



Carry-over effects provide linkages across the annual cycle of a Neotropical migratory bird, the Louisiana Waterthrush *Parkesia motacilla*

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Population limitation models of migratory birds have sought to include impacts from events across the full annual cycle. Previous work has shown that events occurring in winter result in some individuals transitioning to the breeding grounds earlier or in better physical condition than others, thereby affecting reproductive success (carry-over effects). However, evidence for carry-over effects from breeding to wintering grounds has been shown less often. We used feather corticosterone (CORT_f) levels of the migratory Louisiana Waterthrush *Parkesia motacilla* as a measure of the physiological state of birds at the time of moult on the breeding territory to investigate whether carry-over effects provide linkages across the annual cycle of this stream-obligate bird. We show that birds arriving on wintering grounds with lower CORT_f scores, indicating reduced energetic challenges or stressors at the time of moult, occupied higher quality territories, and that these birds then achieved a better body condition during the overwinter period. Body condition, in turn, was important in determining whether adult birds returned the following winter, with birds in better condition returning at higher rates. Together these data suggest a carry-over effect from the breeding grounds to the wintering grounds that is further extended with respect to annual return rates. Very few other studies have linked conditions during the previous breeding season with latent effects during the subsequent overwintering period or with annual survival. This study shows that the effects of variation in energetic challenges or stressors can potentially carry over from the natal stream and accumulate over more than one life-history period before being manifested in reduced survival. This is of particular relevance to models of population limitation in migratory birds.

Keywords: feather corticosterone, Hispaniola, overwintering period, *Parkesia motacilla*, population limitation.

Ecological studies of overwintering migratory birds have focused on the need for habitat-specific demographic data in assessing habitat preferences (Holmes *et al.* 1989, Wunderle & Latta 2000) and

population limitation (Sherry & Holmes 1995). A general model for understanding the demography of North American migratory birds (Sherry & Holmes 1995) suggests that migrant bird populations can be limited by conditions on either the breeding or the wintering grounds, or by factors that occur during migration. The model emphasizes the importance of density dependence and variation in habitat quality on the rates of repro-

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duction and survival. In one of the only tests of the Sherry and Holmes (1995) model, Latta and Faaborg (2002) linked population responses and individual condition of wintering Cape May Warblers *Setophaga tigrina* to prevailing ecological conditions across three habitats to show how demography interacts with habitat quality, mediated by foraging ecology, to limit populations. A population response to differences in habitat quality was observed through differences in foraging behaviour, sex- and age-class segregation, and among-habitat differences in the survival indices of overwinter site persistence and annual return rate.

Population limitation in migratory birds may also involve carry-over effects between seasons. Variation in conditions at one point in life may have future implications for fitness and population growth rates (Metcalf & Monaghan 2001), and these effects can manifest themselves between seasons (Norris 2005). Carry-over effects thus refer to events and processes occurring in one season that result in individuals making the transition between seasons in different states or levels of condition, thereby affecting individual performance in a subsequent period (Inger *et al.* 2010, Harrison *et al.* 2011). Carry-over effects may directly impact individual fitness, and may affect population dynamics if body condition or stress levels influence survival or reproductive success. For example, stable isotope analyses of the American Redstart *Setophaga ruticilla* indicated winter habitat quality of individuals arriving on the breeding grounds (Marra *et al.* 1998) and showed that birds from inferior scrub habitat arrived on the breeding grounds later and produced fewer young (Norris *et al.* 2004). Carry-over effects may be more common than recognized (Harrison *et al.* 2011), as dominance has been widely reported among wintering warblers of the Parulidae (Wunderle & Latta 2000, Latta & Faaborg 2001, 2002), and negative reproductive impacts of birds arriving late on the breeding grounds are known from many species (e.g. Perrins 1970, Lozano *et al.* 1996, Verboven & Visser 1998).

A number of theoretical models predict how carry-over effects from the wintering to the breeding grounds might influence population dynamics through changes in reproductive success (Norris 2005, Runge & Marra 2005, Ratikainen *et al.* 2008). However, carry-over effects from the breeding to the wintering grounds are less often recognized (Nilsson & Svensson 1996, Inger *et al.*

2010, Harrison *et al.* 2011), in part because of the difficulty of assessing physiological condition and tracking individual birds across seasons. The presence of corticosterone in feathers (CORT_f), however, has allowed the measurement of an ecologically meaningful response to prolonged stressors, so CORT_f can be used to understand carry-over effects from the breeding to the wintering grounds. CORT_f is expected to represent the variation over time in basal CORT and the CORT released in response to stressors during growth of the feather (Bortolotti *et al.* 2008, Bortolotti 2010). Birds respond to unpredictable stimuli or stressors by activating the hypothalamic-pituitary-adrenal (HPA) axis, which ultimately involves the secretion and release of CORT hormones from the adrenal glands (Sapolsky *et al.* 2000). The short-term elevation of CORT helps individuals to maintain homeostasis, promoting behaviours important for improving survival (Sapolsky *et al.* 2000, Romero 2004). CORT is also a regulator of the energy balance of individuals and plays an important role in migration, moult and reproduction (Romero 2004, Landys *et al.* 2006). However, chronically elevated levels of CORT can have negative consequences for fitness and survival (Wingfield & Romero 2001, Blas *et al.* 2007, Bonier *et al.* 2009).

