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Corticosterone in territorial male Swainson's Thrushes varies in relation to forest age but not vegetation cover

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Abstract Glucocorticoids are thought to be related to habitat quality and may provide information about the relative health of individuals. We used a model selection approach to test whether plasma glucocorticoid levels of the Swainson's thrush (*Catharus ustulatus*) were associated with two attributes that may reflect breeding habitat quality in coniferous plantation forests: stand age and vegetation cover. For baseline corticosterone, the top model included stand age with limited support for models that included vegetation cover. Mean baseline corticosterone for territorial male thrushes sampled in mature stands was 78.2 % higher than territorial males sampled in early seral stands. For handling-induced corticosterone, there was limited separation among candidate models, and only one model, containing stand age and Julian day, was better supported than the null model. Despite previous research that has shown hardwood cover is an important component of breeding habitat quality for thrushes, our investigation found limited evidence that vegetation cover was associated with either baseline or handling-induced corticosterone levels. Given that early seral and mature conifer forests are characterized by markedly different habitat features, we hypothesize that the observed differences in baseline corticosterone represent either reduced fitness of male thrushes in mature stands or an adaptive adjustment of glucocorticoid levels to match local environmental conditions that equalize fitness across stands of different ages.

Keywords *Catharus ustulatus* · Corticosterone · Early seral forest · Glucocorticoids · Habitat quality · Stress response · Swainson's Thrush

Zusammenfassung

Der Corticosteronspiegel territorialer Zwergdrossel-Männchen variiert in Abhängigkeit vom Waldalter und nicht von der Vegetationsbedeckung

Es wird vermutet, dass Glucocorticoide im Zusammenhang mit der Habitatqualität stehen und daher Aufschlüsse über den relativen Gesundheitszustand von Individuen ermöglichen könnten. Wir verwendeten einen Modellselektionsansatz, um zu prüfen, ob der Plasmaspiegel an Glucocorticoiden bei der Zwergdrossel (*Catharus ustulatus*) mit zwei Kenngrößen zusammenhängt, welche möglicherweise die Bruthabitatqualität wirtschaftlich genutzter Nadelwälder widerspiegeln könnten, nämlich Bestandsalter und Vegetationsbedeckung. Im Falle des Corticosteron-Grundspiegels beinhaltete das beste Modell das Bestandsalter und es gab eine eingeschränkte Bestätigung für Modelle, die die Vegetationsbedeckung berücksichtigten. Der durchschnittliche Grundspiegel an Corticosteron lag bei territorialen Zwergdrossel-Männchen in gereiften Wäldern um 78.2 % höher als in Proben von territorialen Männchen aus frühen Waldstadien. Im Falle des durch Eingriffe induzierten Corticosteronspiegels ließen sich die Kandidatenmodelle nur begrenzt auftrennen und nur für ein Modell, das Bestandsalter und die Julianische Tageszahl beinhaltete, ergab sich eine stärkere

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Bestätigung als für das Nullhypothese-Modell. Obwohl in früheren Studien gezeigt wurde, dass die Bedeckung mit Hartholzvegetation ein wichtiger Bestandteil der Bruthabitatqualität für die Drosseln ist, ergab sich in unserer Untersuchung nur ein schwacher Zusammenhang zwischen der Vegetationsbedeckung einerseits und dem basalen oder dem durch Eingriffe induzierten Corticosteronspiegel. In Anbetracht dessen, dass Frühstadien und Reifestadien von Koniferenwäldern sich durch deutlich verschiedene Habitatmerkmale auszeichnen, stellen wir die Hypothese auf, dass die beobachteten Unterschiede im basalen Corticosteronspiegel entweder eine geringere Fitness der Drosselmännchen in älteren Waldbeständen widerspiegeln, oder aber eine adaptive Anpassung des Glucocorticoidspiegels an die lokalen Umweltbedingungen darstellt, welche zu einer ausgeglichenen Fitness in Waldbeständen verschiedenen Alters führt.

Introduction

In vertebrates, glucocorticoid hormones are critical to several important physiological functions, especially energy metabolism (McEwen et al. 1997; Sapolsky et al. 2000). By mobilizing energy, glucocorticoids play a central role in helping animals cope with unpredictable stressors in their environment (Wingfield et al. 1998; Romero 2004). When confronted with an acute stressor (e.g., interaction with a predator), individuals typically mount a “stress response” whereby circulating levels of glucocorticoids increase rapidly in the blood from baseline levels to prepare individuals for physiological challenges that are associated with a particular stressor (Sapolsky et al. 2000; Romero 2004). In turn, increases in glucocorticoid levels lead to physiological and behavioral changes that help individuals to survive the period of exposure to the stressor (Wingfield et al. 1998). Once the stressor is no longer perceived as a threat, a negative feedback system returns glucocorticoids to baseline levels (Romero 2004) allowing individuals to resume activities that were not essential for survival during the period of exposure to the stressor (e.g., territoriality, parental care).

