a 1°C increase in average daily mean temperature was associated with a 3% increase in feather CORT (Table 2; Figure 2c).

3.2 | Random effects and barred owls on juvenile spotted owl feather CORT

Despite the strong support for the best model, which had an AIC_c score 21.7 units lower than the intercept-only model and 6.1 AIC_c units lower than the general model (Table 2), the conditional R^2 value for this model was 0.30 and the marginal R^2 was 0.06. The difference between the two R^2 values indicates that most of the variation in the data was explained by random effects. This is largely due to the uneven distribution of the data, which confounded the effects of time and study area, two components known to be important to spotted owl demographics (Franklin et al., 2021). Contrary to our predictions, analysis of the general model indicated weak support for a negative relationship between BO presence and feather CORT ($\hat{\beta}_{BO} = -0.059$, 95% CI's = -0.116 to -0.002; Table 2).

4 | DISCUSSION

At baseline concentrations, CORT is involved in metabolism, immunity and electrolyte balance, but concentrations increase rapidly in response to negative stimuli and activate secondary pathways, known as the stress response (Romero & Fairhurst, 2016; Sapolsky et al., 2000; Wingfield, 2005). Understanding the factors that result in increases in CORT can help wildlife ecologists make predictions about how individual physiological responses translate into population-level changes. We used feathers collected from most of the spotted owl range over 17 years to focus on juvenile physiology with detailed insight into individual and landscape characteristics relevant to conservation efforts.

4.1 | Late spring precipitation and juvenile feather CORT

Precipitation from May 22 to June 4 was related to juvenile feather CORT concentrations, even though precipitation during that period

was not particularly high (0–8.6 mm) compared to other periods during the breeding season. However, it is a critical time when spotted owls are fledging, transitioning from growing their juvenile plumage to beginning their prebasic moult, developing flight muscles and increasing locomotor activity—all while exposed to a novel environment (Forsman et al., 1984). These factors combine to make this stage an energetically taxing period in which, due to poor flight ability, juveniles are highly vulnerable to predation and their environment (Forsman et al., 1984). Limited mobility may also leave juveniles exposed to precipitation and wet down severely alters thermal conductance (Bakken et al., 2006; Steen & Gabrielsen, 1988), which may increase energy demands for homeothermy, increasing CORT and reallocating energy from growth and development.

In addition to increased energetic demands, provisioning rates in raptors tend to decrease with increasing precipitation, which may contribute to the physiological state of juveniles during fledging (Dawson & Bortolotti, 2000; Robinson et al., 2017). The relationship between precipitation and feather CORT may be strongest, not when precipitation is highest, but when energetic demands are already particularly high, and thus juveniles are sensitive to small increases in energy costs. Spring precipitation has increased in the Pacific Northwest, with further increases projected in some areas of their range; however, winter precipitation is projected to increase across the spotted owl range over the next century (USGCRP, 2017). Increased precipitation in winter and spring may make this period even more challenging for fledging spotted owls, as they must either avoid or endure increased precipitation. Avoidance requires moving to an area of overhead cover to escape precipitation, and that movement requires energy expenditure. Enduring means staying in place and using energy to maintain homeothermy. In either strategy, energy is used to respond to precipitation, therefore limiting energetic investments in growth, which may have long-term consequences for survival and recruitment (Maness & Anderson, 2013; Mikkelsen, 2021).

4.2 | Juvenile condition and feather CORT

Juvenile mass is a common proxy for overall body condition in avian species and is associated with higher survival and recruitment (Covas et al., 2002; Maness & Anderson, 2013; Mikkelsen, 2021; Monrós et al., 2002). Because CORT is a metabolic hormone that mobilizes both lipids and proteins for immediate use (Sapolsky et al., 2000; Wingfield et al., 1998; Vera et al., 2017), greater juvenile mass should be related to lower corticosterone. We found that feather CORT in juvenile spotted owls decreased as juvenile mass increased, consistent with other studies that reported feather CORT as an indicator of individual physiological condition (Lamb et al., 2016; López-Jiménez et al., 2016).

Because of annual variation in the distribution of samples across the range, the effects of time and study area were confounded and could not be included in this analysis. However, of the seven study areas included, four locations had sufficient samples to estimate trends through time. Three study areas in Oregon (Coast Range,

Tyee, and Klamath) showed a trend of decreasing juvenile mass through time, while juveniles in Cle Elum, Washington, showed no trend through time (Appendix S2, Figure S2). This may be an indicator of increasing challenges during spotted owl development or a reduction in available resources and should be taken into further consideration, as mass is associated with higher recruitment and survival probability (Mikkelsen, 2021).

Besides an indicator of overall condition, juvenile mass also indicates energy reserves to maintain homeothermy under adverse weather conditions (Houston & McNamara, 1993; Rizzolo et al., 2015). The interaction between juvenile mass and precipitation suggests that increasing juvenile mass ameliorated the negative effect of increasing precipitation. This may be due to heavier birds having more resources to maintain homeothermy, a lower surface to volume ratio that is less conducive to heat loss to the environment, or larger birds being more developed with better flight and climbing skills to reach covered perches.