As the primary avian glucocorticoid, CORT can be measured reliably in feathers and provides an integrated measure of HPA activity (Bortolotti *et al.* 2008, Bortolotti 2010, Koren *et al.* 2012, Jenni-Eiermann *et al.* 2015). The concentration of CORT_f depends on plasma CORT levels during feather growth (Bortolotti *et al.* 2008, Lattin *et al.* 2011, Fairhurst *et al.* 2013, Jenni-Eiermann *et al.* 2015). Fairhurst *et al.* (2013) showed experimentally a positive correlation between CORT_f levels and both baseline and stress-induced plasma levels. As single, instantaneous samples of blood glucocorticoid levels cannot encapsulate effects of a temporally dynamic environment (Bortolotti *et al.* 2008, Bortolotti 2010), the use of CORT_f overcomes the problem of how to measure prolonged stressors that may have a seasonal component.

Although CORT_f can be a reliable measure of the physiological state of the bird at the time of moult, even when a feather is collected during the non-breeding period, it remains unknown what specific cause(s) are responsible for variation in CORT_f. CORT_f levels may represent inherent quality differences between individuals (Crossin

et al. 2013, Kouwenberg *et al.* 2013). More frequently cited, however, are numerous ecological factors that could contribute to variation in CORT secretion during the time feathers are grown. These factors may include coping with environmental perturbations (e.g. habitat change, inclement weather), reliability of food supplies, population density, the presence of predators, pathogens and parasites, and social conflicts (Carrete *et al.* 2013, Harriman *et al.* 2014, Kouwenberg *et al.* 2015). Higher CORT levels in adults could also be explained by greater reproductive output and increased parental effort (Bonier *et al.* 2009, Done *et al.* 2011, Crossin *et al.* 2013).

In this study we investigated whether carry-over effects provide linkages across the annual cycle of a Neotropical migratory bird, the Louisiana Waterthrush *Parkesia motacilla*. The Louisiana Waterthrush is a small (approximately 20 g), stream-obligate bird with behavioural dominance resulting in some individuals obtaining higher quality territories than other individuals on both the breeding (Robinson 1995, Mulvihill *et al.* 2008) and the wintering grounds (Master *et al.* 2002, Hallworth *et al.* 2011). Waterthrushes have been shown to respond to the ecological integrity of riparian ecosystems on the breeding grounds with decreased reproductive success and lower return rates on suboptimal streams (Mattsson & Cooper 2006, Mulvihill *et al.* 2008). We predicted that: (1) individuals occupying higher quality winter territories would be predominantly birds arriving from the breeding grounds with lower CORT_f levels; (2) individuals with a higher body condition on winter territories would be birds arriving from the breeding grounds with lower CORT_f levels; and (3) individuals with lower CORT_f scores and better body condition would be more likely to return to the overwintering site the following year.

METHODS

Fieldwork was conducted from September 2008 to March 2011 in the Cordillera Septentrional of the Dominican Republic at Loma de la Joya (19°25'N, 70°16'W), near San Francisco de Macorís, Duarte province. We selected for study a total of > 10.0 km of six montane streams (range = 1.0–3.3 km per stream; mean = 1.7 km) based on their having appropriate habitat for Louisiana Waterthrush, and variation in surrounding land uses suggesting variation in water and habitat quality. The

streams selected were Río Bijao, Río Frío, Río Jagua, La Malena, Río Bonito and La Malenita.

Data collection

Birds were target-sampled with mist-nets (12 m × 3 m × 30 mm mesh) set strategically in or near the stream. Playback of Waterthrush 'chip' notes was sometimes used to aid in captures, but frequency of use was similar among sites and years, and playback attracted only targeted territorial individuals. Most (approximately 80%) captures were made early in the overwintering period (September–October). The age (immature = HY/SY, hatching year/second year; adult = AHY/ASY, after hatching year/after second year) of all mist-netted birds was determined by plumage characteristics. We measured wing chord and weighed birds to the nearest 0.1 g on a 30-g Pesola scale, and calculated a body condition index (BCI) for each individual using the unstandardized residuals of the regression between log₁₀ of bird mass and log₁₀ of the wing chord. All birds were ringed with both a numbered metal ring and colour rings for identification of individuals in the field. In both years nearly all (mean = 91.2%) Louisiana Waterthrushes resident on a stream were captured and marked.

