

Baseline corticosterone is positively related to juvenile survival in a migrant passerine bird

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Summary

1. Glucocorticoid hormones are an integral part of the vertebrate stress response, and theoretical models argue for a link between glucocorticoid levels and individual fitness. The cort-fitness hypothesis posits that elevated levels of baseline glucocorticoids are reflective of an individual in poor condition and with a reduced likelihood of survival. Surprisingly, this hypothesis remains virtually untested for the juvenile life-history stage, a period that is often characterized by high mortality rates.

2. To address this issue, we explored whether glucocorticoid levels just prior to fledging were related to survival during the juvenile period in the Swainson's thrush (*Catharus ustulatus*), a short-lived, temperate-breeding passerine bird. Over 2 years, we blood-sampled nestling thrushes to quantify glucocorticoid levels and then used radio telemetry to assess whether individuals died or survived to emigrate from the study area. Finally, we measured vegetation characteristics at the nest and at locations used by individuals during the juvenile period to quantify the relative importance of habitat features and glucocorticoid levels on survival.

3. Predation was the leading cause of death, and overall juvenile survival rate was 34.6%. We found that survival was positively associated with baseline corticosterone and, to a lesser extent, size-corrected body mass and date of fledging. Contrary to expectations, we found no evidence that the amount of vegetative cover at the nest site or at locations used during the juvenile period was associated with survival.

5. Although we cannot completely rule out the cort-fitness hypothesis, our data appear to support the cort-activity hypothesis and suggest that elevated baseline corticosterone levels in juvenile thrushes may be linked to enhanced post-fledging survival via increased locomotor activity that promotes foraging, more effective escape from predators or both.

Key-words: *Catharus ustulatus*, corticosterone, cort-activity hypothesis, cort-fitness hypothesis, juvenile survival, Swainson's thrush

Introduction

Glucocorticoid hormones are common to all vertebrates and play a key role in the regulation of several important processes such as locomotor activity, energy metabolism and feeding behaviour (Romero 2004). Glucocorticoids are perhaps best known for their role in modulating physiology and behaviour of individuals as they cope with unpredictable environmental stressors (e.g. predators, inclement weather; Wingfield *et al.* 1998; Sapolsky, Romero & Munck 2000). Recently, much interest has focused on

understanding the extent to which baseline glucocorticoid levels provide information about the quality and fitness of an individual (Wingfield *et al.* 1998; Romero 2004; Bonier *et al.* 2009a). If a relationship exists between baseline glucocorticoids and individual fitness, it may take two possible forms. First, baseline glucocorticoids may be negatively associated with an individual's fitness such that individuals with the lowest levels have the best fitness prospects (i.e. the 'cort-fitness hypothesis'; Bonier *et al.* 2009a). This hypothesis is based on the premise that as the degree of environmental challenge increases, there is a concurrent increase in baseline glucocorticoid level and a decrease in individual fitness (Bonier *et al.* 2009a). Higher levels of

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baseline glucocorticoids are associated with reduced fitness because glucocorticoid activity can reallocate critical resources away from normal activities and, after periods of chronic exposure, can lead to deleterious effects (Bonier *et al.* 2009a). A second, non-exclusive explanation is the 'cort-activity hypothesis', which argues that as the degree of environmental challenge increases, there is a concurrent increase in baseline glucocorticoids and individual fitness via physiological and behavioural modifications undertaken to cope with such a challenge. In particular, elevated levels of baseline glucocorticoids are associated with increased individual fitness through increased locomotory and anti-predator activities (Breuner & Hahn 2003; Comendant *et al.* 2003; Cote *et al.* 2006). Both hypotheses rely on the assumption that baseline glucocorticoids serve as a proxy for environmental challenges and invoke a link between baseline glucocorticoid and fitness; however, they differ in the direction of the relationship between glucocorticoids and individual fitness measures.

