

Juvenile Northern Spotted Owls with higher mass and intermediate levels of corticosterone have greater long-term survival

Ashlee J. Mikkelsen,^{1,*} Damon B. Lesmeister,^{2,3,4} Kathleen M. O'Reilly,⁵ and Katie M. Dugger^{4,6}

¹Department of Natural Sciences and Environmental Health, University of South-Eastern Norway, Vestfold-Telemark, Norway

²USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon, USA

³Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, Oregon, USA

⁴Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, Oregon, USA

⁵Department of Biology, University of Portland, Portland, Oregon, USA

⁶U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, Oregon, USA

*Corresponding author: Ashlee.Mikkelsen@usn.no

ABSTRACT

Early life experiences have carry-over effects that manifest in later life stages. Challenging rearing environments result in more energy invested in immediate survival and less energy on growth and maturation, which can decrease survival in both the short- and long-term. One way to measure differences in energy allocation to growth between individuals is through physiological indices, such as concentrations of the metabolic hormone corticosterone, and body condition. Corticosterone increases in response to challenges to homeostasis and mobilizes stored fat and muscle to meet energetic demands. Maintaining elevated corticosterone can result in poor body condition and decreased survival. Juvenile or pre-breeding age classes are typically a substantial portion of the total population and serve key functions in population dynamics in many long-lived species. Thus, understanding how the rearing environment may influence demographics across life-history stages is crucial to understanding larger population dynamics. Yet, demographic models and conservation planning often lack vital rate estimates for early life stages because, prior to breeding, animals cannot be effectively sampled (i.e., they are unobservable). We used corticosterone concentrations in feathers and body mass of fledged juvenile Northern Spotted Owls (*Strix occidentalis caurina*) as indicators of potential energetic limitations early in life and used a multi-state modeling framework to quantify the effect of these indicators on apparent annual survival prior to claiming a territory (pre-territorial birds) and the probability of recruiting into the territorial population. Apparent annual survival for pre-territorial birds was higher for birds with greater mass, earlier banding dates, and intermediate levels of corticosterone. Birds with greater mass at banding were also more likely to recruit into the territorial population. Our results demonstrate the importance of early development and traditionally excluded life-history stages on long-term demographics. Although early life stages are difficult to observe, monitoring and conservation efforts may be improved by increasing studies on pre-territorial animals, control of Barred Owls, and conservation of forest structures important for Spotted Owls. This may contribute to increased juvenile survival and recruitment.

Keywords: avian development, conservation, corticosterone, demographic modeling, energetic tradeoffs, life-history, Northern Spotted Owls, recruitment, *Strix occidentalis caurina*

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LAY SUMMARY

- Animals have many mechanisms for responding to physical challenges and maintaining homeostasis. For instance, certain hormones make fat and protein available for immediate use to meet these challenges.
- However, this uses energy that could be otherwise spent on growth and maturation, resulting in smaller animals with lower probability of survival and finding territories or mates.
- We used hormone concentrations and masses of juvenile Northern Spotted Owls as indicators of environmental challenges and related them to survival and recruitment (i.e., the probability of gaining a territory for the first time).
- Survival and recruitment increased with greater mass, and survival was highest for owls with intermediate hormone concentrations and those banded earlier in the season.
- Population monitoring and conservation of imperiled species may be improved with increased efforts to study the conditions of juvenile life stages, Barred Owl management, and review habitat designations that might improve recruitment probabilities.

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Los juveniles de *Strix occidentalis caurina* con mayor masa y niveles intermedios de corticosterona tienen una mayor supervivencia a largo plazo

RESUMEN

Las experiencias tempranas de la vida tienen efectos que se manifiestan en etapas posteriores de la vida. Los ambientes de cría desafiantes resultan en más energía invertida en la supervivencia inmediata y menos energía en el crecimiento y la maduración, lo que puede disminuir la supervivencia a corto y largo plazo. Una forma de medir las diferencias en la asignación de energía al crecimiento entre individuos es a través de índices fisiológicos, como las concentraciones de la hormona metabólica corticosterona y la condición corporal. La corticosterona aumenta en respuesta a los desafíos homeostáticos y moviliza grasa y músculo almacenados para satisfacer las demandas energéticas. Mantener niveles elevados de corticosterona puede resultar en una mala condición corporal y disminución de la supervivencia. Las clases de edad de juveniles o individuos pre-reproductivos son típicamente una porción sustancial de la población total y sirven funciones clave en la dinámica poblacional de muchas especies longevas. Por lo tanto, comprender cómo el ambiente de cría puede influir en la demografía a través de las etapas de la historia de vida es crucial para comprender las dinámicas poblacionales más grandes. Sin embargo, los modelos demográficos y la planificación de la conservación a menudo carecen de estimaciones de tasas vitales para las primeras etapas de la vida porque, antes de la reproducción, los animales no pueden ser muestreados de modo efectivo (es decir, son no observables). Utilizamos las concentraciones de corticosterona en plumas y la masa corporal de *Strix occidentalis caurina* como indicadores de posibles limitaciones energéticas tempranas en la vida y utilizamos un marco de modelado de múltiples estados para cuantificar el efecto de estos indicadores en la supervivencia anual aparente antes de reclamar un territorio (aves pre-territoriales) y la probabilidad de reclutamiento en la población territorial. La supervivencia anual aparente para las aves pre-territoriales fue mayor en aves con mayor masa corporal, fechas de anillamiento más tempranas y niveles intermedios de corticosterona. Las aves con mayor masa corporal al momento del anillamiento también tuvieron más probabilidades de reclutarse en la población territorial. Nuestros resultados demuestran la importancia del desarrollo temprano y de las etapas de la historia de vida tradicionalmente excluidas en las tendencias demográficas a largo plazo. Aunque las primeras etapas de vida son difíciles de observar, los esfuerzos de monitoreo y conservación pueden mejorarse mediante el aumento de estudios en animales pre-territoriales, el control de individuos de *S. o. caurina* y la conservación de las estructuras boscosas importantes para esta especie. Esto puede contribuir a un aumento en la supervivencia y el reclutamiento de los juveniles.

Palabras clave: compensaciones energéticas, conservación, corticosterona, desarrollo aviar, historia de vida, modelado demográfico, reclutamiento, *Strix occidentalis caurina*

INTRODUCTION

Sub-adult or pre-breeding life stages are difficult to study, and typically have a lower contribution to annual population growth rates than adult survival, resulting in their exclusion from demographic studies and conservation planning (Lenda *et al.* 2012, Robles and Ciudad 2017). However, nonbreeding animals typically make up a large proportion of a population and serve important roles in population dynamics, such as driving annual variation in population growth rates, buffering against stochastic effects, and acting as colonizers (Penteriani *et al.* 2005, Lenda *et al.* 2012, Robles and Ciudad 2017). Thus, they can have important impacts on population dynamics (Gaillard *et al.* 2000, Franklin *et al.* 2000).