Following ringing we employed extensive resighting efforts to monitor survival of colour-ringed birds. We calculated both within-year survival (overwinter site persistence, September–February) and between-year survival (annual return), with the latter defined as the proportion of within-year site-persistent birds (from the previous winter) that were captured or resighted in the subsequent winter. Because site persistence was high across all years and sites (approximately 90%) and varied little, we used only annual return as our measure of survivorship. Although return rate reflects survival through the breeding season and two migrations, it is frequently used as an indicator of habitat quality and as a reliable measure of survival (Wunderle & Latta 2000, Latta & Faaborg 2001, 2002, Marra & Holmes 2001, Faaborg *et al.* 2010). Return can also be biased, however, if there are high rates of emigration or territory-switching. The location of all of our study streams in a single watershed aided us in reducing the possibility that returning birds switched streams, thereby inflating mortality estimates, and this was never observed.

Waterthrushes depend primarily on aquatic macroinvertebrates for food (Robinson 1995) and prefer streams with a prey biomass containing a high proportion of Ephemeroptera, Plecoptera and Trichoptera (Mattsson & Cooper 2006). We characterized stream and territory quality based on 80 Surber samples per stream (Pringle & Ramírez 1998, Mulvihill *et al.* 2008), and 4–8 Surber samples per territory. Surber samplers are nets that allow the collection of macroinvertebrates from riffle habitat within a standardized area of stream bottom. Each year, four Surber samples were taken at each of 10 approximately equidistantly located points per stream. At each of these 10 points we located the nearest riffle upstream and the nearest riffle downstream, and then sampled macroinvertebrates at the midpoint in the width of the stream, and midway between the right-hand bank and the stream midpoint in each of these two riffles. The macroinvertebrates were then sorted, identified to family and counted. We pooled samples to calculate the mean proportion of Ephemeroptera, Plecoptera and Trichoptera (% EPT) in each territory to reflect macroinvertebrate distributions and territory quality.

Sexing birds

We used the *CHD* genes on the Z and W chromosomes to determine the sex of all birds. Blood samples of 5–10 μL were obtained by wing venipuncture and preserved in Queen's lysis buffer or on FTA cards (Whatman Ltd, Maidstone, Kent, UK). DNA was extracted using the FTA Purification Reagent (Whatman Ltd) and the Qiagen DNeasy Blood and Tissue kit (Qiagen Inc., Valencia, CA, USA) according to the manufacturer's instructions, and was stored in $1\times$ Tris-EDTA buffer at -20°C . The *CHD* genes were amplified from each DNA sample by means of the polymerase chain reaction, using a multiplexed cocktail of primers 3007F, 3112R and 2987F (Ellegren & Fridolfsson 1997), and Illustra PuRe Taq Ready-To-Go PCR Beads (GE Healthcare, Pittsburgh, PA, USA). Each sample was amplified and electrophoresed twice through a 1.5% agarose gel to confirm the sex. The *CHD-W* copy of the gene is present only in female birds and is larger than the *CHD-Z* copy, which is found in both sexes. Individuals displaying both bands on the electrophoretic gel were therefore scored as

females, and those showing only a single smaller band were scored as males.

Measurement of CORT_f

We used CORT_f to represent physiological condition of the individuals from the breeding period. Louisiana Waterthrushes moult and regrow feathers on the breeding stream immediately following nesting (Eaton 1958, Robinson 1995, Mulvihill *et al.* 2009), often during the fledgling period and prior to departure for the autumn migration. Therefore, CORT_f levels reflect the energetic challenges or stressors faced by a bird during the moulting period on the natal stream or breeding grounds. We analysed CORT_f levels by extracting CORT from the outer rectrix (R6) using a methanol-based extraction technique (Bortolotti *et al.* 2008). Whole feathers were used in this study so as to measure CORT averaged over as long a period as possible. We first measured the length of each feather excluding the calamus, which was removed and discarded. Then each feather was cut into pieces of $< 5\text{ mm}^2$ and placed in a glass vial to which 10 mL of methanol was added (HPLC grade, VWR International, Mississauga, ON, Canada). The vials were capped and placed in a sonicating water bath at room temperature for 30 min, followed by incubation at 50°C overnight in a shaking water bath. Using vacuum filtration, the methanol containing the hormones was separated from the feather bits; vials were washed with an additional 5 mL of methanol and added to the original methanol extract. Vials with the methanol extract were placed open in a 50°C water bath in a fume hood under air to evaporate until they were completely dry. When the evaporation of the samples was completed, the extract residues were reconstituted with 600 μL of phosphate-buffered saline (PBS; 0.05 M, pH 7.6) and frozen at -20°C until CORT was measured. We extracted CORT_f from all samples in one single batch and assessed the recovery efficiency of the extraction by including three feather samples spiked with a small amount (approximately 5000 d.p.m.) of ^3H -CORT (Amersham Biosciences Corp., Piscataway, NJ, USA); 90% of the radioactivity was recovered in the reconstituted samples. For more details about feather extraction see Bortolotti *et al.* (2008). CORT concentration was determined using radioimmunoassay (RIA) as in previous studies (Blas *et al.* 2005, Bortolotti *et al.* 2008). Anti-