To date, there has been limited study of the relationship between glucocorticoid levels and survival, a key aspect of fitness (Breuner, Patterson & Hahn 2008; Bonier *et al.* 2009a). Indeed, only two studies have focused on the relationship between glucocorticoids and survival during the juvenile period and both focused on large, long-lived animals (Blas *et al.* 2007; Goutte *et al.* 2010). Because the relationship between glucocorticoids and fitness likely differs among species (Ricklefs & Wikelski 2002; Hau *et al.* 2010; Martin *et al.* 2011), studies of small, short-lived species are needed for a better understanding of glucocorticoid–fitness relationships. This is particularly true for the juvenile period, as this life-history stage is typically characterized by lower survival rates (Sullivan 1989; Gardali *et al.* 2003), and hence experiences strong directional selection with subsequent effects on population structure (Anders *et al.* 1997).

In this study, we asked whether baseline corticosterone, the primary glucocorticoid hormone in birds, was related to survival during the juvenile period in a short-lived, temperate-breeding passerine bird, the Swainson's thrush (*Catharus ustulatus*; hereafter thrush). Specifically, we tested whether the cort-fitness hypothesis or the cort-activity hypothesis better explained the relationship between survival and glucocorticoids in free-living juvenile thrushes. According to the cort-fitness hypothesis, baseline corticosterone in nestlings should be negatively associated with juvenile survival; in contrast, the cort-activity hypothesis argues that baseline corticosterone should be positively associated with juvenile survival. We also quantified handling-induced corticosterone (i.e. a stress response) because this measure is indicative of an individual's ability to respond to an acute stressor and may also be linked to fitness (Romero 2004; Breuner, Patterson & Hahn 2008). Because juvenile survival is frequently influenced by environmental conditions at the nest site (Norris 2005; Harrison *et al.* 2011) and during post-fledging dispersal (Cohen & Lindell 2004; King *et al.* 2006; Whittaker & Marzluff

2009; Vitz & Rodewald 2011), we also tested whether juvenile survival was associated with vegetation characteristics of the nest site and of locations where individuals were detected during the post-fledging period. We focused on the total vegetative cover and hardwood vegetative cover because these habitat features are important for thrushes during the breeding season (White *et al.* 2005; Hagar 2007; Ellis, Kroll & Betts 2012).

Materials and methods

STUDY AREA AND SPECIES

We conducted this study from June to September during the 2009–2010 breeding seasons in the Coast Range of western Oregon (Benton and Polk counties). Sixteen study plots were located in young conifer plantations (i.e. 7–12 years old), which were planted with Douglas-fir (*Pseudotsuga menziesii*) within a year of harvest. Study plots were selected randomly from a large pool of stands ($n = 102$) to represent the natural gradient in hardwood cover for young conifer plantations in this area (i.e. <5–35%; Ellis 2010). Douglas-fir was the dominant plant species on study plots, with varying levels of hardwood species [e.g. vine maple (*Acer circinatum*), red alder (*Alder rubra*)] and understory plants (e.g. *Rubus* spp., *Vaccinium* spp.). The thrush is a long-distance migrant passerine that nests in a wide range of forested habitats in western Oregon from early June until mid-August. Female thrushes usually lay a single clutch of four to five eggs each season, and parents provide care for juveniles for at least 2 weeks after fledging, with juveniles moving only short distances in the first week after fledging (White & Faaborg 2008).

RADIO TELEMETRY AND BLOOD SAMPLING OF THRUSHES

We used radio telemetry to follow marked female thrushes to their nests because dense vegetation and the furtive behaviour of breeding females prevented us from locating nests through traditional nest-searching techniques. We captured female thrushes from June to July in each year (46 in 2009, 39 in 2010) using passive mist netting. Each female was fitted with a ca. 1.0-g radio transmitter (Advanced Telemetry Systems, Isanti, MN, USA) that weighed approximately 3% of each female's body mass and was attached using the harness method (Rappole & Tipton 1991). We located nests ($n = 47$) by tracking females through standard radio telemetry techniques and opportunistically through related research activities. Nest failure rate was high (63.8%, 30 of 47 nests), so survival was assessed in 28 nestlings from 17 successful nests.