Recently, much interest has focused on determining the extent to which glucocorticoids are informative about the relative health of individuals or populations within conservation and management settings (Bonier et al. 2009a; Wikelski and Cooke 2006; Busch and Hayward 2009). This is because glucocorticoids play an important role in maintaining energy balance, and circulating levels often increase when environmental conditions become challenging (e.g., via inclement weather, habitat alteration) and can lead to individuals experiencing energy imbalances (Sapolsky et al. 2000; McEwen and Wingfield 2003; Romero et al. 2009). In general, high baseline glucocorticoid levels are thought to be indicative of individuals in worse condition with a reduced likelihood of future fitness gains, an idea formalized as the cort-fitness hypothesis (Bonier et al. 2009a). Because it focuses on the relationship between intrinsic physiological measures and the degree of environmental challenge, this framework may be helpful for identifying links between habitat quality and the health of individuals and populations within conservation and management settings (Bonier et al. 2009a; Busch and Hayward 2009).

Plantation forests provide a significant portion of the raw materials used to satisfy the ever-increasing worldwide demand for wood products (Shepherd 1993). However, the intensive management practices used to increase wood production in plantation forests can have negative consequences for biodiversity (Brockerhoff et al. 2008; Lindenmayer 2009). For example, herbicides are often used in an attempt to control plant species that compete with merchantable trees during stand initiation (Shepard et al. 2004; Hayes et al. 2005; Carnus et al. 2006). This can result in negative consequences for wildlife because many species depend on non-merchantable plant species during critical life stages (Easton and Martin 1998, Hagar 2007; Betts et al. 2010, 2013). The influence of intensive forest management practices on ecological communities is especially evident in landscapes dominated by plantation forests such as those in the U.S. Pacific Northwest (Adams et al. 2005) where forest composition has changed substantially in recent decades (Kennedy and Spies 2005). Such changes include a reduction in compositionally diverse early seral forest that has coincided with long-term population declines of passerine bird species that use early seral forest stands for breeding (Betts et al. 2010). Despite clear and obvious changes to habitat components, we still have a poor understanding of the health of animal populations that rely on plantation forests as habitat for critical biological processes (Brockerhoff et al. 2008; Lindenmayer 2009), including how the physiological health of individuals is linked to changes in habitat that arise due to management practices. This is especially true for forest-dwelling bird communities.

In this study, we investigated the relationship between plasma glucocorticoid levels and two attributes that may reflect breeding habitat quality on plantation forests of the Pacific Northwest: the stand age and extent of vegetation cover. We focused our study on a migrant passerine bird, the Swainson’s Thrush (*Catharus ustulatus*, hereafter thrush) because it is a forest-nesting species that regularly uses conifer forests of varying ages as breeding habitat and has experienced long-term, range-wide population declines (Sauer et al. 2012). The thrush requires an interspersion of hardwood vegetation with coniferous forest during the nesting (McGarigal and McComb 1995; Hagar 2007; Ellis and Betts 2011) and the post-fledging stages of the breeding season (White et al. 2005; Ellis et al. 2012). Thrushes preferentially place their nests in patches that contain higher densities of deciduous trees (Easton and Martin 2002), and these are selected by juvenile thrushes during the post-fledging period (White et al. 2005; Jenkins et al. 2013). Thus, a greater level of hardwood cover on a male's territory is thought to be indicative of higher quality breeding habitat within the coniferous forest matrix. However, hardwood vegetation is targeted for chemical removal by herbicides on the industrial forest lands (Easton and Martin 2002) throughout much of the breeding range of the thrush, so forest management practices have strong potential to alter the quality of breeding habitat for the thrush by affecting the level of hardwood cover and, in turn, the quality of individual thrush territories.

In this study, we measured the glucocorticoid levels of territorial male thrushes captured in early seral (i.e., <15 years) and mature (i.e., 50–60 years) coniferous forest stands and related these physiological measures to vegetation components of each male's territory. We predicted that baseline corticosterone, the primary glucocorticoid hormone in birds, was inversely related to the amount of hardwood cover measured on territories of males sampled during the preparental phase (sensu Holberton and Wingfield 2003). In contrast, we expected no relationship between baseline corticosterone and the extent of coniferous cover and the amount of total cover (i.e., hardwood cover + coniferous cover). Because foraging and nesting substrates for the thrush are variable and occur across vegetation strata within forests (Mack and Yong 2000), we made no a priori predictions regarding the direction of the relationship between baseline corticosterone and vegetation strata.