serum and purified CORT for standards were purchased from Sigma Chemicals (Anti-Corticosterone product no. C8784, lot no. 090M4752; purified CORT product no. C-2505, lot no. 22K1439). Samples were duplicated and randomly measured using RIA. A parallel relationship was found between serial dilutions of reconstituted feather extracts and the CORT standard curve, suggesting that the extracts of Louisiana Waterthrushes did not contain substances that interfere with the RIA. Assay variability was determined as the % coefficient of variation (CV) resulting from repeated measurement of six samples spiked with a known amount of CORT. Samples were measured in one single assay with CV of 3.7% and limit of detection (ED 80) of 9.83 pg per assay tube.

Data are expressed as pg CORT/mm because of the nature of CORT deposition in feathers. The incorporation of CORT into the feathers happens mainly at the blood quill (Jenni-Eiermann *et al.* 2015) and it is thought to be time-dependent (Bortolotti *et al.* 2008, 2009, Bortolotti 2010, Jenni-Eiermann *et al.* 2015). Mass variation along the feather, or among parts of the feather, creates biases, as concentrations become lower as feather mass increases (Bortolotti *et al.* 2008, 2009, Bortolotti 2010, Lattin *et al.* 2011). We used only the outer rectrix (R6) in our study, and thus all feathers had the same morphology and similar size (mean \pm sd = 49.41 \pm 2.42 mm) avoiding any influence that differences in feather structure could have on CORT concentrations (Bortolotti *et al.* 2009, Lattin *et al.* 2011). Hormone analyses were performed at the University of Saskatchewan, Canada.

Data analysis

Data were tested for normality using the Kolmogorov–Smirnov test. We used generalized linear mixed models (GLMMs), performed in SAS 9.3 (SAS Institute, Inc. 2012) to assess how characteristics of birds differed among winter territories of variable quality, what factors affected scores of body condition and what factors predicted the return of birds to overwintering sites in a subsequent year. In GLMM 1, %EPT was the dependent variable (with a square-root transformation to achieve normality), and year, age, sex, BCI, CORT_f and interactions between all pairs of variables were included as independent variables. In

GLMM 2, BCI was the dependent variable with a normal distribution, and year, age, sex, CORT_f and interactions between all pairs of variables were included as independent variables. In GLMM 3, return was the dependent variable with a binomial distribution (returning or not), and year, age, sex, BCI, %EPT, CORT_f and interactions between all pairs of variables were included as independent variables. In the three models, the variable stream (six streams) was fitted as a random factor to control for its potentially confounding effect. All models were built through a backward stepwise procedure.

RESULTS

From September 2008 to March 2011 we ringed and monitored 76 Louisiana Waterthrushes ($n = 39$ in year 1, $n = 37$ in year 2; year 3 required only to determine annual returns) in defended territories along six montane streams in the Cordillera Septentrional of the Dominican Republic. Of these, 31.6% were adults and 38.1% males. Across all streams and years the rate of annual return was 34.7%.

Surveys of Louisiana Waterthrushes and macroinvertebrates indicated that neither age ($P = 0.230$) nor sex ($P = 0.860$) of Louisiana Waterthrush was significantly related to the %EPT in the bird's territory. However, results from GLMM 1 showed a significant negative relationship between %EPT and CORT_f (Table 1), suggesting that birds arriving on the winter territory with lower CORT_f scores occupied territories with higher %EPT (Fig. 1). We also found a significant negative correlation between %EPT and the interaction of CORT_f and age (Table 1). Analysing this interaction separately by age class, we found that the correlation between %EPT and CORT_f was significant for AHY birds ($F_{1,14} = 6.66$, $P = 0.022$) but not HY birds ($P = 0.862$; Fig. 1). %EPT was also positively correlated with BCI (Table 1), indicating that birds on higher quality territories had a better body condition. We found significant interactions between BCI and age, and BCI and sex (Table 1). These interactions were analysed separately by age class and sex; the correlation between %EPT and BCI was significant for AHY birds ($F_{1,14} = 8.01$, $P = 0.013$) but not for HY birds ($P = 0.862$), and the relationship between %EPT and BCI was significant for males ($F_{1,18} = 4.31$, $P = 0.052$) but not females ($P = 0.857$).

Table 1. Results of generalized linear mixed models (GLMMs) to determine how characteristics of birds differed among winter territories of variable quality (%EPT), what factors affected scores of body condition (BCI) and what factors predicted the return of birds to overwintering sites in a subsequent year in the Cordillera Septentrional of the Dominican Republic.