A challenging rearing environment can decrease survival and dispersal of young animals (Graffen 1988, Monaghan 2008) and can have long-lasting effects on subsequent life stages (Metcalf and Monaghan 2001, Douhard *et al.* 2014). Less food availability due to decreased primary production or limited prey decreases energy available for growth and survival of developing offspring (Maness and Anderson 2013, Ronget *et al.* 2018). Repeated exposure to inclement weather can result in more energy expended on homeothermy (Rodríguez *et al.* 2016), and the presence of predators or competitors can alter behavior that negatively impacts growth, maturation, and survival (Berger and Gotthard 2008, Hua *et al.* 2014). Thus, in poor environments, juveniles must make tradeoffs between expending resources on immediate demands (i.e., homeostasis or predator avoidance) vs. spending resources on long-term investments (i.e., growth and fat storage; Metcalf and Monaghan 2001, Douhard *et al.* 2014). Challenging early conditions can have carry-over effects on later life-stages (Metcalf and Monaghan 2001, Monaghan 2008, Douhard *et al.* 2014), decreasing subsequent survival and reproduction. Thus, while early life stages may not be the largest contributors to overall annual population growth rates, a challenging rearing environment may have effects that

persist through transitions into key demographic classes, such as breeding adults. A better understanding of how rearing environment and energetic tradeoffs can have long-term effects on subsequent life stages is paramount to conservation planning and management.

Energetic tradeoffs, however, are difficult to measure directly, but steroid hormone profiles are good indices of the physiological challenges experienced by animals (Busch and Hayward 2009, Dantzer *et al.* 2014, Vera *et al.* 2017, Mikkelsen *et al.* 2021). Corticosterone (CORT) is a metabolic steroid hormone in reptiles, amphibians, rodents, and birds that is essential for critical physiological functions, such as protein synthesis and immunity (Vera *et al.* 2017). CORT also rapidly increases in response to challenges to homeostasis (i.e., inclement weather, infections, starving), resulting in mobilization of fats and proteins and shifting resources away from storage, maintenance, and growth for immediate use and survival (Busch and Hayward 2009, Dantzer *et al.* 2014). Thus, CORT functions as an effective index of physiological condition related to energetic tradeoffs between immediate needs and long-term investments (Bortolotti *et al.* 2008, Dantzer *et al.* 2014). While adaptive in the short-term, prolonged exposure to elevated CORT can be detrimental, resulting in depressed immunocompetence and survival (Busch and Hayward 2009, Dantzer *et al.* 2014, Vera *et al.* 2017). Animals with sufficient resources to meet metabolic demands or who have fewer metabolic demands overall should have lower circulating CORT concentrations and suffer less of the negative effects of prolonged CORT exposure than peers who are resource limited.

Body mass is another important indicator of rearing environment, incorporating investments in skeletal and organ growth, as well as fat stores (Piersma and Davidson 1991, Labocha and Hayes 2012), and acting as an integrative measure of both short- and long-term energy storage. Thus, animals with abundant resources and few demands will have

greater mass than animals that are resource limited or live in a challenging environment. While better body condition is associated with increased survival, recruitment, and life-span (Labocha and Hayes 2012, Maness and Anderson 2013, Ronget *et al.* 2018), most studies consider only short-term effects (typically a season or single year). As a result, there remains a gap in our understanding—not only concerning life-history tradeoffs and carry-over effects from one life stage to another—but also how these tradeoffs alter population dynamics, even in widely studied taxa.

For instance, the Northern Spotted Owl (*Strix occidentalis caurina*) has been extensively monitored for over 30 years, but demographic studies have focused on territorial breeders, with the first years of life prior to settling on a territory rarely included (Dugger *et al.* 2016, Franklin *et al.* 2021). Therefore, there is uncertainty regarding the probability of juveniles recruiting into the territorial population and the underlying mechanisms influencing recruitment, despite extensive monitoring efforts. Northern Spotted Owls are long-lived, late-seral forest obligates (Forsman *et al.* 1984, USFWS 1990) endemic to southwest Canada and the Pacific Northwest, USA. The sub-species is “endangered” under the Canadian Species at Risk Act (COSEWIC 2008) and “threatened” under the United States Endangered Species Act (USFWS 1990), but due to continued population declines and unresolved threats, the sub-species now warrants “endangered” status in the USA (USFWS 2020). Northern Spotted Owls (hereafter Spotted Owl) have altricial young that hatch in spring and disperse in fall to spend several months to years prospecting for a territory and mate (Forsman *et al.* 1984). Dispersing juveniles are non-territorial and difficult to detect (Forsman *et al.* 1984, 2002), which makes survival during this period challenging to estimate. However, Spotted Owl studies provide a wealth of long-term monitoring data (Franklin *et al.* 2021), making them an ideal model for examining relationships between early-life development and demography.

Currently, the congeneric Barred Owl (*Strix varia*) is one of the greatest threats to Spotted Owls (USFWS 2020, Franklin *et al.* 2021, Wiens *et al.* 2021). Both species use similar resources, but Barred Owls are larger, more aggressive, exist in higher densities, and have a more generalist life-history (Wiens *et al.* 2011, Lesmeister *et al.* 2018). Barred owls displace Spotted Owls, and competition between these two species increases rates and distances of breeding dispersal (after territory acquisition; Jenkins *et al.* 2019a, 2021), and may also increase the distances Spotted Owls must move during natal dispersal before finding available territories. Starvation and predation are the two greatest causes of mortality during natal dispersal (Forsman *et al.* 1984, 2002; Miller *et al.* 1997). Being forced to move over longer distances increases both the energetic costs and probability of encountering a predator, resulting in an increased mortality risk (Miller *et al.* 1997). In addition, competition for prey between Barred Owls and Spotted Owls may result in increased nutritional stress for juvenile Spotted Owls, limiting available resources for growth and increasing CORT concentrations.

We used long-term, capture-mark-resight data across 7 study areas in Oregon and Washington state (USA) to estimate (1) apparent annual survival (Φ) of pre-territorial and territorial Spotted Owls and (2) recruitment (ψ) of pre-territorial Spotted Owls into the territorial population over 17 years. We examined relationships between vital rates and CORT extracted from feathers, juvenile mass, and Barred

Owl presence to examine whether differences in indices of metabolic demands and challenging environments would have carry-over effects that resulted in subsequent survival and recruitment differences. We predicted (1) a negative relationship between Barred Owl presence and survival for both territorial and pre-territorial Spotted Owls as well as recruitment rates of pre-territorial owls, (2) a negative relationship between CORT and pre-territorial survival and/or recruitment, and (3) a positive relationship between pre-territorial survival and/or recruitment and mass.

MATERIALS AND METHODS

Study Areas

We used capture histories, feathers, and banding data collected from 2001 to 2017 as part of a long-term demographic monitoring program for Spotted Owls (Lint *et al.* 1999). Study areas included Cle Elum and Olympic Peninsula in Washington state, and Coast Range, H.J. Andrews, Tyee, Klamath, and South Cascades in Oregon state (Figure 1). These study areas cover almost 10% of the range of Spotted Owls and have varying topography, climate, land management, and forest structure, as described in prior publications (Forsman *et al.* 2011, Dugger *et al.* 2016). Cle Elum, Coast Range, Tyee, and Klamath study areas contain a blend of federal and private lands, whereas Olympic Peninsula, H.J. Andrews, and South Cascades largely cover federal lands.

Field Methods and Feather Collection

Our field crews monitored historic Spotted Owl territories annually, using standard protocols to estimate occupancy, survival, and reproductive output of individually marked owls (Franklin *et al.* 1996). After juvenile owls left the nest, surveyors captured and banded owls with individually numbered U.S. Fish and Wildlife Service bands and color bands. When crews recaptured birds marked as juveniles for the first time, they confirmed their USFWS bands and replaced their cohort-specific color bands with a unique color-band that allowed identification of birds through resighting alone (Forsman *et al.* 1984).