We visited successful nests shortly before fledging (i.e. 9–10 days after eggs hatched) to collect physiological data and affix telemetry transmitters to 1–2 nestlings in the brood (Fig. 1). In instances when >2 nestlings were available, we selected two focal nestlings that represented the range of body sizes within the brood based on visual estimation (nestling body mass range over all nests: 17.6–24.8 g). Within 3 min of arriving at the nest, we sampled blood from each focal nestling to quantify baseline corticosterone levels. We took blood samples by pricking the alar vein with a sterile 27-gauge needle and collecting blood (c. 75 μ L) into a heparinized capillary tube. We held nestlings in an artificial nest and then took a second blood sample 30 min after the baseline sample to quantify the corticosterone response because of handling (Romero 2004; Breuner, Patterson & Hahn 2008). We restricted blood sampling to these two periods to minimize any possible negative effects on survival from blood sampling (Sims &



Fig. 1. Young Swainson's thrush (*Catharus ustulatus*) fitted with radio telemetry transmitters immediately prior to fledging. Prior to affixing transmitters, we sampled blood to examine the relationship between glucocorticoid levels and juvenile survival.

Holberton 2000). After sampling, blood flow was stanching with cotton, and samples were immediately stored on ice. After the second blood sample was taken, we recorded the mass of each nestling on a digital scale, measured right tarsus length and then attached a ca. 1.0-g radio transmitter using the approach described previously. We did not determine the sex of focal individuals because thrushes are monomorphic, so sex determination would have required collecting additional blood beyond that required for glucocorticoid analyses; therefore, we assumed that there were no sex-specific differences in the survival rate of juvenile thrushes.

We located juvenile thrushes, starting the day after attachment of the radio transmitter and then once every 1–2 days thereafter, until death or dispersal from the study area using standard radio telemetry techniques (Anders *et al.* 1997). We started at different points throughout the day (0700–1800) and attempted to alternate between morning and afternoon periods on consecutive visits, although this was not always possible because of logistical constraints. For each tracking session, we recorded the location of the juvenile with a hand-held GPS receiver and attempted to confirm its status (i.e. dead or alive). For two individuals, we recovered a transmitter in new condition without any physical remains within 3 days of attachment (i.e. attachment loops intact, transmitter undamaged). In each case, we considered the thrush to have shed its transmitter while still alive, so we did not include these two individuals in our calculation of overall mortality rate. However, these two individuals were included in our analysis of juvenile survival following the guidelines of Cox proportional hazards survival analysis (Murray 2006).

If we did not make visual contact with an individual for two consecutive visits and we tracked the signal to the same location both times, we conducted a detailed search to determine its fate. We deemed a juvenile dead when we discovered all or part of its carcass with the transmitter. We considered a juvenile to have dispersed from the natal area if we could not locate it after searching intensively on ≥ 3 consecutive visits, and all individuals that were considered to have dispersed were assumed to have survived in our analysis. We adopted this approach because (i) transmitters gave strong signals that covered a large area and were easily located from hilltops on our study sites; (ii) we relocated transmitters from depredated thrushes that were found in underground burrows, buried in deep leaf litter, and had passed through the gut of predators; and (iii) several dispersing individuals were located dozens of times over a relatively long period (i.e. up to 55 days after transmitter attachment) and disappeared from the study area

during the period when thrushes were departing on their autumn migration.

VEGETATION SAMPLING

We sampled vegetation composition within a 25-m radius centred on each successful nest. Measurements were taken at four sampling points: one was centred directly on the nest, and the other three were located 25 m distant from the centre of the nest. The bearing of the initial off-nest point was chosen randomly, with the second and third points located 120 and 240° from the initial bearing. At each of the four points, we used a 3-m radius circle to quantify vegetation cover. In each circle, we visually estimated the amount of cover provided by each plant species that covered at least 5% of the 28.3 m² sample area in one of three distinct vegetation strata: herbaceous (0–0.5 m), shrub (0.5–2.0 m) and canopy (>2.0 m). If a plant species was found in more than one stratum, we only recorded the stratum in which it provided the greatest cover. For analysis, we first summed the amount of cover for all plant species over all three strata in each 3-m radius sampling point, and we then averaged cover estimates over each of the four sampling points grouping species together to estimate (i) the total amount of hardwood cover (with classifications based on Ellis & Betts 2011) and (ii) the total amount of vegetative cover of all plant species. This approach can lead to summed cover values >100%.