Dependent variable	Fixed effects	Estimate	se	df	F	P
%EPT (GLMM 1)	Intercept	6.074	1.212	5	5.01 ^c	0.004
	Age	1.654 ^a	1.364 ^a	63	1.47	0.230
	Sex	-0.068 ^b	0.383 ^b	63	0.03	0.860
	BCI	17.987	10.215	63	4.58	0.036
	CORT _f	-0.021	0.095	63	5.89	0.018
	BCI x Age	-31.018 ^a	13.452 ^a	63	5.32	0.024
	CORT _f x Age	-0.470 ^a	0.213 ^a	63	4.86	0.031
	BCI x Sex	-34.895 ^b	12.862 ^b	63	7.36	0.009
BCI (GLMM 2)	Intercept	0.029	0.010	5	2.78 ^c	0.039
	Sex	-0.015 ^b	0.006 ^b	68	5.10	0.027
	CORT _f	-0.003	0.001	68	5.76	0.019
Return (GLMM 3)	Intercept	1.963	1.464	5	1.34 ^c	0.238
	Age	-7.000 ^a	3.038 ^a	62	5.31	0.025
	Sex	-1.643 ^b	0.697 ^b	62	5.55	0.022
	BCI	-17.319	13.519	62	1.08	0.302
	EPT	-0.009	0.014	62	1.89	0.174
	CORT _f	-0.292	0.175	62	0.94	0.336
	BCI x Age	62.784 ^a	27.387 ^a	62	5.26	0.025
	EPT x Age	0.054 ^a	0.027 ^a	62	4.14	0.046
	CORT _f x Age	0.969 ^a	0.412 ^a	62	5.52	0.022

^aEstimate and se for age = 1; for age = 2 the Estimate is 0. ^bEstimate and se for sex = 1; for sex = 2 the Estimate is 0. ^ct-value.

With GLMM 2, we tested the prediction that birds with a higher BCI on winter territories would be individuals with a lower CORT_f score from the breeding grounds. As predicted, we found a significant negative correlation of CORT_f with BCI (Table 1), with birds with low CORT_f having a higher BCI (Fig. 2). We also found a significant difference in BCI between sexes (Table 1), with females having higher body condition scores than males.

Finally, using annual return as a measure of survival, in GLMM 3 we found significant differences in return rate between age classes and sex (Table 1), with females more likely to return than males (43% of females returned vs. 21% of males), and AHY individuals more likely to return than HY birds (46% of adults vs. 25% of immatures). The interaction between BCI and age was also significant in the model (Table 1). Analysing this relationship separately by age class we found that AHY individuals that returned had higher scores of body condition than the AHY birds that did not return and this relationship approached significance ($F_{1,14} = 3.65$, $P = 0.077$). The body condition of HY birds that returned was similar to that of birds that did not return ($F_{1,42} = 1.40$,

$P = 0.244$; Fig. 3). The interaction between CORT_f and age was also significant (Table 1) because AHY birds had lower CORT_f scores than HY birds; this difference was significant for birds that did not return but not for those birds that did return (Fig. 3). Analysing this relationship between return and CORT_f by age class we found that the relationship approached significance for AHY birds ($F_{1,14} = 3.87$, $P = 0.069$) but it was not significant for HY individuals ($F_{1,42} = 2.55$, $P = 0.118$). The interaction between %EPT and age was also significant (Table 1). Analysing this relationship separately by age class we found that the relationship approached significance for AHY birds ($F_{1,14} = 3.67$, $P = 0.076$) because adults that returned held territories in the previous winter with higher %EPT, but among HY birds there was no significant difference ($F_{1,42} = 0.41$, $P = 0.526$).

DISCUSSION

Our study suggests that in the Cordillera Septentrional of the Dominican Republic, the effects of variation in energetic challenges to the Louisiana Waterthrush on the breeding grounds can carry over to the wintering grounds and that these