During banding, field crews weighed birds and collected small samples of body feathers from the breast, back, or head, placed them in plastic bags, and stored them at room temperature (19–22°C). We collected feathers opportunistically, thus the number and feather tract sampled varied. All relevant state and federal permits were acquired and maintained for all study areas, and protocols for handling owls were approved under animal care and use permits overseen by Oregon State University's Institutional Animal Care and Use Committee.

Lab Methods

Circulating CORT can cause decreased feather mass or growth rates (Jenni-Eiermann *et al.* 2015, Patterson *et al.* 2015), resulting in concentrated CORT in feathers of similar lengths, but with different mass, which can conceal important relationships between feather CORT and environmental variables (Lattin *et al.* 2011, Patterson *et al.* 2015). To control for this, we standardized feather CORT values by overall sample mass (picograms CORT per milligram feather) rather than feather length (Freeman and Newman 2018, Will *et al.* 2019). We assayed feather samples between 5 and 90 mg using radioimmunoassay following the study by Bortolotti *et*

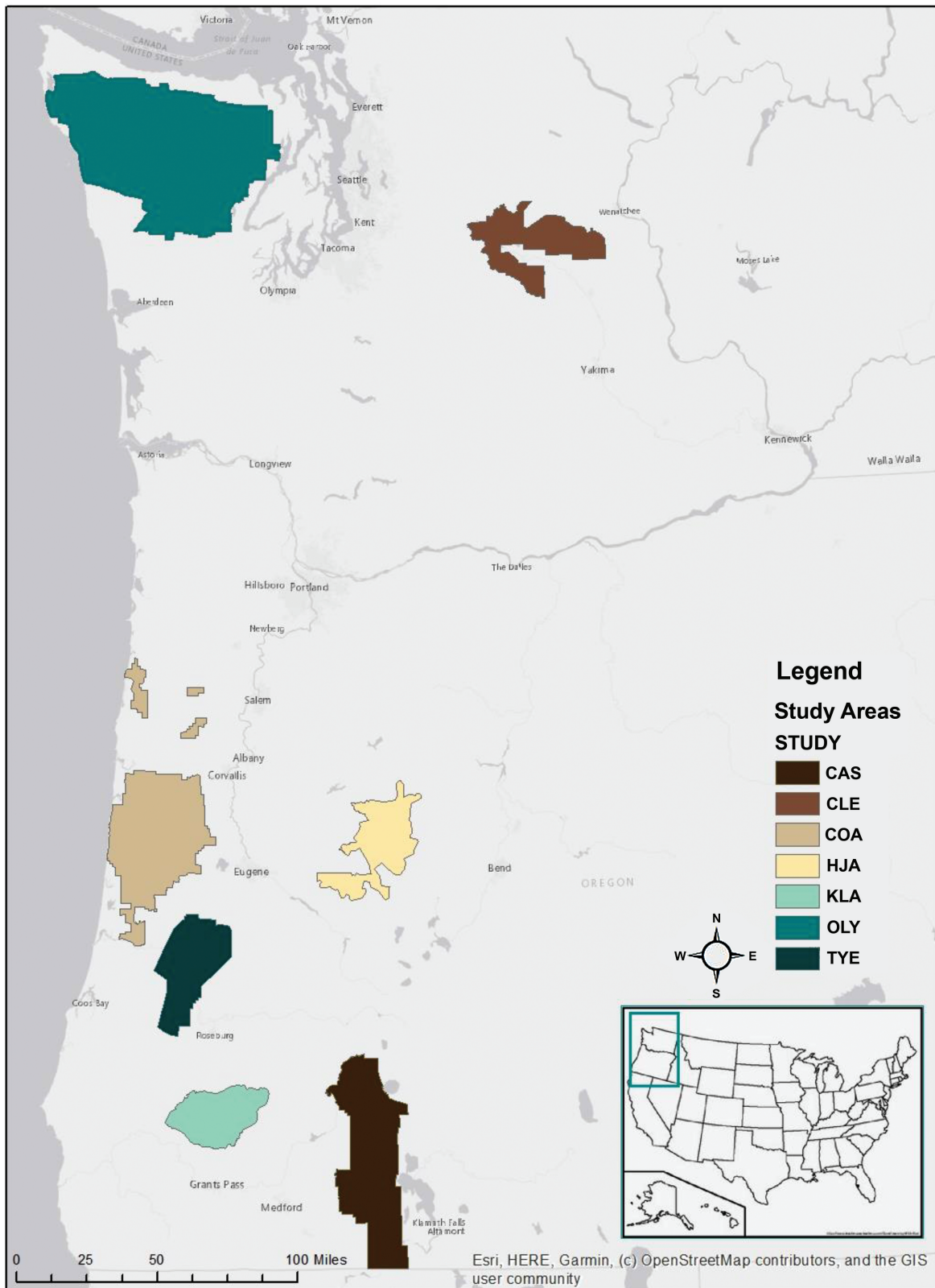


FIGURE 1. Locations of seven Northern Spotted Owl monitoring study areas in Oregon and Washington, 2001–2017. Study areas included Cle Elum (CLE), Olympic peninsula (OLY), Coast Range (COA), H.J. Andrews (HJA), Tye (TYE), Klamath (KLA), and South Cascades (CAS).

al. (2008). We removed each calamus and weighed feathers to the nearest tenth of a milligram and measured along the rachis to the nearest millimeter. We cut the feathers into pieces < 5 mm² and placed them in a 20-mL test tube with 7 mL of

high-pressure liquid chromatography grade methanol (VWR international, LLC.). After the addition of a cap, we put the samples in a sonicating water bath at room temperature for 30 min and then a shaking water bath at 50°C overnight.

TABLE 1. Descriptions and abbreviations of territorial states, estimated demographic parameters, and covariates used in modelling recruitment and survival for Northern Spotted Owls on seven study areas in Washington and Oregon, 2001–2017.

Category	Abbreviation	Description
Territorial states	PT	Categorical variable that denotes pre-territorial owls that have fledged and presumably dispersed but have yet to claim a territory. All owls enter the PT state when they fledge and are initially captured and banded. Time spent in this state ranges from 0 to 12 year.
	TR	Categorical variable that denotes territorial owls that have successfully fledged, dispersed, and claimed a territory to defend. Contains a mix of ages 1–17.
Demographic parameters	p	Probability that an owl is detected given that it is alive and on the study area during the survey interval (March–August).
	ψ	Probability that a pre-territorial owl settles on a territory and becomes territorial, thus transitioning from PT to TR (recruitment).
	Φ^{PT}, Φ^{TR}	Probability that an owl survives the interval from t to $t + 1$, where t represents the breeding season of a given year (March–August) for each territorial state (pre-territorial and territorial).
Covariates	FCORT	Individual covariate representing the linear relationship between demographic parameters and juvenile feather corticosterone.
	lnFCORT	Individual covariate representing the log-linear relationship between demographic parameters and juvenile feather corticosterone, calculated by taking the natural log of FCORT.