4.3 | Spring temperatures and juvenile feather CORT

The temperature covariate with the most support in the data encompassed temperatures from May 8 to May 21 which ranged from 5.3 to 16.6°C. Typically, in temperate climates, spring seasons marked by cold temperatures and heavy precipitation are negatively associated with survival and reproduction (Dugger et al., 2016; Rockweit et al., 2012). Therefore, increasing temperatures should benefit juvenile spotted owls. However, juvenile spotted owl feather CORT had a positive relationship with temperature during this time, indicating that warm temperatures rather than cold temperatures were associated with physiological responses in juveniles. Like boreal owl species, spotted owl feathers are highly insulative, resulting in relatively low tolerance for high ambient temperatures (Barrows, 1981). Just as poor flight skills can leave fledglings exposed to precipitation, limited mobility may also result in fledglings with little thermal cover, thereby increasing energetic demands to maintain homeothermy and risking hyperthermia (Barrows, 1981). Recent studies that have focused on early avian development show that even small increases in temperatures during nestling and post-fledging can impact demographics (Greño et al., 2007; Rodríguez et al., 2016). Juveniles suffering from hyperthermia tend to be lethargic with a loss of appetite, and reduced growth rates (Geraert et al., 1996). Experimentally heating nest cavities by 1°C during incubation reduced fledging success in prothonotary warblers *Parulidae protonotaria* and reduced body condition in Carolina wrens *Thryothorus ludovicianus* (Mueller et al., 2019). Maintenance costs come with trade-offs in future investments (Van De Pol et al., 2006), and even at moderate temperatures, our model results indicated a physiological toll of increasing temperatures. Temperatures have increased by 0.3–0.8°C across the Pacific Northwest with further increases of 2.1–2.6°C by the mid-21st century (USGCRP, 2017), which corresponds to a 6.3%–7.8% increase in feather CORT based on our results.

4.4 | Covariates with little or no support

The general model (WT+PPT₄+TEMP₃+BO+EAS_M+EAS_F+N/R FOREST+WT*PPT₄+WT*TEMP₃) indicated that barred owls had a negative relationship with feather CORT, which was counter to our predictions. Because barred owls displace spotted owls and compete for similar prey (Lesmeister et al., 2018; Wiens et al., 2014), we expected that increased presence of barred owls would increase competitive pressure, resulting in higher juvenile feather CORT (Santicchia et al., 2018). However, the effect of barred owls had little support in our analysis. We also predicted an association between other potential stressors during developing; however, we did not find support for a relationship between feather CORT and the amount of nesting and roosting forest (N/R FOREST), possibly because we considered N/R FOREST across the entire natal territory, rather than at a local scale. Our sample of juvenile feathers was unevenly distributed among study areas and years, which may have weakened measurable effects of spatial landscape characteristics because temporal and spatial variation were somewhat confounded and accounted for by the random effects of study area and year. We also found no relationship with adult experience on a natal site (EAS). We assumed that an adult's familiarity with a territory would increase foraging efficiency. However, provisioning rates and parental investment may be better explained by age, overall breeding experience or may not vary widely between spotted owl pairs. Spotted owls predominately consume nocturnal mammals (i.e. flying squirrels, *Glaucomys* spp., woodrats *Neotoma* spp. and lagomorphs; Forsman et al., 1984; Wiens et al., 2014). Provisioning may be predominately driven by prey availability of these groups, in that even the most dedicated and experienced parent may not be able to compensate for low prey densities by switching prey species. A spotted owl adult's ability to provide for young may also be confounded by competition with barred owls, both directly for prey, and through competitive displacement of spotted owls to lower quality forests (Jenkins et al., 2021; Lesmeister et al., 2018; Singleton et al., 2010; Wiens et al., 2014).

5 | CONCLUSIONS

Juvenile spotted owl feather CORT was related to both the external environment and individual variation through juvenile mass, precipitation, temperature, and the interaction between mass and precipitation. These relationships illustrated the link between the environment and hormonal condition. Juvenile mass is a common proxy for body condition (Labocha & Hayes, 2012; Peig & Green, 2010; Piersma & Davidson, 1991) and is associated with greater survival and recruitment probabilities in spotted owls (Mikkelsen, 2021) and other species (Maness & Anderson, 2013; Ronget et al., 2018). Feather CORT is also associated with survival in spotted owls (Mikkelsen, 2021); thus, understanding how increasing temperatures and precipitation alter the physiology of less-studied life-history stages might provide insights into potential population responses, particularly in areas,

such as the Pacific Northwest, forecasted to experience changes in temperature and precipitation (USGCRP, 2017). Changes in precipitation and higher temperatures related to climate change will likely result in higher metabolic demands and higher feather CORT concentrations, which may negatively impact long-term population demographics.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

AUTHORS' CONTRIBUTIONS

D.B.L. and K.M.D. conceived the ideas and designed the methodology; D.B.L., K.M.D. and A.J.M. collected the data; K.M.O. performed the laboratory protocols; A.J.M., K.M.O. and D.B.L. analysed the data; A.J.M. and D.B.L. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ETHICS STATEMENT

All handling and marking of northern spotted owls was authorized and in compliance with regulations of the U.S. Fish and Wildlife Service, Oregon Department of Fish and Wildlife, Washington Department of Fish and Wildlife, and the Federal Bird Banding Lab. All protocols were approved by the Oregon State University Institutional Animal Care and Use Committee.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.zs7h44j9s> (Mikkelsen et al.2021).

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