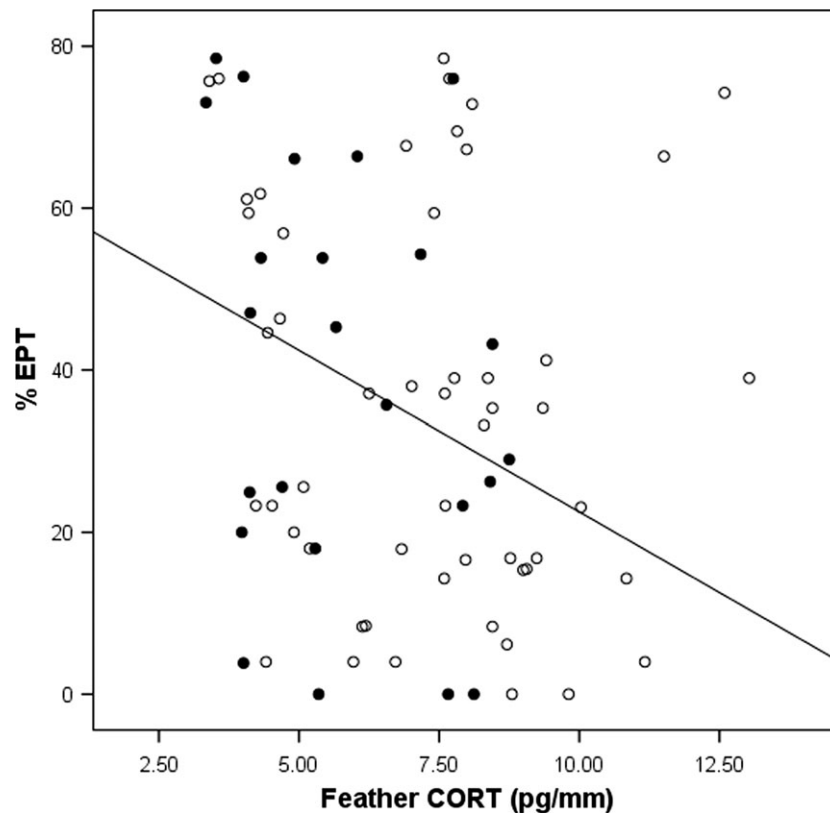


Figure 1. Relationship between the proportion of prey biomass representing the %EPT (Ephemeroptera, Plecoptera and Trichoptera) in each overwintering territory, and individual feather CORT (pg/mm) levels for adult (black circles) and immature (white circles) Louisiana Waterthrush in the Cordillera Septentrional of the Dominican Republic. Regression line corresponds to the adult relationship.

effects can be extended and accumulate over more than one life-history period to affect rates of annual return to the wintering territory.

Using $CORT_f$ as a proxy for post-breeding physiological condition, we found a significant relationship between $CORT_f$ and invertebrate numbers on the overwintering territory, and this was stronger for adult birds than for immature birds. This suggests that individuals that faced increased energetic challenges or stressors during feather moult occupied poorer quality territories in the winter. A similar pattern relating $CORT_f$ from the breeding grounds to non-breeding habitat quality was shown for the Black-capped Chickadee *Poecile atricapillus*, in which Grava *et al.* (2013) showed that CORT from natal feathers predicted the type of habitat in which the birds ultimately settled during the autumn. Schultner *et al.* (2014) also demonstrated experimentally a CORT-mediated carry-over effect between breeding and wintering grounds in the Black-legged Kittiwake *Rissa tri-*

dactyla, with CORT-treated females adjusting their departure from the breeding grounds and then spending a longer period on the wintering grounds than control birds.

We do not know how the observed relationship between $CORT_f$ and invertebrate densities operates, but it could be that Louisiana Waterthrushes with lower $CORT_f$ have fewer energetic challenges or stressors and are able to attain higher quality territories because they are able to migrate sooner (Descamps *et al.* 2011, Harms *et al.* 2015). Data on exact arrival dates for these individuals would help to support this hypothesis, but these are lacking. Alternatively, birds with lower $CORT_f$ may, upon arrival, be better able to compete among conspecifics for optimal territories with high %EPT. Studies of competition among conspecifics of Neotropical migratory birds for high-quality winter territories have frequently shown strong patterns of dominance by age and/or sex (Holmes *et al.* 1989, Wunderle 1995, Latta &

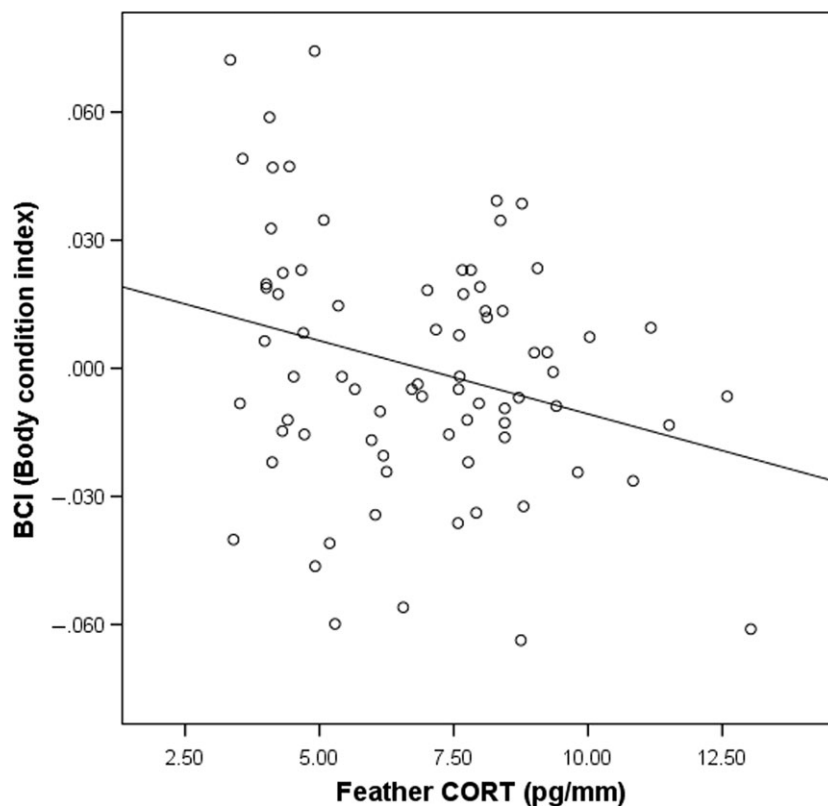


Figure 2. Relationship between BCI (body condition index) and feather CORT (pg/mm) levels for Louisiana Waterthrush sampled on their overwintering grounds in the Cordillera Septentrional of the Dominican Republic.