Using individual 23-cm glass Pasteur pipets, we transferred the methanol extract to a 14-mL test tube. We rinsed feathers in the original 20 mL test tube with 3 mL of methanol for 2 hr and then added the extract to the sample in the 14 mL test tube. We used an evaporator rack blowing air over our samples in a water bath at 40°C to evaporate the methanol. When tubes were dry, we reconstituted feather CORT in 250 mL of buffer solution. After vortexing samples and refrigerating overnight, we aliquoted the extracts into duplicate 5 mL tubes and conducted a radioimmunoassay (MP Biomedicals, LLC; Immunochem Double antibody Corticosterone ^{125}I RIA Kit, Cat. No. 07-120103) following manufacturer's instructions with the modification of using half volumes for all components. We used serial dilutions to conduct a parallelism test to validate the use of the MP Bio kit and confirm that the samples followed the standard curve and determined the optimum dilution to be 1 part (12.5 μL) extracted corticosterone and 3 parts (37.5 μL) buffer solution. Inter-assay variation was 9.2% across seven assays and intra-assay variation was 1.9%.

Covariate Development

Feather CORT

We determined that 15 feather CORT values beyond 2 SD from the overall mean were outliers related to extraction procedures. Because these 15 birds constituted <1.5% of the total sample, and the scope of this study went beyond the effects of CORT alone, we retained these birds in the data and replaced the outlying CORT concentrations with the mean (156.12 pg mg^{-1}). To ensure this would have no impact on inferences, we ran the most supported model with and without these samples. There were no changes to model coefficients, but when we included these samples, there was an increase in precision of the estimated effect of feather CORT.

When crews initially captured and banded juveniles, the exact age of owls varied by territory and year, and observers did not know dates of clutch initiation or hatch date. Thus, juvenile feather CORT represents a general period of early development when contour feathers are grown but does not correspond to exact dates (Supplementary Material). Previous

studies have reported linear, log-linear, and quadratic relationships between CORT and fitness (Busch and Hayward 2009, Dantzer *et al.* 2014); thus, we included each of these potential relationships in model sets when evaluating associations with feather CORT (FCORT; Table 1).

Mass

Field crews offered live mice to adult owls who then fed them to juveniles, disclosing the juvenile's location to the bander. In cases where the fledgling ate mice delivered by adults just before capture and banding, the bander subtracted the mass of the prey item (s ; domestic house mouse, *Mus musculus* ~15 g) from the total juvenile mass (MASS; Table 1). Due to variation in surveyor effort and the need to reduce handling time during inclement weather, some crews released juveniles without recording mass. We developed procedures to account for missing mass data so we could include all banded juveniles in the analysis (Supplementary Material).

Banding date covariate

There was a weak positive relationship between banding date (BD; Table 1) and MASS ($r = 0.49$, Supplementary Material). As we did not have hatch dates for juveniles, it was possible that birds banded later in the season were heavier because they were older than birds banded earlier, which would make body condition confounded by age. While we did not find evidence to support this (Supplementary Material), variation in fledgling survival relative to hatch date has been reported for many species (Maness and Anderson 2013). To account for potential variation in post-fledgling survival relative to hatch date within the season, we used the day of year when a bird was banded (BD) as a covariate in our analysis.

Barred Owl covariate

Throughout the study, we recorded Barred Owl detections during Spotted Owl surveys and calculated a Barred Owl (BO; Table 1) covariate as the annual proportion of territories across Oregon and Washington surveyed ≥ 3 times during the breeding season and had one or more Barred Owl detections recorded (Forsman *et al.* 2011, Wiens *et al.* 2011). Once a

Barred Owl was detected on a territory, we assumed no local extinction, and any incidences of non-detection in the future were a result of imperfect detection (Wiens *et al.* 2011, 2021). Thus, the BO covariate reflects a coarse cumulative index of the Barred Owl range expansion within our study areas but does not reflect whether a Barred Owl was directly affecting resource availability in the vicinity of Spotted Owl nests.

Temporal trends

Besides individual covariates, we also modeled temporal effects on vital rates to evaluate annual patterns unaccounted for by the annual increases in cumulative Barred Owl detections, or other sources of annual variation (Anthony *et al.* 2006, Franklin *et al.* 2021). We modeled general annual variation (t), a linear (T), quadratic (TT), and log-linear time trend ($\ln T$; Table 1) on the probability of detection (Anthony *et al.* 2006) and t , T , and $\ln T$ on survival and recruitment as there was no ecological rationale or evidence from previous studies supporting a quadratic time trend on these vital rates (Franklin *et al.* 2021). Feathers were not collected on all study areas in all years, so study area differences were confounded with temporal variation; therefore, we focused on general time trends across all study areas.

Analytical Methods

We used multi-state Cormack-Jolly-Seber open population models in Program MARK (vs. 9.0; <http://www.phidot.org/software/mark/downloads/>; Chapter 10; Cooch and White 2019) with an unobservable state (Lebreton *et al.* 2003) to generate model selection results and estimates of probability of detection (p), apparent annual survival (Φ) and the probability of transitioning between pre-territorial and territorial states (ψ ; owls banded as fledglings become unobservable for varying numbers of years prior to establishing territories). Estimates of apparent survival can be negatively biased because capture-mark-recapture models cannot differentiate between permanent emigration and mortality (Chapter 10; Cooch and White 2019). However, Spotted Owls disperse short distances relative to the size of surveyed demographic areas and have an estimated probability of 0–0.1 to disperse out of study areas as large as those in this study, thus we believe the bias associated with our estimates due to permanent emigration is low (Forsman *et al.* 2002, Zimmerman *et al.* 2007, Hollenbeck *et al.* 2018). Additionally, we used the unobservable state with deterministic transitions and constraints on the probability of detection following Lebreton *et al.* (2003) to address the period when birds banded as young were unobservable before gaining a territory (i.e., temporary emigration). After an owl was observed defending a territory during at least one nesting season (March to August), it transitioned into the observable, territorial (TR) state (Table 1). Each year, a territorial bird may not breed, or be detected, yet they are “observable” ($p > 0.00$) and cannot transition back to the unobservable, pre-territorial state (PT). Thus, to maintain this important deterministic transition, we fixed the probability of transitioning from the territorial state back to the pre-territorial state to zero. In addition, we fixed the probability of detection to zero for birds in the unobservable, pre-territorial (PT) state as they cannot be detected until they gain a territory.

To evaluate model support, we used an information-theoretic approach and Akaike’s Information-theoretic

Criterion for small sample sizes (AIC_c), relative differences in AIC_c (ΔAIC_c), and AIC_c weight (w_i) (Burnham and Anderson 2002). Prior to model building, we screened covariates for collinearity using Pearson covariance matrix. Because BO was an annual covariate, we used annual means of individual covariates to test for correlations. The only variables with covariance > 0.50 were BO and year, which were highly correlated, so we never included the BO covariate or other temporal parameters together in the same model. We used a combination of build-up and secondary candidate set modeling to minimize the total number of models evaluated (Morin *et al.* 2020). We began by modeling p and retained the most supported structure in all subsequent models. We then modeled survival and recruitment separately but followed identical protocols: we first determined the best time structure, then added covariates and interactions to the time structure for increasingly complex models.

We considered all survival and recruitment structures within five ΔAIC_c units of the top model to be competitive (Morin *et al.* 2020) and carried those into the final stage of modeling where we evaluated all combinations of recruitment and survival structures in the final model set. When drawing inference, we considered the model with the lowest AIC_c score and highest w_i to have the most support. We also considered the extent to which 95% confidence intervals (CIs) for $\lambda\beta$ estimates overlapped zero to evaluate strength of evidence for specific effects. Confidence intervals that did not contain zero indicated the strongest support, ~10% of the CIs overlapping zero indicated moderate support, and CIs widely overlapping zero were considered to have weak support (Forsman *et al.* 2011). We applied the median c -hat goodness of fit test on the most general model that included state by time interactions on all model parameters (i.e., $\Phi_{(t)}^{NT,TR}$, $p_{(t)}^{TR}$, $\psi_{(t)}^{NTtoTR}$) to test for over-dispersion (Cooch and White, 2019).