In addition to studies of baseline glucocorticoids, a growing body of evidence suggests the reactivity of the glucocorticoid stress response may also be linked to fitness (Breuner et al. 2008) independently of baseline glucocorticoid measures (Sapolsky et al. 2000; Romero 2004). Therefore, we also measured absolute corticosterone levels in males 30 min after capture to assess glucocorticoid reactivity arising from a standardized stressor. We predicted that the corticosterone levels of males measured 30 min after capture would exhibit the same relationship to habitat measures and vegetation cover as baseline corticosterone. We made no a priori predictions about the direction of the relationship between corticosterone measures and stand age, as several studies have found high thrush densities in early successional habitats (Hansen et al. 1995; Ellis and Betts 2011), and its association with stand age is inconclusive in the Pacific Northwest (Mack and Yong 2000).

Methods

Study area

We captured and measured Swainson's Thrushes in the Coast Range Mountains of western Oregon, USA, at the start of the 2009 breeding season. We worked in two study areas that were separated by ca. 100 km; one comprised 16 early seral Douglas-fir stands (i.e., 7–12 years post-harvest) whereas the other included 12 mature Douglas-fir stands (i.e., 50–60 years post-harvest). These stands were selected because they represent common stand ages on coniferous plantation forests of the Pacific Northwest. Early seral stands were replanted with Douglas-fir (*Pseudotsuga menziesii*) within a year of harvest and were selected randomly from a large pool ($n = 102$) to represent the natural gradient in hardwood cover for early seral conifer plantations in this region (i.e., <5 to 35 %; see Ellis et al. 2012). All mature stands were initially planted with Douglas-fir as part of an ongoing, long-term study (see Cahall et al. 2013), with each stand undergoing one of three treatments in late 1994, with four replicates per treatment: no thinning (i.e., control, 410–700 trees/ha), moderate thinning (i.e., 240–320 trees/ha), or heavy thinning (i.e., 180–220 trees/ha). On both early seral and mature stands, the overstory was comprised primarily of Douglas-fir and interspersed with hardwood (e.g., vine maple *Acer circinatum*, red alder *Alder rubra*) and various understory plant species (e.g., *Rubus* spp., *Vaccinium* spp., swordfern *Polystichum munitum*, Oregon grape *Mahonia nervosa*).

Although ongoing research objectives prevented us from interspersing early seral and mature stands in this study, a direct comparison between thrushes breeding on early seral and mature stands is appropriate for several reasons. First, the techniques we used to capture the thrushes, quantify hormones, and measure territory vegetation characteristics were identical in both early seral and mature stands. Second, both study areas occur within the central portion of the 1,900-km-long breeding range of the nominate subspecies (Mack and Yong 2000), and there is no evidence of population differentiation between our sampling locations. Finally, the landscape in which our study was conducted is a matrix of coniferous forest that contains stands that range from recently harvested sites to old growth stands. Tree harvest regulations in this region restrict the size and location of timber harvest activities to ensure that adjacent stands differ in age and that no single stand age predominates in the landscape. This leads to a patchwork of coniferous forest stand ages, all of which are used for breeding by the thrush. Taken together, these factors provide a reasonable basis for direct comparisons of male thrushes captured in early seral and mature stands during the breeding season.

Study species and blood sampling

In the Pacific Northwest, Swainson's Thrushes are common in coniferous forests during the summer breeding season (June–mid-August) and often nest in commercial conifer plantations that are interspersed with hardwood plant species (McGarigal and McComb 1995; Hagar 2007). Thrushes are thought to be socially monogamous and raise only a single brood in a breeding season, but they will attempt additional nests if their initial attempt(s) are unsuccessful (Mack and Yong 2000; Rivers et al., unpublished data). The female builds the nest and incubates the eggs for 12–14 days without any assistance from the male (Mack and Yong 2000). Males begin to feed young shortly after hatching and continue to do so throughout the post-fledging period.

We captured and blood-sampled territorial male thrushes on early seral and mature stands concurrently from 7 to 30 June 2009, which coincided with the start of the local breeding season. All required permits 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. To capture birds, we first listened for territorial song from singing males; once a male was detected, we moved to the vicinity of his vocalizations and erected a 6-m mist-net, which was visually obscured by natural vegetation. We then hid a small speaker under the center of the net that played a continuous loop of advertising song of the thrush to simulate a territorial intrusion of an unknown male thrush (see Angelier et al. 2010). Immediately upon capture, we removed each individual from the mist-net, pricked the alar vein with a sterile 27-gauge needle, and collected whole blood (~75 μl) into a heparinized capillary tube; this served as the baseline corticosterone sample. All blood samples were taken within 3 min of capture to ensure that baseline corticosterone levels were measured, as samples taken after 3 min may not reflect baseline conditions (Romero and Romero 2002; Romero and Reed 2005). To minimize circadian variation in baseline corticosterone, we captured all thrushes between 0600 and 1000 hours local time. After obtaining an adequate sample, we stanched blood flow with cotton and immediately placed the sample on ice. After the baseline sample was taken, we placed each individual into an opaque cloth bag and help it in a quiet, secure location. We then took a second blood sample 30 min after the baseline sample to quantify the acute stress response (Romero and Romero 2002). Finally, we measured right tarsus length (to 0.1 mm) and body mass (to 0.1 g), attached a unique combination of color bands for individual identification, and then released the individual. Once the bird was released, we marked the center of the mist-net and plotted its location on a GPS handheld unit for subsequent vegetation measurements.