For each location at which a live juvenile was encountered through radio telemetry, a single 3-m radius vegetation plot was used to quantify vegetation cover using the same procedures as described previously. To assess the link between vegetation used during the post-fledging period on survival, we restricted our analysis to the 8 days immediately following fledging as nearly all juvenile mortality occurred during this period, a pattern typical of passerine birds (e.g. Cohen & Lindell 2004; King *et al.* 2006). For analysis, we summed the amount of cover for all plant species over all three strata in each point at which a live individual was detected, and then, we averaged cover estimates over all location points to estimate the total amount of hardwood cover and the total amount of vegetative cover of all plant species. For those individuals found dead after leaving the nest and prior to their first check during the post-fledging period ($n = 9$ individuals), we used nest cover data as a measure of cover used during the juvenile period because juvenile thrushes are unable to move large distances immediately after fledging (White & Faaborg 2008) and because individuals in our study were often found dead within the vicinity in which nest vegetation plots were measured.

LABORATORY PROCEDURES

We centrifuged blood at 4650 *g* for 10 min within 8 h of being drawn; we then removed plasma and froze it at -20°C . At the completion of fieldwork, we shipped samples to the University of South Florida on dry ice where all laboratory analysis took place. We used a commercially available enzyme immunoassay (EIA) kit (cat# 900-097; Assay Designs, Ann Arbor, MI, USA) to measure corticosterone in plasma (Breuner *et al.* 2006). We did not validate the assay for the thrush and instead used assay conditions found to be effective for several other songbird species [white-crowned sparrow (*Zonotrichia leucophrys*): Wada, Hahn & Breuner 2007; house sparrow (*Passer domesticus*): Kuhlman & Martin 2010; grey catbird (*Dumetella carolinensis*) Owen *et al.* 2010, 2011]. Briefly, we added a 10% steroid displacement reagent (5 μL) to 5 μL of plasma; 5 min later, we added an assay buffer (240 μL) to each sample, vortexed and aliquoted in duplicate (100 μL per well) to assay plates. We measured standard curves (ranging from 200 000 to 32 pg mL⁻¹) in duplicate in a five-step serial dilution on all

plates. We incubated samples with conjugated corticosterone and antibody for 2 h at room temperature while they were shaken. We then emptied wells and washed them three times before substrate was added to all wells; plates were then incubated 1 h at room temperature without shaking. Finally, we added stop solution and read each plate at 405 nm (corrected at 590 nm). The detection limit for the assay is 27 pg (Assay Designs), and no sample concentration fell below this limit. We randomly allocated samples among five plates, and intra- and interplate variation were 12.95% and 8.65% respectively.

STATISTICAL ANALYSIS

We used Cox proportional hazards mixed regression models in program R [v2.7.1; COXME package (Therneau 2009)] to model juvenile survival because this approach (i) can account for non-independence in survival of individuals that originate from the same nest via the use of a random effect, (ii) allows for inclusion of censored individuals whose mortality status could not be determined (e.g. transmitter shed prematurely, radio signal disappeared from study site) and (iii) can assess the relative importance of multiple, time-dependent covariates on survival without having to assume a specific hazard function (Murray 2006). Thus, Cox proportional hazards models allowed us to estimate the cumulative survival probability of juvenile thrushes, examine the influence of physiological and vegetation covariates on survival and incorporate data from each individual up until their time of death or emigration from the study area. As noted earlier, individuals that were not detected after repeated searches within their natal area were considered to have survived and emigrated, so we considered these individuals as censored in our survival analysis because censored individuals provide meaningful data on minimum survival time (Murray 2006).