Faaborg 2001, 2002), with males and AHY birds generally dominant over females and HY individuals. But in other cases, age- or sex-based dominance is not observed (Brown *et al.* 2000, Koronkiewicz *et al.* 2006, Sogge *et al.* 2007, Brown & Sherry 2008a,b, Smith *et al.* 2008), and this is most frequently the case in monomorphic species (Brown & Sherry 2008a, Faaborg *et al.* 2010) such as the Louisiana Waterthrush. We found little direct evidence of competition and segregation of Louisiana Waterthrush by sex or age class, as neither sex nor age was a significant predictor of the %EPT of the territory. But our finding of significant interactions between BCI and both age and sex with regard to %EPT on a territory, and the correlation of BCI and $CORT_f$, suggests that better physiological condition is related to physical condition (as reflected in the BCI), and that differences in BCI among individuals play a role in dominance interactions, resulting in some birds gaining access to territories with a higher %EPT. The correlation between body condition

(BCI) and high-quality food resources of overwintering migrants is generally accepted, even if inadequately tested (Latta & Faaborg 2002, Sherry *et al.* 2005, Brown & Sherry 2008a), but the role of physiological condition in attaining high-quality territories has seldom been shown.

We also showed that females have a significantly higher BCI than males, even though there was no significant difference between the sexes in territory quality. This suggests that females may do better across a wider range of territory quality (%EPT) than do males. Although we know of no studies that have documented partitioning of food resources within Louisiana Waterthrush populations, some ages or sexes of many species may be expected to be more flexible or more experienced in accessing a wider variety of diet items in a wider variety of locations (Marchetti & Price 1989, Slagsvold & Wiebe 2007, Inger *et al.* 2010), and such variation could partially explain these results. In addition, females of some overwintering migrants, including Louisiana Waterthrush, are sometimes tolerated when

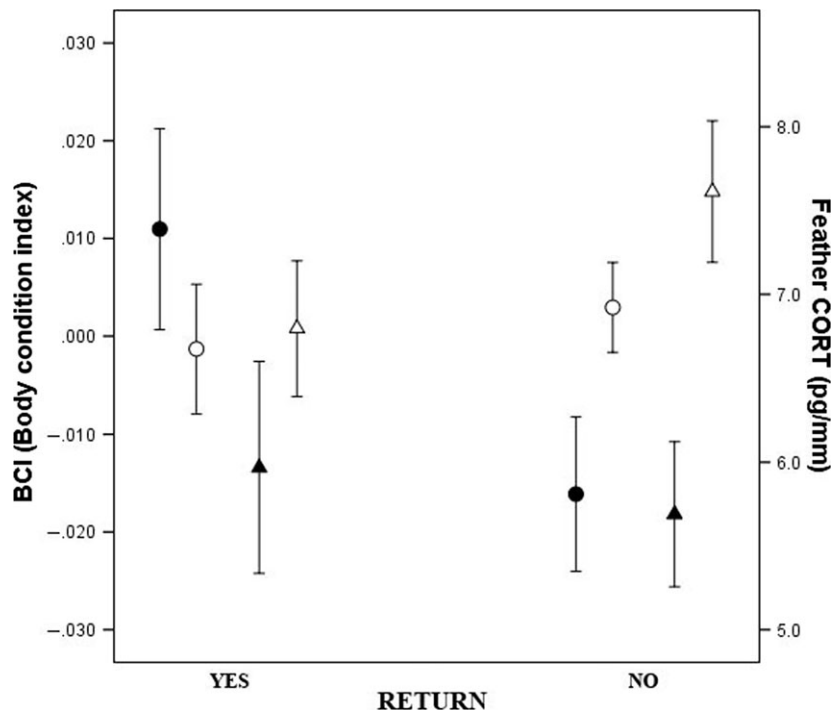


Figure 3. Mean values of BCI (body condition index) scores on the left axis (circles) and feather CORT (pg/mm) levels on the right axis (triangles) in adult (black) and immature (white) Louisiana Waterthrushes that return or do not return to their overwintering grounds in the Cordillera Septentrional of the Dominican Republic. Error bars represent the standard error of the mean.

encroaching on male territories (Faaborg *et al.* 2010), thus potentially finding better access to food resources. More broadly, migrants without a dominance hierarchy may be more likely to adjust their within-home-range activity in response to variation in food availability (Brown & Sherry 2008a), and this may be particularly relevant in the Louisiana Waterthrush, for which preferred macroinvertebrates may be widely but patchily distributed in mid-stream riffles (Prosser & Brooks 1998, Mattsson & Cooper 2006). Caution should be taken in interpreting these data, however, as undescribed sexual dimorphism could also play a role in differences in our BCI if, for example, females have relatively shorter wings for overall body size.