When starting song playback to capture thrushes, we used a stopwatch to quantify (1) the time elapsed from the start of playback to the point at which we finished taking the baseline blood sample (hereafter "playback to bleed time") and (2) the time elapsed from the time an individual first contacted the mist-net to the point at which we finished taking the baseline blood sample (hereafter "capture to bleed time"). On a limited number of occasions, when no males were singing (i.e., <10 % of captures), we played 1–2 songs to elicit territorial song and determine male location. Although using playback to elicit singing in territorial males had the potential to influence baseline corticosterone levels, we found no relationship between baseline corticosterone levels and the elapsed time between the start of playback and the time we finished collection of the baseline blood sample (see "Results"). This indicates that our limited use of song playback to locate territorial males did not impact baseline corticosterone levels in male thrushes (see Angelier et al. 2010).

After capture, we attempted to quantify the stage of the breeding cycle and the territory size for each individual sampled. Unfortunately, we experienced great difficulty in re-sighting banded individuals because of the furtive nature of this species, the dense vegetation on our study sites, and because previously-captured males typically did not respond to conspecific song playback, even when the song types used to lure males for re-sighting differed from those played during initial capture. These factors made it impossible for us to determine the stage of the breeding cycle or the territory size of sampled individuals. However, a related study that was conducted concurrently with this investigation (Rivers et al., unpublished data) found that most thrush nests (73 %, 27 of 37) located in early seral stands were in the preparental phase during the sampling period for males in the current study. We therefore assumed that the males in our sample were measured prior to the onset of nestling feeding behavior. Nevertheless, even if some males in our dataset did feed offspring and that behavior altered glucocorticoid levels, this would only contribute random noise to our dataset and not lead to a systematic bias because male arrival, the onset of territorial behavior, and our sampling was concurrent in early seral and mature stands (Rivers et al. unpublished data).

Laboratory procedures

Within 8 h of collection, we centrifuged blood at 4,650*g* for 10 min, removed the plasma, and then froze it at −20 °C. At the completion of fieldwork, we shipped samples on dry ice to the University of South Florida where laboratory analysis took place. We used a commercially available corticosterone enzyme immunoassay EIA kit (Assay Designs, Ann Arbor, MI, USA; cat# 900-097) to measure CORT from plasma (Breuner et al. 2006; Kuhlman and Martin 2010). 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 in duplicate in a five-step serial dilution (ranging from 200,000 to 32 pg/ml) on all plates, and all samples fell within this range. We added conjugated corticosterone and antibody to samples and then incubated them for 2 h at room temperature while shaking. 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 was 27 pg based on the manufacturer's specifications (Assay Designs). Further, cross-reactivity with other endogenous steroids (e.g., progesterone, testosterone, aldosterone) were low (<2 %). Samples were randomly allocated among 5 plates; inter-plate variation (the average variation of the samples across plates) was 8.65 %. Average intra-plate variation (variation among duplicate samples) was 12.95 %; intra-plate variation might be expected to be higher than inter-plate variation as low values (as with baseline levels of corticosterone) should result in higher variation between samples.

Vegetation measurements

We measured the vegetation composition within a 25-m radius centered on the mist-net where each male was captured. We used this approach because (1) male thrushes respond to conspecific song when defending their territories (Mack and Yong 2000), so a male responding to playback can reasonably be considered to be exhibiting defense of his breeding territory, and (2) we were unable to quantify territory size because of difficulties with re-sighting males after their initial capture as described above. We took vegetation measurements at four sampling points: one point was centered directly on the mist-net and the other three were located 25 m from the central point. Because it was impossible to assess the territory size of males, we were forced to assume that the vegetation measured at the netting site was representative of the vegetation on a male's breeding territory. The bearing of the first off-net sampling point was chosen randomly, with the second and third points at 120° and 240° from the initial bearing. At each of the four points, we used a 3-m-radius circle (i.e., 28.3 m^2) to quantify vegetation cover. Within each circle, we visually estimated the amount of cover provided by each plant species that covered at least 5 % of the sampling are in one of three distinct vegetation strata: herbaceous vegetation (0–0.5 m), shrub vegetation (0.5–2.0 m), and canopy vegetation (>2.0 m). If we found a species in more than one stratum, we only recorded the stratum in which it provided the greatest cover. For analysis, we summed cover estimates over the four sampling points separately for each of the three strata. We grouped species together to estimate (1) the percent cover provided by hardwood species, (2) the percent cover provided by conifer species, and (3) the percent vegetation cover which included both hardwood and conifer species. Plant classifications were based on Ellis and Betts (2011), and we note this approach can result in summed cover values of >100 % in some cases because of overlapping plants within a stratum.