RESULTS

Data Summary

We conducted this analysis using encounter histories from 1,061 Spotted Owls banded as fledglings during 2001–2017. Of this total, 381 (35.9% of 2,385 total detections) were resighted after recruiting into the territorial breeding population. The age at which pre-territorial birds recruited into the territorial population ranged from 1 to 12 year, but the mean was 2.2 year (SD = 1.89), and the median was 2 year. Many pre-territorial birds recruited into the territorial population at age 1 (49%), 19% recruited at age 2, 16% at age 3, and the remaining 16% were distributed between age classes of 4–12. Most birds (93%) in this study came from the five study areas in Oregon, with 67% coming from just two study areas: Klamath and Tyee. This non-uniform sample distribution resulted from a combination of surveyor effort and different Spotted Owl population sizes and reproductive output among study areas. Estimates of median $\hat{c} = 1.01$, 95% CI: 0.24–1.78) and that no adjustments to account for overdispersion were needed. The probability of detecting territorial birds was high (0.84–0.99) and our results indicated strong support for a quadratic trend, with capture probabilities declining from 2002 to 2012 ($\hat{p}_{(2002)} = 0.99$, 95% CIs: 0.97–1.00, $\hat{p}_{(2012)} = 0.84$, 95% CIs: 0.80–0.87) and then increasing ($\hat{p}_{(2017)} = 0.94$, 95% CIs: 0.85–0.97). The final model set included 16 models representing all combinations

TABLE 2. Pre-territorial survival was lower than territorial Owls in Oregon and Washington and varied annually 2001–2017, but across all years, survival in the pre-territorial state was also affected by banding date, juvenile mass, and feather corticosterone concentrations. Final model selection results from the multi-state analysis of relationships between corticosteroids, body mass, and apparent annual survival and recruitment of Northern Spotted Owls.

Model	ΔAIC_c^a	w_i^b	k^c	Deviance ^d
$\Phi_{(BD+MASS+FCORT^2+t)}^{PT}, \Phi_{(t)}^{TR} P(TT) \psi_{(lnT*MASS)}$	0.0	0.260	28	3472.5
$\Phi_{(BD+MASS+t)}^{PT}, \Phi_{(t)}^{TR} P(TT) \psi_{(lnT*MASS)}$	1.0	0.156	26	3477.6
$\Phi_{(BD+MASS+FCORT^2)}^{PT}, \Phi_{(t)}^{TR} P(TT) \psi_{(BO*MASS)}$	1.1	0.152	28	3473.5
$\Phi_{(BD+MASS+FCORT^2)}^{PT}, \Phi_{(t)}^{TR} P(TT) \psi_{(lnT*MASS)}$	1.9	0.099	28	3474.4
$\Phi_{(BD+MASS)}^{PT}, \Phi_{(t)}^{TR} P(TT) \psi_{(BO*MASS)}$	2.7	0.069	26	3479.2
$\Phi_{(BD+MASS)}^{PT}, \Phi_{(t)}^{TR} P(TT) \psi_{(lnT*MASS)}$	3.4	0.047	26	3480.0
$\Phi_{(BD+MASS+FCORT^2+t)}^{PT}, \Phi_{(t)}^{TR} P(TT) \psi_{(BO*MASS)}$	3.8	0.039	28	3476.2
$\Phi_{(BD+MASS+t)}^{PT}, \Phi_{(t)}^{TR} P(TT) \psi_{(lnT*MASS)}$	4.2	0.033	25	3482.7
$\Phi_{(BD+MASS+FCORT^2+t)}^{PT}, \Phi_{(t)}^{TR} P(TT) \psi_{(lnT*MASS)}$	4.2	0.032	27	3478.7
$\Phi_{(BD+MASS+FCORT^2)}^{PT}, \Phi_{(t)}^{TR} P(TT) \psi_{(lnT*MASS)}$	4.3	0.030	27	3478.8
$\Phi_{(BD+MASS)}^{PT}, \Phi_{(t)}^{TR} P(TT) \psi_{(lnT*MASS)}$	4.9	0.022	25	3483.5
$\Phi_{(BD+MASS+t)}^{PT}, \Phi_{(t)}^{TR} P(TT) \psi_{(BO*MASS)}$	5.1	0.020	26	3481.7
$\Phi_{(BD+MASS+FCORT^2+t)}^{PT}, \Phi_{(t)}^{TR} P(TT) \psi_{(BO*MASS)}$	5.3	0.019	27	3479.8
$\Phi_{(BD+MASS)}^{PT}, \Phi_{(t)}^{TR} P(TT) \psi_{(BO*MASS)}$	5.8	0.014	25	3484.4
$\Phi_{(BD+MASS+FCORT^2+t)}^{PT}, \Phi_{(t)}^{TR} P(TT) \psi_{(BO*MASS)}$	8.2	0.004	27	3482.7
$\Phi_{(BD+MASS+t)}^{PT}, \Phi_{(t)}^{TR} P(TT) \psi_{(BO*MASS)}$	8.3	0.004	25	3486.9
$\Phi_{(BD+MASS+t)}^{PT}, \Phi_{(t)}^{TR} P(TT) \psi_{(BO*MASS)}$	27.9	0.000	22	3512.6

^aDifference in Akaike's information criteria corrected for small sample sizes relative to the model with the lowest AIC_c (ΔAIC_c).

^bAkaike weight (w_i).

^cNumber of parameters (k).

^dModel deviance.

Model covariates: general (t), linear (T), quadratic (TT), and log-linear (lnT) temporal structures.

Barred Owl presence (BO), banding date (BD), mass at banding ($MASS$), and quadratic juvenile feather corticosterone concentrations ($FCORT^2$).

Demographic parameters: recruitment (ψ) and apparent annual survival (Φ^{PT} = pre-territorial; Φ^{TR} = territorial).

of the 4 best survival structures and the 4 best recruitment structures from the previous modeling stages ($4 \Phi \times 4 \psi \times 1p = 16$ models).

Recruitment Probability

A negative log-linear trend (lnT) on the probability of recruitment was the most-supported temporal structure, suggesting strong declines in recruitment over time that leveled off at low probabilities near the end of the study. Important covariates associated with recruitment rates included the positive effect of mass and the negative effect of Barred Owl presence. In the final model set, 3 of the top 4 models had identical recruitment structures with an interaction between $MASS$ and lnT , whereas one model contained the interaction between $MASS$ and BO (Table 2). The negative effect of Barred Owl presence on recruitment had moderate support, as confidence intervals slightly overlapped zero (5.4%; $\beta_{(BO)} = 11.2$, 95% CIs: -1.4 to 23.8). The strength of the $MASS$ effect, present in the top two models, diminished as recruitment rates declined throughout the study, reaching levels so low that even though mass differed among birds, it had little additional effect. The probability of recruitment for birds with mean juvenile mass (546 g) ranged from a high of 0.27 in 2002 (95% CIs: 0.18–0.38) to a low of 0.07 in 2017 (95% CIs: 0.05–0.12; Figure 2).