To conduct our analysis, we initially modelled the influence of physiological and vegetation covariates on survival separately because of concerns that combining all covariate types and nuisance factors into a single model could lead to problems of model overfitting (Babyak 2004). In our first model, we included both baseline corticosterone and handling-induced corticosterone measures because there was no evidence of multicollinearity between the two measures ($r = 0.14$). Thus, we modelled juvenile survival as a function of baseline corticosterone, handling-induced corticosterone and four nuisance factors [i.e. year, date of fledging, size-corrected body mass and bleed time (i.e. elapsed time between our initial contact with a nestling and the time when we completed baseline blood sampling)]. In addition, we included study site as a random effect to address the potential lack of independence among birds fledging in close proximity, and nest (nested within study site) as a random effect to address the potential lack of independence among individuals originating from the same nest. We then used a stepwise backwards model selection approach by sequentially removing non-significant variables ($P > 0.10$) until we arrived at a final model that was limited to physiological covariates and nuisance factors, which had a significant association with juvenile survival. Although such stepwise approaches have been criticized (Babyak 2004; Mundry & Nunn 2009), we adopted this approach because mixed Cox models are not likelihood-based, making information theoretical model selection procedures (e.g. Akaike's Information Criterion [AIC]) unreliable. Importantly, parameter estimates of significant factors did not change qualitatively when all variables were retained in any of the models.

In the second step in our analysis, we modelled the relationship between juvenile survival and the four vegetation covariates that were measured at nest sites and at the points where live juveniles were located during the first part of the post-fledging period. Because our initial analysis found evidence of multicollinearity between some combinations of vegetation variables ($r = 0.32$ – 0.83

for all pair-wise correlations), we began by modelling juvenile survival separately for each vegetation covariate. Thus, each model included the vegetation covariate of interest (i.e. hardwood cover at the nest, total cover at the nest, hardwood cover at juvenile locations, total cover at juvenile locations), three nuisance factors (i.e. year, date of fledging and size-corrected body mass) and the two random factors described previously (i.e. study site, nest nested within study site). We then used the same stepwise backwards model selection approach as described previously to sequentially remove non-significant variables ($P > 0.10$). In the last step in our analysis, we created a single global model that included the significant covariates and nuisance factors from the final physiological model and the final vegetation models using stepwise forward model selection.

When interpreting Cox proportional hazards models, the hazards ratio [i.e. $\exp(\beta)$] is the statistic of interest. Specifically, when $\exp(\beta) < 1$, the hazard decreases (and survival increases) per unit increase in a variable, and when $\exp(\beta) > 1$, the hazard increases (and survival decreases) per unit increase in a variable. However, model interpretation should not be restricted only to covariates, but instead should explore additional information contained within the hazard function and its survival distribution (see Murray 2006). Therefore, we also present our results graphically. We used a dichotomous approach with our graphical analysis (unlike our statistical analysis) because the influence of covariates on survival is time-dependent and because it is not possible to portray fitted relationships with bivariate plots. Cut-off points for this graphical analysis were selected by dividing data evenly into two discrete groups based on the median value of covariates. All variables were z -transformed prior to analysis to allow direct comparison among effect sizes. We report means and 95% confidence intervals unless otherwise noted, and significance levels for all tests were set at $P < 0.05$.

Results

Juvenile thrushes were monitored for up to 55 days in their natal area, and all individuals that were considered to have dispersed successfully did so an average of 40 days (range: 25–55) after fledging. Predation was the leading cause of death, and overall survival rate was 34.6%. All but one of 17 individuals found dead during the juvenile period died within the first 11 days after fledging. Our best physiological model found that juvenile survival was positively associated with baseline corticosterone [$z = -2.68$, $P = 0.007$, $\beta = -1.147$ (-2.024 , -0.270)] and, to a lesser extent, size-corrected body mass [$z = -2.00$, $P = 0.045$, $\beta = -0.331$ (-0.670 , 0.007)] and date of fledging [$z = -1.96$, $P = 0.050$, $\beta = -0.668$ (-1.365 , 0.029); Fig. 2]. In contrast, we did not detect an association between survival and the magnitude of the acute stress response [$z = -0.48$, $P = 0.630$, $\beta = -0.148$ (-0.778 , 0.482)], bleed time [$z = -0.71$, $P = 0.480$, $\beta = -0.294$ (-1.143 , 0.554)] or year [$z = -0.35$, $P = 0.720$, $\beta = -0.241$ (-1.639 , 1.157)].