Statistical analysis

To analyze our data, we used a model selection approach where we considered a priori models that were restricted to key parameters of biological relevance for examining the relationship between glucocorticoids and habitat quality measures (vegetation cover and stand age). We used mixed linear models to test the relationship between glucocorticoid measures (baseline, handling-induced), stand age (early seral, mature), and six vegetation measures (total hardwood cover, total hardwood $cover^2$, total conifer cover, total conifer $cover^2$, total vegetation cover, total vegetation $cover^2$) in each of three vertical strata (i.e., herbaceous, shrub, canopy layer). We deemed it necessary to test for squared effects of cover because of the potential for non-linear relationships between physiological and habitat quality measures (Bonier et al. 2009a). Nevertheless, because of the large number of vegetation measurements, we used a preliminary univariate assessment to screen vegetation candidate variables by eliminating variables that had standard deviations larger their parameter estimates (see Ritchie et al. 2009). This resulted in 8 vegetation variables (see "Results"), all of which were log-transformed prior to analysis to meet assumptions of regression models. For analysis, we considered vegetation measures as fixed effects in our models and included 'plot' as a random effect to account for the potential lack of independence among birds captured within a plot. We modeled the two glucocorticoid measures separately because these processes have different functions (Sapolsky et al. 2000; Romero 2004) and thus may have differential relationships with fitness components (Breuner et al. 2008; Bonier et al. 2009a). For baseline corticosterone models, we examined three covariates (i.e., playback to bleed time, residual body mass, Julian day); we did not include capture to bleed time because our analysis was restricted to males caught within 3 min of contacting mist-nets, a period

Table 1 Results of linear mixed models used in modeling baseline corticosterone levels in preparental male Swainson's Thrushes (*Catharus ustulatus*) in western Oregon, USA, 2009

Model[a]	*K*[b]	ΔAIC[c]	w_i[d]	ER[e]
Stand age	3	0.0	0.776	1.0
Total cover (canopy layer)	4	3.1	0.165	4.7
Total cover (canopy layer)^2	5	6.9	0.025	31.5
Total cover (shrub layer)	4	9.7	0.006	127.7
Null	3	10.1	0.005	156.0
Hardwood cover (canopy layer)	4	10.5	0.004	190.6
Softwood cover (shrub layer)	4	10.7	0.004	210.6
Playback to bleed	4	11.0	0.003	244.7
Softwood cover (shrub layer)^2	5	11.2	0.003	270.4
Total cover (shrub layer)^2	5	11.3	0.003	284.3
Residual mass	4	11.7	0.002	347.2
Julian day	4	12.0	0.002	403.4
Hardwood cover (canopy layer)^2	5	12.4	0.002	492.7
Residual mass + Julian day	5	13.5	0.001	854.1

Models are ranked according to differences in Akaike's Information Criterion (ΔAIC)

[a] Stand age, age class of forest stand; hardwood cover, cover of hardwood species; hardwood cover^2, cover of hardwood species squared; softwood cover, cover of conifer species; softwood cover, cover of conifer species squared; total cover, cover of all foliage species; total cover^2, cover of all foliage species squared; Julian day, day of capture on Julian calendar; residual mass, residuals from regression of body mass on right tarsus length; playback to bleed, time elapsed between the start of song playback and finish of baseline bleed. Model parameters in parentheses denote the vegetation strata (i.e., shrub, canopy) in which vegetation cover was measured

[b] Denotes number of parameters in model

[c] Top-ranking model had AIC = 261.8

[d] Relative likelihood of the current model (*i*) based on AIC value

[e] Evidence ratio

during which corticosterone levels do not increase due to capture or handling (Romero and Romero 2002; Romero and Reed 2005). We examined two covariates for handling-induced corticosterone models (i.e., residual body mass, Julian day). We calculated residual body mass as the residual of body mass regressed on right tarsus length. In our initial analysis, we found no relationship between the time of capture and baseline corticosterone (Pearson's $r = -0.092$, $P = 0.502$) or handling-induced corticosterone (Pearson's $r = -0.158$, $P = 0.245$); therefore, we did not include the time of capture as a covariate in our analysis. We used Akaike's Information Criterion (AIC) as a basis for discriminating among best-supported models using a maximum likelihood approach; restricted maximum likelihood was used to obtain parameter estimates and associated 95 % confidence intervals. All analyses were conducted using PROC MIXED in SAS v.9.2.