Apparent Survival Probability

Annual variation (t) was the best time structure for apparent annual survival of both pre-territorial and territorial birds, but a constant annual survival rate for pre-territorial birds

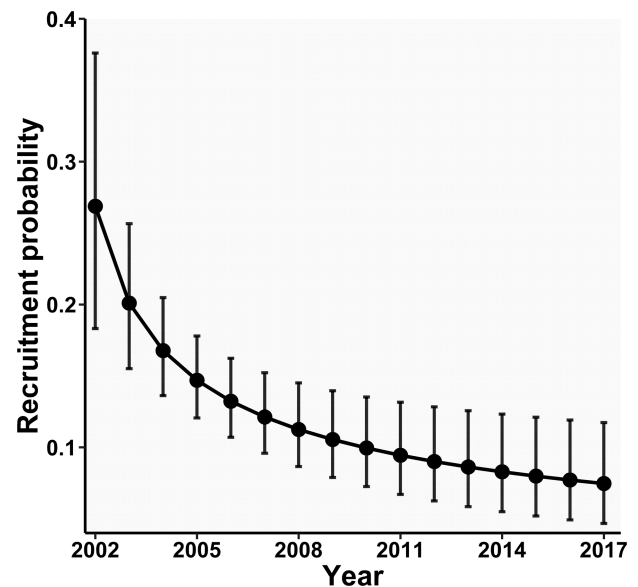


FIGURE 2. Recruitment probability declined throughout the study, but the decline was steeper in early years. Annual estimates of recruitment probabilities are plotted through time, including point estimates and 95% confidence intervals for the mean mass (546 g). Annual estimates represent the probability that a previously pre-territorial Northern Spotted Owl is detected defending a territory in the current breeding season, thus recruiting into the territorial portion of the population, on seven study areas in Washington and Oregon, 2001–2017. Estimates come from the best-supported model that included an interaction between a negative log-linear time trend (lnT) and the effect of juvenile mass at banding ($MASS$; $\varphi_{(BD+MASS+FCORT^2+t)}^{PT}, \varphi_{(t)}^{TR} P(TT) \psi_{(lnT*MASS)}$).

was also competitive. The top survival model included the additive effects of territorial state, FCORT², MASS, and BD on apparent annual survival of pre-territorial birds (Table 2). The additive effects of BD and MASS occurred in all competitive models ($\leq 2 \Delta AIC_c$), and FCORT² occurred in three of the four.

When MASS, BD and FCORT² were held at their means, annual survival of pre-territorial birds was 0.18 lower than survival of territorial birds, with the lowest survival in 2017 ($\hat{\Phi}_{(2017)}^{(PT)} = 0.26$, 95% CIs: 0.16–0.40, $\hat{\Phi}_{(2017)}^{(TR)} = 0.52$, 95% CIs: 0.39–0.65) and the highest in 2005 ($\hat{\Phi}_{(2005)}^{(PT)} = 0.95$, 95% CIs: 0.65–0.99, $\hat{\Phi}_{(2005)}^{(TR)} = 0.98$, 95% CIs: 0.85–1.0) (Figure 3A). Survival of pre-territorial birds declined in association with later band dates (Table 3). When all other variables were held at their means, apparent annual survival for pre-territorial birds across all years declined with later banding dates (Figure 3C), ranging from a high of 0.86 (95% CIs: 0.79–0.90) on the earliest date (13 May), to a low of 0.39 (95% CIs: 0.24–0.56) for birds banded on the latest date (19 September). MASS had a positive relationship with pre-territorial survival (Table 3; Figure 3B). Across all years in this study when other covariates were held at their means, the lightest juveniles (320 g) had an estimated apparent annual survival probability of 0.39 (95% CIs: 0.16–0.68) which increased to 0.93 (95% CIs: 0.68–0.99) for the heaviest birds (885 g; Figure 3B). When all other variables were held at their means, birds with the lowest feather CORT concentrations had $\Phi^{PT} = 0.54$ (95% CIs: 0.37–0.70), which increased to $\Phi^{PT} = 0.70$ (95% CIs: 0.56–0.82) at intermediate FCORT concentrations ($\sim 317 \text{ pg mg}^{-1}$), followed by a decrease back down to a low of $\Phi^{PT} = 0.25$ (95% CIs: 0.03–0.81) for birds with high feather CORT concentrations (Figure 3D).

DISCUSSION

In our 16-year study we banded 1,061 Spotted Owls as fledglings and resighted 381 of them as territory holders. We found that apparent annual survival of pre-territorial Spotted Owls was highest for those with intermediate CORT concentrations, which has also been reported in Cliff Swallows (*Petrochelidon pyrrhonota*; Brown *et al.* 2005) and Thorn-tailed Rayaditos (*Aphrastura spinicauda*; Quirici *et al.* 2021). We also found that apparent survival was highest for birds with greater mass and those banded earlier in the season.

Due to small sample sizes in feather CORT beyond 500 pg mg^{-1} , our confidence intervals become wider, indicating more uncertainty in the relationship between apparent survival and the highest feather CORT concentrations. Nonetheless, the quadratic relationship had over 3.5 times greater model weight than the log-linear relationship and over 6.5 times more support than the linear model. A quadratic relationship is consistent with the biological role of corticosterone—it is essential at low to moderate concentrations but can become detrimental at high concentrations. Thus, survival should be low when CORT concentrations are either too low or too high.

Reduced survival in birds with feather CORT beyond intermediate concentrations may indicate a crucial threshold, beyond which fitness declines (Busch and Hayward 2009, Dantzer *et al.* 2014, Vera *et al.* 2017). Because owls in the pre-territorial state included a mix of age classes that

varied annually, the effect of juvenile feather CORT on survival may last beyond the first year of life—illustrating the potential for long-term consequences of challenging rearing conditions (Busch and Hayward 2009, Dantzer *et al.* 2014). Prolonged exposure to elevated CORT can result in immunosuppression, protein catabolism, or permanent disruption in life-history processes (Busch and Hayward 2009, Dantzer *et al.* 2014, Vera *et al.* 2017), which is likely related to the decrease in survival in some birds with high feather CORT concentrations.

We expected low feather CORT concentrations to indicate favorable rearing conditions with fewer challenges and energetic tradeoffs, resulting in increased survival, yet we found that survival was lower for juveniles with low feather CORT concentrations. While most research in ecology focuses on the negative associations of CORT exposure documented in the biomedical field (Dantzer *et al.* 2014, Vera *et al.* 2017), the stress response is likely advantageous (Busch and Hayward 2009, Dantzer *et al.* 2014, Vera *et al.* 2017). Juveniles with intermediate feather CORT concentrations may have mounted a more appropriate physiological response to environmental stressors than their peers by increasing anti-predator behaviors (Breuner and Hahn 2003), energy intake, or begging (Kitaysky *et al.* 2001). The inability to respond to challenges may arise from either inherent physiological insensitivity or from desensitization, which is the dampening of CORT production because of chronic or prolonged stressors (Rich and Romero 2005, Cyr and Romero 2007). Thus, lower survival associated with the lowest feather CORT levels may reflect the effects of chronic stress or severely challenging environments.

In addition to the effects of feather CORT, banding date had a negative relationship with pre-territorial survival, which was contrary to predictions. We expected that juveniles banded earlier, in the spring, would be recent fledglings that were still poor fliers and more vulnerable to predation relative to birds banded in summer or fall who would have been older, more proficient fliers (Forsman *et al.* 1984). Additionally, juveniles banded early in the season had a longer time interval to survive before the next time step relative to those birds banded later in the season. For these two reasons, we expected juveniles banded later in the season to have higher subsequent survival. However, the relationship we observed between banding date and survival reflects the well-established relationship of increased survival with earlier clutch initiation or hatch date (Maness and Anderson 2013). Owls banded later in the season likely represent late or even second broods rather than older juveniles banded later in the season because of logistics or surveyor effort.