Body condition is of critical importance to overwintering migrants, as it has been shown to affect overwinter site persistence (Johnson & Sherry 2001, Latta & Faaborg 2001) and annual return rates (Latta 2003) of a number of species. Ultimately these demographically important indices of survival are critical in assessing the overwintering ecology of migratory birds (Holmes *et al.* 1989, Faaborg *et al.* 2010). Among our Louisiana Waterthrush population, overwinter site persistence was

remarkably high (approximately 90%) when compared with that recorded in other species of migrants on Hispaniola, which frequently ranges from ~45 to 75% (Latta & Faaborg 2001). This very high site persistence suggests that once a territory is obtained in appropriate habitat, food may not be limiting this Louisiana Waterthrush population, and that predation is apparently minimal in these riparian habitats.

Annual return rates, which included the confounding factors of winter survival, breeding season survival, two migrations as well as site fidelity, were more variable. Females returned at significantly higher rates than males, and adults returned at significantly higher rates than immature birds. That females return at higher rates than males is somewhat unusual (Latta & Faaborg 2001, 2002) but may be less surprising given the lack of well-defined age- or sex-based dominance hierarchies of this monomorphic species, and the significantly higher body condition (BCI) of the females. But our study shows that for AHY birds in particular, the significantly higher rate of return is related to $CORT_f$, %EPT and BCI, where AHY individuals with lower $CORT_f$ from the breeding grounds,

occupying winter territories with higher %EPT, and with a higher BCI, survive and return to overwintering territories at greater rates. Carry-over effects like this from the breeding grounds to the overwintering site have seldom been recorded, but Grava *et al.* (2013) showed not only that natal $CORT_f$ predicted the type of winter habitat in Black-capped Chickadees, but that habitat quality then influenced critically important syrinx and song development. Koren *et al.* (2012) showed that House Sparrows *Passer domesticus* with high $CORT_f$ had low survival rates through the following winter. Crossin *et al.* (2013) also used $CORT_f$ to show that female Giant Petrels *Macronectes* spp. experienced a cost of successful reproduction through delayed moult prior to winter migration, and that these individuals were also much more likely to defer breeding in the following year.

The carry-over effect from the moulting period on the Louisiana Waterthrush breeding ground was also reflected in a significant interaction between $CORT_f$ levels and age class with respect to return rates to overwintering sites. All adults and returning immature birds shared a similar range of relatively low $CORT_f$ levels, but immature birds that did not return had significantly higher $CORT_f$ levels. This suggests that immatures that did not return were those individuals that had faced particularly difficult energetic challenges or stressors on their natal stream, and this was reflected not only in their high $CORT_f$ levels but also in lower survival rates beyond their first overwinter period. Although not frequently measured, survival of inexperienced young birds through the first year of life is thought to be quite low (Faaborg *et al.* 2010), and high levels of $CORT_f$ in immatures leaving their natal streams may be more indicative of future opportunities or losses than is body condition on the overwintering grounds. Very few other studies have reported events occurring during the previous autumn with latent effects on subsequent summer reproduction or survival. However, Harms *et al.* (2015) recently found that in Common Eider *Somateria mollissima*, $CORT_f$ levels at moulting predicted arrival date and body condition the following year, as well as reproductive success and survival in the face of unique environmental challenges.

Our study, showing that the effects of variation in energetic challenges or stressors can carry over from the breeding ground to overwintering sites, and the accumulation of these effects across seasons resulting in reduced survival, is of particular interest

for models of population limitation of migratory birds. Fitness consequences cannot always be measured in terms of fecundity but rather may also be expressed in terms of survival. Carry-over effects may result in declines in body condition and reduced competitive abilities, which may in turn propagate further carry-over effects to accumulate in the next or future seasons (Inger *et al.* 2010, Harrison *et al.* 2011, Harriman *et al.* 2014, Sild *et al.* 2014). Previous studies of another parulid warbler (Palm Warbler *Setophaga palmarum*) wintering on Hispaniola have shown remarkable declines in body condition associated with infestations of an ectoparasitic mite, *Knemidokoptes jamaicensis*, probably acquired on the breeding grounds (Latta 2003). Even though most infected birds survived the wintering period, not a single infected individual returned the following year. Thus, even though stressors may not have immediate fitness consequences, local conditions can still influence the bird's physiological condition and ability to compete, and affect survival and the population growth rate (Inger *et al.* 2010, Harrison *et al.* 2011). However, further work on the costs and benefits associated with carry-over effects from both the breeding and the wintering grounds needs to be done and integrated into models of population regulation (Sherry & Holmes 1995, Norris 2005, Runge & Marra 2005, Ratikainen *et al.* 2008).

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