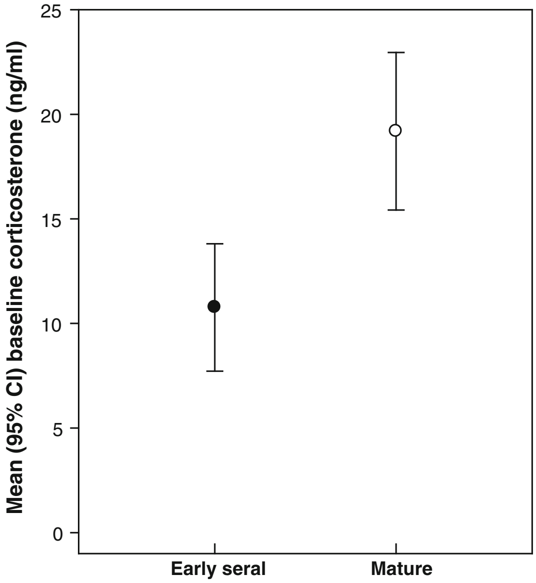

Fig. 1 Mean (95 % CI) baseline corticosterone levels of territorial male Swainson's Thrushes (*Catharus ustulatus*) captured on early seral (*filled circle*) and mature (*open circle*) Douglas-fir plantations in western Oregon, USA

Results

We captured and bled 47 male Swainson's Thrushes: 29 from early seral stands and 18 from mature stands. Males from early seral stands were similar in size [body mass: 29.0 g (95 % CI 28.2, 29.8); tarsus: 30.8 mm (95 % CI 30.3–31.4)] to those captured in mature stands [body mass: 29.7 g (95 % CI: 28.7, 30.7); tarsus: 30.0 mm (95 % CI: 29.3–30.7)]. In addition, males in early seral and mature stands did not differ in residual body mass, an index of body condition [early seral stands: −0.38 (95 % CI −1.15, 0.39); mature stands: 0.59 (95 % CI −0.37, 1.55)].

The model for baseline corticosterone that received the greatest support included stand age, and had 4.7× the weight of evidence to the second best model that included total vegetation cover in the canopy layer (Table 1). These two models had much better support than any of the remaining models ($\Delta\text{AIC} > 6.5$, evidence ratio $[\text{ER}] > 31.0$). In the top model, mean baseline corticosterone levels were substantially higher (78.2 %) higher in mature stands [19.19 ng/ml (95 % 15.42, 22.96); Fig. 1] than in early seral stands [10.77 ng/ml (95 % CI 7.72, 13.81)]. In the second best model, baseline corticosterone increased as the percent total vegetation cover of the canopy increased [$\beta = 1.51$ (95 % CI 0.39, 2.63)]. The model containing residual body mass received very little support, and there was no apparent relationship between residual body mass and either corticosterone measure in early seral and mature stands (Fig. 2).