Consistent with findings from other species (Maness and Anderson 2013, Ronget *et al.* 2018), survival in the pre-territorial state was also related to body condition, as Spotted Owls with greater juvenile mass had a higher probability of surviving to recruit into the territorial population. Presumably, heavier birds were reared in favorable conditions with fewer energetic demands and more resources that increased investment in growth and fat stores, making them more resilient to variable weather and starvation, as they likely had more fat to burn to maintain essential bodily functions before catabolizing muscles or organs (Bar 2014, Ronget *et al.* 2018; Mikkelsen *et al.* 2021). This may be particularly important to Spotted Owls, as starvation is one of the most common

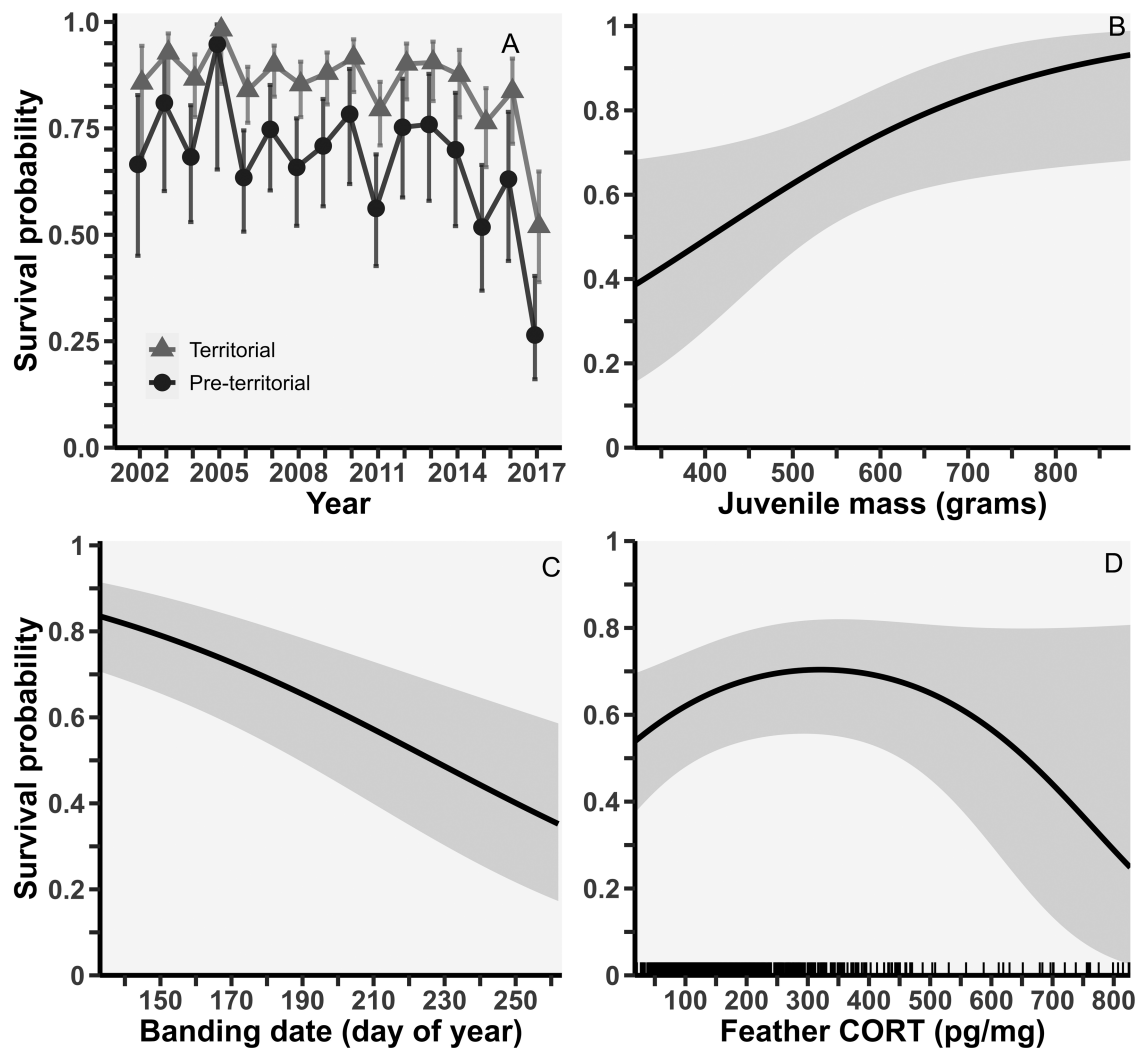


FIGURE 3. There was a lot of annual variation in survival probabilities for Northern Spotted Owls on seven study areas in Washington and Oregon, 2001–2017; but across all years, survival increased with fledging mass (B), decreased with banding date (C), and was greatest at median corticosterone concentrations (D). All estimates were based on the best-supported model that included the effects of territorial status, juvenile mass (MASS), banding date (BD), and a quadratic relationship with juvenile feather corticosterone (FCORT; $\varphi_{(BD+MASS+FCORT^2+t)}^{PT}$, $\varphi_{(t)}^{TR}$, $P(TT)$, $\psi(MASS + \ln T)$). In panel (A), estimates are plotted separately for both territorial states, including point estimates and 95% confidence intervals. In panels (B–D), the fitted relationships between apparent annual survival and model covariates are denoted by solid black lines with 95% confidence intervals denoted by gray shading. In panel (D), the distribution of FCORT samples is denoted by tick marks along the x-axis.

mortality sources during natal dispersal (Miller *et al.* 1997; Forsman *et al.* 2002)

Furthermore, larger birds or those in better body condition may be better at competing for territories or mates, as social and physical dominance are often associated with territory tenure and quality (Maness and Anderson 2013). The probability of recruitment into the territorial population for juveniles at the mean mass when banded were comparable to estimates of recruitment probabilities reported elsewhere (Dugger *et al.* 2016, Rockweit *et al.* 2017), but recruitment probabilities for the heaviest juveniles in our study were much higher.

While most birds recruited into the territorial population by age 3, 16% of banded juveniles in this study recruited later in life (between ages of 4–12), which may represent birds who emigrated off the study area and bred elsewhere, then immigrated back, though, as detailed above, Spotted Owls have short natal dispersal distances and low probability of breeding dispersal, therefore this is unlikely the explanation for these birds (Forsman *et al.* 1984, 2002; Jenkins *et al.* 2019a,

2021). We hypothesized that these owls represent long-term “floaters” (i.e., they struggled to find a vacant territory amidst a landscape with increasing Barred Owl presence).