We also did not detect an association between juvenile survival and nest site characteristics [nest hardwood cover: $z = 0.95$, $P = 0.34$, $\beta = 0.327$ (-0.379 , 1.033); nest total cover: $z = 0.28$, $P = 0.78$, $\beta = 0.079$ (-0.508 , 0.666)], nor did we detect an association between juvenile survival and the vegetation cover at locations used during the juvenile period [hardwood cover: $z = -0.92$, $P = 0.36$, $\beta = -0.336$

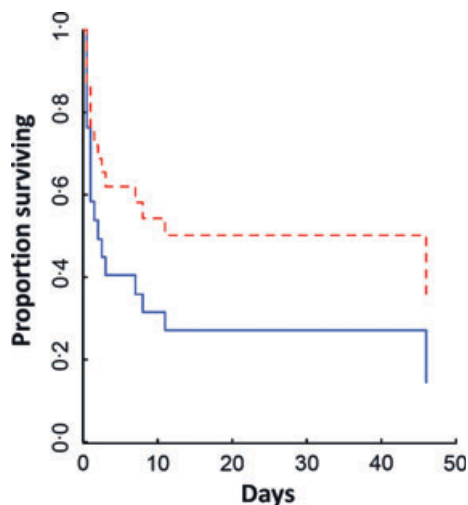


Fig. 2. Baseline corticosterone level is positively related to juvenile survival in Swainson's thrushes. Estimated survival functions of individuals with high (>9 ng mL $^{-1}$, dashed red line; $n = 14$) and low baseline corticosterone (<9 ng mL $^{-1}$, solid blue line; $n = 13$). Although baseline corticosterone was analysed as a continuous variable (see text), it is displayed here as dichotomous variable for illustrative purposes. Significant nuisance factors (i.e. mass and fledging date) were held at their average values.

($-1.080, 0.409$); total cover: $z = -0.99, P = 0.32, \beta = -0.344$ ($-1.059, 0.270$)). In addition, we did not detect an association between juvenile survival and the three nuisance factors (year, fledge date, size-corrected body mass) in any of the four vegetation models (all $P \geq 0.30$). Because no significant vegetation covariates or nuisance factors were associated with juvenile survival, our best global model is equivalent to the final physiological model that found juvenile survival was positively associated with baseline corticosterone, date of fledging and size-corrected body mass (Table 1). The assumption of proportional hazards was met for all significant variables in the final model (baseline corticosterone: $r = 0.00, \chi^2 = 6.24 \times 10^{-05}, P = 0.99$; size-corrected body mass: $r = -0.36, \chi^2 = 2.55, P = 0.11$; date of fledging: $r = 0.21, \chi^2 = 0.626, P = 0.43$).

Discussion

Our study found that juvenile thrush survival was positively associated with baseline corticosterone levels measured close to the time of fledging. Because baseline corticosterone at the time of fledging probably reflects conditions at the nest site during development (Love &