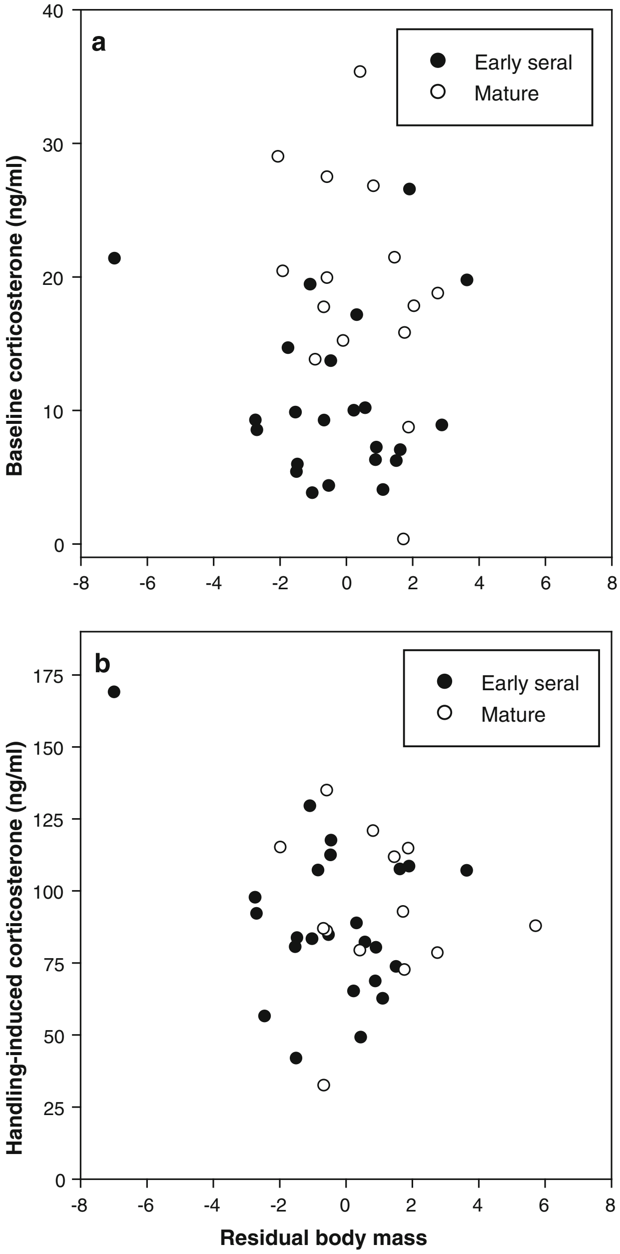

Fig. 2 Relationship between residual body mass and **a** baseline corticosterone and **b** handling-induced corticosterone for territorial male Swainson's Thrushes captured on early seral (*filled circle*) and mature (*open circle*) Douglas-fir plantations in western Oregon, USA. Residual body mass was calculated as the residual of body mass regressed on right tarsus length

Table 2 Results of linear mixed models used in modeling handling-induced corticosterone levels in preparental male Swainson's Thrushes in western Oregon, USA, 2009

Model[a]	K[b]	ΔAIC[c]	w_i[d]	ER[e]
Julian day + stand age	4	0.0	0.238	1.0
Null	3	0.9	0.152	1.6
Residual mass	4	1.0	0.144	1.6
Julian day + softwood cover (shrub)	5	1.0	0.144	1.6
Julian day	4	2.1	0.083	2.9
Julian day + softwood cover (shrub)^2	6	3.0	0.053	4.5
Julian day + total cover (canopy)	5	3.1	0.051	4.7
Julian day + total cover (shrub)	5	3.2	0.048	5.0
Julian day + hardwood cover (canopy)	5	4.0	0.032	7.4
Julian day + total cover (canopy)^2	6	5.1	0.019	12.8
Julian day + hardwood cover (canopy)^2	6	5.2	0.018	13.5
Julian day + total cover (shrub)^2	6	5.2	0.018	13.5

Models are ranked according to differences in Akaike's Information Criterion (ΔAIC)

[a] Stand age, age of forest stand; hardwood cover, cover of hardwood species; hardwood cover, cover of hardwood species squared; softwood cover, cover of conifer species; softwood cover^2, cover of conifer species squared; total cover, cover of all foliage species; total cover, cover of all foliage species squared; Julian day, Julian day of capture; residual mass, residuals from regression of body mass on right tarsus length. Model parameters in parentheses denote the vegetation strata (i.e., shrub, canopy) in which vegetation cover was measured

[b] Denotes number of parameters in model

[c] Top-ranking model had AIC = 353.1

[d] Relative likelihood of the current model (i) based on AIC value

[e] Evidence ratio

In contrast to models for baseline corticosterone, there was no strong separation among the candidate models for handling-induced corticosterone. The best-supported model contained Julian day and stand age, and this was the only model that had more support than the null model (Table 2). The top five models had all had an ER < 3.0, although only one of these models contained a measure of vegetation cover (i.e., Julian day + softwood cover in the shrub layer). Importantly, parameter estimates for the factors in the best supported non-null models (i.e., those ranked 1st, 3rd, and 4th in Table 2) had 95 % confidence intervals that were broad and overlapped with zero, indicating these models had poor precision and limited predictive power.

Discussion

Our results revealed that stand age, a key component of habitat structure, was associated with variation in baseline corticosterone levels. Specifically, the mean baseline corticosterone level of Swainson's Thrushes captured in mature stands was substantially higher, on average, than that for thrushes captured in early seral stands. Although we were unable to determine the exact reproductive status of each male, males were measured concurrently on both sites and during the preparental phase of the breeding season, and samples were taken using identical techniques in the field and laboratory. When these results are considered within the framework of the cort-fitness hypothesis (Bonier et al. 2009a), they suggest that the higher baseline corticosterone levels of males in mature stands may have been indicative of individuals in worse condition and reduced fitness relative to males in early seral stands. However, an alternative perspective argues that individuals in mature stands may have encountered greater environmental challenges and responded adaptively by increasing baseline corticosterone levels (Bonier et al. 2011). The latter view does not imply that males in mature stands were in worse condition because of higher baseline corticosterone levels, but instead explains such differences as an adaptive regulation of glucocorticoid levels to environmental conditions that led to equivalent fitness payoffs for males in stands of both ages. Distinguishing between these two alternatives requires data on components of fitness (e.g., reproductive success) for males inhabiting the two stands: the cort-fitness hypothesis predicts males in mature stands with higher baseline levels had reduced fitness, whereas the adaptive regulation hypothesis predicts equivalent fitness payoffs between males in early seral and mature stands despite differences in baseline corticosterone. Unfortunately, it was not possible to measure fitness components in our study as thrush nests were extremely difficult to locate even when females were fitted with radio-tags and tracked via radio telemetry (see Rivers et al. 2012). Nevertheless, other studies have shown that corticosterone levels can be positively linked to components of fitness (Moore and Jessop 2003; Wingfield and Sapolsky 2003; Ouyang et al. 2011; Bonier et al. 2011), including a related study in which we found baseline corticosterone was positively linked to survival in juvenile thrushes during the post-fledging period (Rivers et al. 2012).