Barred Owls decrease the occupancy, survival, and calling behavior of territorial Spotted Owls, and their density has increased throughout the Spotted Owl’s range (Wiens *et al.* 2011, Lesmeister *et al.* 2018, Franklin *et al.* 2021). We did not find a direct link between our BO covariate and survival or recruitment of pre-territorial birds, but the covariate was spatially coarse and could not capture the fine-scale effects of BO density in the vicinity of nests. A post hoc analyses indicated that while Barred Owls have increased through time, Spotted Owl juvenile mass decreased throughout this study ($\hat{\beta}_{\text{year}} = -2.35$, $\text{SE} = 0.50$, 95% CI: -3.33 to -1.37), and there is a negative correlation between our Barred Owl metric and Spotted Owl juvenile mass ($\hat{\beta}_{\text{BarredOwl}} = -48.78$, $\text{SE} = 11.57$, 95% CI: -71.46 to -26.10). Thus, Barred Owls likely have negative impacts on the pre-territorial segment of the Spotted Owl population, likely through depletion of

TABLE 3. Model coefficients for covariates from the top model indicate strong support for the effects of banding date, juvenile mass, and moderate support for the effect of feather corticosterone concentrations on annual probability of survival in the pre-territorial state, while there was only weak support for a difference in annual survival between the two territorial states. There was also strong support for a decline in annual recruitment probability that was modified by juvenile mass. Below we present the results from the top model estimating apparent annual survival and recruitment for pre-territorial Northern Spotted Owls in Washington and Oregon, 2001–2017.

Parameter	β^a	SE ^b	LCI ^c	UCI ^c
$\Phi_{\text{intercept}}$	1.79	0.53	0.76	2.82
$\Phi_{\text{Pre-territorial}}$	-1.50	1.37	-4.19	1.19
$\Phi_{\text{BD}}^{\text{PT}}$	-0.017	0.004	-0.026	-0.009
$\Phi_{\text{MASS}}^{\text{PT}}$	0.0054	0.0025	0.0005	0.0104
$\Phi_{\text{FCORT}}^{\text{PT}}$	0.0049	0.0023	0.0005	0.0094
$\Phi_{\text{FCORT}^2}^{\text{PT}}$	-0.0000077	0.0000040	-0.0000155	0.0000001
$p_{\text{intercept}}^{\text{TR}}$	5.67	0.89	3.93	7.42
p_{T}^{TR}	-0.768	0.200	-1.160	-0.376
$p_{\text{TT}}^{\text{TR}}$	0.036	0.011	0.015	0.057
$\psi_{\text{intercept}}$	-6.09	1.63	-9.29	-2.90
ψ_{MASS}	0.009	0.003	0.004	0.015
ψ_{InT}	2.117	1.082	-0.004	4.239
$\psi_{\text{InT} \times \text{MASS}}$	-0.005	0.002	-0.009	-0.001

The best model was determined by the lowest Akaike's information criterion adjusted for small sample sizes (AIC_c) and contained the effects of juvenile feather corticosterone (FCORT²), juvenile mass (MASS) and day of year on which it was banded (BD), and annual variation (t) on estimated annual survival (Φ^{PT} , Φ^{TR}) for bird in the pre-territorial state (PT) and annual variation (t) on birds in the territorial state (TR), with an interaction between a log-linear time trend (InT) and juvenile mass (MASS) on recruitment ($\Phi_{(\text{BD} + \text{MASS} + \text{FCORT}^2 + t)}^{\text{PT}}$, $\Phi_{(t)}^{\text{TR}}$, $p_{(\text{TT})}^{\text{TR}}$, $\psi_{(\text{InT} \times \text{MASS})}$).

^aModel coefficients.

^bStandard errors.

^c95% confidence interval.

prey resources or competitive exclusion from productive, preferred forests.

Juvenile mass, and feather corticosterone were not highly correlated ($r = -0.16$), but survival was highest for birds with the highest mass and those with intermediate CORT concentrations. However, few birds shared these characteristics. Birds with intermediate CORT levels had masses near the mean (500–600 g), whereas birds with the highest masses (>650 g) had lower CORT concentrations. Many studies have hypothesized that there is a tradeoff between avian survival and body mass, where small birds suffer from risk of starvation and increased costs of thermoregulation, while large birds lose maneuverability to escape predators or catch prey (Adriaensen *et al.* 1998, Covas *et al.* 2002). In addition, clutch size or parental effort, metrics we could not measure directly in our study, may also influence the relationship between juvenile mass, CORT, and survival. Spotted Owls who fledge with one other nestmate tend to have higher survival than triplets or singletons, which may be related to parental provisioning effort to maximize growth and fitness of chicks—a benefit that may last multiple years (Peery and Gutiérrez 2013). The study methodology precluded us from testing the effect of clutch size, as field crews did not climb trees to determine the number of eggs laid or successfully hatched. Crews could count the number of offspring the day they initially banded fledglings, but that occurred post-fledging. We believe that fledgling counts during banding would be a biased estimate of brood size or parental effort since they include an unknown amount of chick mortality that occurred prior to fledging. However, direct measurements of fledgling mass at banding and CORT levels should reflect resource availability associated with parental foraging effort or brood size. The physiological processes that allocate energy are extremely complex, and we could not control for all potentially im-

portant factors in the interaction between the environment, individual differentiation in physiology, and long-term demographics.

Pre-territorial floaters and their recruitment into the breeding population is an often-overlooked demographic class that can be important to population persistence (Pradel and Lebreton 1999, Penteriani *et al.* 2005, Robles and Ciudad 2017). Occupancy rates, adult survival, and recruitment in Spotted Owls are declining—and there is evidence that fecundity may also be declining (Dugger *et al.* 2016, Franklin *et al.* 2021). Our results indicate that the probability of a bird surviving and becoming territorial to attempt to breed has also been declining. Therefore, there are fewer adult breeders on the landscape producing fewer fledglings and these young birds have a low probability of becoming a territorial breeder creating a negative spiral of ever dwindling numbers of Spotted Owls. Even when adult survival in long-lived species remains high and stable, a population cannot persist if breeders that senesce or die are not replaced (Sergio *et al.* 2021, Warret Rodriguez *et al.* 2021). Therefore, the rearing conditions and resulting energetic tradeoffs that reduce survival and recruitment in pre-breeding individuals are important for population dynamics. For juvenile Spotted Owls below the mean weight, each 50 g increase in mass corresponds to ~0.07 increase in annual survival probability and a 0.03–0.05 increase in annual recruitment probability. For a long-lived species, these annual differences are substantial and can have significant impacts on population dynamics. For imperiled species, understanding early development or pre-breeding life stages may increase the effectiveness of monitoring and conservation efforts. For example, current efforts to control Barred Owls have focused on improving vital rates of territorial Spotted Owls, but lagged effects may also

improve survival of juveniles and recruitment rates (Wiens *et al.* 2021). Coexistence of these species may also be enhanced with management of structurally complex forests as Spotted Owls more commonly use more developed understories and steeper slopes than Barred Owls (Jenkins *et al.* 2019b). During dispersal, juvenile Spotted Owls use similarly complex forests as those selected by adult Spotted Owls (Sovern *et al.* 2015). Control of Barred Owls along with the conservation of forest structures important for Spotted Owls may be important management activities that can contribute to increased juvenile survival and recruitment and the conservation of range wide populations.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement

All relevant state and federal permits were acquired and maintained for all study areas, and protocols for handling owls were approved under animal care and use permits overseen by Oregon State University's Institutional Animal Care and Use Committee.

Conflicts of interest statement

The authors declare no conflicting interests.

Author contributions

DL and KMD conceived the ideas and designed methodology; DL, KMD and AM collected the data; KO performed laboratory protocols; AM, KMD and DL analyzed the data; AM and KMD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability

Analyses reported in this article can be reproduced using the data provided by Mikkelsen *et al.* (2023).

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