Williams 2008), our results suggest a physiological effect that originated in the nest and persisted into the post-fledging period. How might elevated baseline corticosterone levels enhance survival rates of juvenile thrushes after they left the nest? Two non-exclusive explanations appear possible. First, elevated corticosterone may promote the locomotory ability of individuals, allowing them to maintain movement with care-giving parents during the juvenile period. This possibility is supported by studies that have demonstrated (i) thrush offspring often move substantial distances after fledging to follow their parents (White & Faaborg 2008) and (ii) baseline corticosterone levels are linked to increased locomotory activity in adult passerine birds (Breuner, Greenburg & Wingfield 1998; Breuner & Hahn 2003). Second, because most of the mortality of juvenile passerine birds is attributed to predation (e.g. Anders *et al.* 1997; Cohen & Lindell 2004; King *et al.* 2006; this study), elevated baseline corticosterone might have enhanced anti-predation behaviours. Experimental elevation of corticosterone in lizards increases anti-predator behaviour (e.g. faster response time, greater latency to emerge from hiding after a predator encounter; Uller & Olsson 2006; Thaker, Lima & Hews 2009), and corticosterone levels experimentally elevated *in ovo* in the European starling (*Sturnus vulgaris*) led to increased wing area and enhanced juvenile flight performance (Chin *et al.* 2009). Although we lack data on thrush flight performance or anti-predator behaviours, our data support the notion that elevated baseline corticosterone levels at the time of fledging in altricial birds may be a general means of promoting juvenile survival through enhancement of anti-predator behaviours and/or locomotory activities (Wada 2008).

Collectively, our data support the cort-activity hypothesis (Breuner & Hahn 2003; Comendant *et al.* 2003; Cote *et al.* 2006); nevertheless, we cannot completely rule out the cort-fitness hypothesis. Our uncertainty stems from a lack of data on the degree of environmental challenge facing individual thrushes. Specifically, the degree to which environmental challenges impacted thrushes in our study area could have led to baseline corticosterone levels that were not high enough to be associated with reduced juvenile survival. Under more difficult environmental conditions, thrushes may exhibit higher baseline corticosterone levels than reported here, and these levels may be associated with reduced juvenile survival. Nevertheless, our data were collected over 2 years in the naturally occurring environmental conditions for thrushes in our study area, so

Table 1. Hazard ratios with effect sizes (β) and their associated 95% confidence intervals for the final Cox proportional hazards mixed regression model that found baseline corticosterone and two nuisance factors were positively associated with juvenile survival in the Swainson's thrush

	Hazard ratio	z	P	β	95% CI
Baseline corticosterone	0.318	-2.68	0.007	-1.147	-2.024, -0.270
Size-corrected mass	0.718	-2.00	0.045	-0.331	-0.670, 0.007
Date of fledging	0.513	-1.96	0.050	-0.668	-1.365, 0.029

under these conditions, it does appear that juvenile thrushes conform to the cort-activity hypothesis. We recommend that future researchers attempt to quantify simultaneously the degree of environmental challenge faced by individuals and its influence on the relationship between survival and glucocorticoids. Although such data can be difficult to obtain, recent technological advances [e.g. miniaturization in heart rate telemetry (Green 2011)] now make it possible to record physiological parameters that could provide measurements of environmental challenges in free-ranging individuals in real time. Future studies may also benefit from careful manipulation of glucocorticoid levels under controlled settings, keeping in mind the challenges that can complicate this approach (Fusani *et al.* 2005; Fusani 2008).

Our results contrast with two previous studies that found negative associations between juvenile survival and glucocorticoid levels in the European white stork (*Ciconia ciconia*, Blas *et al.* 2007) and the black-legged kittiwake (*Rissa tridactyla*, Goutte *et al.* 2010). One possible explanation for this contrast is that environmental challenges to juveniles were more demanding in the previous studies (Blas *et al.* 2007; Goutte *et al.* 2010). For example, juvenile survival in both large-bodied species appears to be strongly influenced by food resource limitations (Barbraud, Barbraud & Barbraud 1999; Hatch, Robertson & Baird 2009), whereas predators are chiefly responsible for mortality experienced during the juvenile period in thrushes and other passerine birds (e.g. Anders *et al.* 1997; Cohen & Lindell 2004; King *et al.* 2006). In addition, the role of life-history strategy might also be important. The two species in which corticosterone was negatively related to survival are large species with slow-paced life histories relative to the small, short-lived thrush, and these differences may alter how glucocorticoids impact mechanisms underlying variation in juvenile survival (Ricklefs & Wikelski 2002; Hau *et al.* 2010). New studies are required to test the hypothesis that interactions between stressor risk type and body size/life history determine how glucocorticoids affect survival and fitness broadly, as insufficient data currently exist. Another important difference between these previous studies and ours is the aspect of glucocorticoid regulation that was related to fitness. In storks, handling-induced corticosterone was negatively related to juvenile survival (Blas *et al.* 2007), and in kittiwakes, experimentally elevated corticosterone levels over 2 days reduced survival (Goutte *et al.* 2010), whereas baseline corticosterone just prior to fledging was positively related to juvenile survival in thrushes. On the one hand, these comparisons among taxa may be difficult, if not impossible, if similar aspects of glucocorticoid regulation are not considered. On the other, it is noteworthy that glucocorticoid levels appear to be linked to survival in all juvenile birds examined to date, albeit in complex, context- and/or species-dependent manners.