An additional non-mutually exclusive possibility is that males with inherently higher baseline corticosterone are more apt to hold a territory on mature stands. This suggests that relative differences in male baseline corticosterone in stands of different ages may be indicative of settlement patterns that are tied to local environmental conditions (Bonier et al. 2009b) and lead to spatial variation in hormone levels across the landscape. What specific environmental conditions may lead males to settle in different stands is unclear, and a more detailed investigation is needed to determine the cause(s) for the pattern we documented. However, our results do indicate that the differences in thrush baseline corticosterone between early seral and mature stands were not related to vegetation composition and, in particular, the extent of hardwood vegetation cover on territories. Although this may seem surprising, given that hardwood plants provide critical habitat for thrushes during the breeding season (Hagar 2007; White et al. 2005) and are linked to juvenile abundance in this species (Ellis et al. 2012), the lack of relationship may be because hardwood plants were present on thrush territories on both early seral and mature stands at adequate levels.

Unlike baseline corticosterone, there was no strong separation among the best supported models for handling-induced corticosterone. The relative likelihoods of the top 5 best-ranked models (i.e., w_i) ranged from 0.14 to 0.24, indicating that all models had a reasonable chance of being the best model in the candidate set. This result may have been due to model parameter estimates being too imprecise to have any predictive power in our models. For example, the parameter estimates for residual mass in them model ranked third was −2.85 (95 % CI −7.29, 1.59). This poor precision was found for other parameter estimates in the best supported models, making it impossible to draw strong conclusions about how handling-induced corticosterone levels were linked to the factors that we examined.

Data from this study add to previous research that evaluated how forest type was linked to corticosterone levels in a coniferous forest-nesting passerine, the Eurasian Woodcreeper (*Certhia familiaris*; Suorsa et al. 2003). That study found a negative association between corticosterone levels and the age of forests in nestling woodcreepers; however, important differences between the two studies make it difficult to make generalizations about the role of forest composition and structure in relation to stress hormones in birds. First, woodcreepers prefer older coniferous forest (Suorsa et al. 2003) whereas thrushes are known to breed in coniferous forest of all age classes. In addition, a comparison between adult territorial male thrushes and nestling woodcreepers may be confounded by developmental stage as corticosterone values are generally lower in altricial species during the nestling stage (Wada 2008). Finally, the woodcreeper nestlings did not exhibit an increase in corticosterone levels when handled, suggesting that they were at a developmental stage where they did not have a functional response to handling (Wada 2008).

Several other studies have assessed the association between glucocorticoid levels and habitat features in forest-dwelling passerines during the breeding season, with contrasting results. Silverin (1998) found that baseline corticosterone levels of the cavity-nesting Pied Flycatcher (*Ficedula hypoleuca*) were higher in deciduous forest relative to suboptimal coniferous habitat. However, flycatchers in deciduous forest bred at a higher density and experienced more territorial intrusions (Silverin 1998), which can alter corticosterone levels in flycatchers (Silverin 1998) and other species (van Duyse et al. 2004). Whether habitat-specific territorial intrusion rates influenced the differences observed in this study is unknown; however, it is clear that corticosterone levels in male thrushes in this study did not increase in response to an artificial territorial intrusion using song playback alone. A role for breeding density and habitat on corticosterone was also suggested by an examination of mainland and island populations of the cavity-nesting Blue Tit (*Parus caeruleus*; Muller et al. 2007). Although there was a difference in baseline corticosterone between island and mainland populations, no difference was detected between habitats (Muller et al. 2007). Finally, nestling Ovenbirds (*Seiurus aurocapilla*) reared in areas that were recently subjected to logging activity had baseline corticosterone levels that were >2× the level of nestlings from undisturbed stands (Leshyk et al. 2012). Although it was unclear what drove this relationship, the authors argued it was not due to differences in food availability (Leshyk et al. 2012). Our investigation, taken together with these previous studies, provides mounting evidence that corticosterone levels in forest-dwelling passerine birds are linked to structural characteristics of habitat but that additional, unmeasured factors may also influence corticosterone-habitat relationships. However, the number of studies that have assessed habitat-glucocorticoid measures in open-cup nesting passerines during breeding is small, making generalizations difficult. Therefore, we recommend additional studies on this group, especially forest-dwelling species, to provide improved understanding of how anthropogenic disturbance influences glucocorticoid levels via changes in habitat quality.

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