Our study revealed that body size and fledging date also had positive effects on juvenile survival, results that are well supported by previous studies of passerines (e.g. Magrath

1991; Verboven & Visser 1998; Naef-Daenzer, Widmer & Nuber 2001). Unlike previous studies, however, we did not find that juvenile survival was associated with vegetation characteristics. These results are somewhat surprising, given that vegetation can provide juvenile passerine birds with cover from predators and food resources for adults to provision young (King *et al.* 2006; Vitz & Rodewald 2007; Mitchell, Taylor & Warkentin 2010; Streby, Peterson & Anderson 2011). One possible explanation for this pattern is a potentially complex relationship between vegetation characteristics and predators in our study system. The main predators of juvenile thrushes in our system (snakes) are themselves subject to predation by higher-order predators (e.g. raptors). Thus, taking refuge in locations with greater vegetative cover might actually increase predation risk on juvenile thrushes because it may also reduce predation risk to important predators of the thrush. We hypothesize that juvenile survival is maximized when thrushes have vegetation that provides them ample concealment from predators but also provides enough physical space to escape terrestrial predators rapidly through powered flight.

Although glucocorticoids have previously been found to be related to adult survival (Cote *et al.* 2006; Cabezas *et al.* 2007; Angelier, Holberton & Marra 2009; O'Connor *et al.* 2010; Romero & Wikelski 2010), our study is the first to find such a link between baseline corticosterone levels and juvenile survival in a passerine bird under free-living conditions. Furthermore, it is among the first to determine that glucocorticoids are more strongly related to juvenile survival than environmental factors (e.g. vegetation cover used during the post-fledging period). Whether baseline corticosterone levels influence the success of juvenile thrushes during their first migratory journey or on their wintering grounds is still unknown, although data from other species indicate that glucocorticoid levels may impact survival between life-history stages (Angelier, Holberton & Marra 2009; Bonier *et al.* 2009b).

Acknowledgements

Grants from the National Council for Air and Stream Improvement, Oregon State University, the United States Department of Agriculture, Agriculture Food and Research Initiative (AFRI-2009-04457) to M.G.B., and the National Science Foundation (NSF-IOS 0920475) to L.B.M. provided funding for this work. Weyerhaeuser, Forest Capital, and the Oregon Department of Forestry kindly allowed us access to study sites. We thank Camille Beasley, Sinead Borchert, Rebecca Cahall, Keith Castleman, Laurie Clark, Tana Ellis, Lyla Hunt, Lauren MacFarland, Dana McCoskey, Haley Stafford, Ryan Trimbath and Aaron Young for assistance in the field; Camille Freitag, Liz Etherington and Tom Manning for logistical support; Jennifer White for helpful discussion; and Joe Nocera and several reviewers for insightful helpful comments on previous versions of this manuscript. Permits for our research were provided by the Institutional Animal Care and Use Committee at Oregon State University, the Oregon Department of Fish and Wildlife, and the United States Fish and Wildlife Service.

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Received 14 December 2011; accepted 21 May 2012

Handling Editor: Jennifer Grindstaff