CORTICOSTERONE SECRETION, ENERGETIC CONDITION, AND A TEST OF THE MIGRATION MODULATION HYPOTHESIS IN THE HERMIT THRUSH (CATHARUS GUTTATA), A SHORT-DISTANCE MIGRANT

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Abstract.—Recent evidence suggests that migration may be extremely important in limiting populations of migratory songbirds. Understanding the relationship between changes in corticosterone secretion and energy reserves during migration is essential to understanding how environmental conditions such as weather, food availability, predation pressure, and habitat quality may be affecting birds en route. Several studies have found that baseline corticosterone is often elevated, and response to capture and handling stress reduced (migration modulation hypothesis), in birds sampled during the migratory period. However, because neither corticosterone secretion nor energetic condition within groups of birds sampled either in laboratory or in field varied significantly (Holberton et al. 1996, Holberton 1999), it was unknown whether corticosterone secretion could be modulated to track changes in energetic condition within the migratory period. Here, we investigated patterns of corticosterone secretion associated with variation in energetic condition in 18 free-living Hermit Thrushes (Catharus guttatus) sampled during autumn migration. Mean baseline corticosterone (mean ± SE) was 37.22 ± 7.70 ng mL−1 and increased during the 30-min interval up to 54.52 ± 6.01 ng mL−1. Lean birds were more likely to exhibit higher levels of baseline corticosterone and a reduced adrenocortical response, compared with birds that had greater energy reserves. Collectively, the results support the migration modulation hypothesis and illustrate that baseline and stress-induced corticosterone secretion can be modulated to meet the changing energy needs of birds during the migratory period. Received 6 February 2003, accepted 12 May 2004.

Resumen.—Evidencia reciente sugiere que la migración puede ser extremadamente importante en limitar las poblaciones de aves canoras migratorias. Entender la relación entre los cambios en la secreción de corticoesterona y las reservas de energía durante la migración es esencial para dilucidar cómo las condiciones ambientales tales como el clima, la disponibilidad de alimento, la presión de depredadores y la calidad del hábitat pueden afectar a las aves durante la migración. Varios estudios han encontrado que en aves muestreadas durante el periodo de migración el nivel basal de corticoesterona se encuentra generalmente elevado y la respuesta al estrés de la captura y la manipulación se ve reducida (hipótesis de la modulación migratoria). Sin embargo, debido a que ni la secreción de corticoesterona ni la condición energética en los grupos de aves muestreados en el laboratorio o en el campo variaron significativamente (Holberton et al. 1996, Holberton 1999), no fue posible saber si la secreción de corticoesterona podría ser modulada para acompañar los cambios en la condición energética durante el periodo migratorio. En este estudio, investigamos los patrones de secreción de corticoesterona asociados a la variación en la condición energética en 18 individuos silvestres de Catharus guttatus que fueron muestreados durante la migración de otoño. El nivel basal promedio de corticoesterona (media ± EE) fue 37.22 ± 7.70 ng mL−1 y éste aumentó durante un intervalo de 30 minutos hasta 54.52 ± 6.01 ng mL−1. Las aves más magras tuvieron una mayor probabilidad de tener niveles basales de corticoesterona más altos y una respuesta adenocortical reducida en comparación con las aves que tenían reservas energéticas mayores. En conjunto, los resultados apoyan la hipótesis de modulación migratoria y muestran que la secreción de corticoesterona basal e inducida por estrés puede ser modulada para cumplir con las necesidades energéticas variables de las aves durante el periodo de migración.

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Recent research on conservation of Neotropical migrants has focused on linking population-limiting events on the wintering grounds with those on the breeding grounds (Marra et al. 1998, Sillett et al. 2000, Norris et al. 2003). The importance of the migratory period in limiting populations has historically been overlooked (Moore et al. 1995, Hutto 2000), but interest in understanding population limitation across the annual cycle is growing. Migrants can spend a significant portion of the annual cycle traveling to and from the breeding grounds. While en route, individuals may have little knowledge of resource availability, predation pressure, or the weather they might encounter (Butler 2000). Long-term data from Black-throated Blue Warblers (Dendroica caerulea) recently indicated that, while the sources of mortality have not been identified, more than 85% of apparent annual mortality occurs during the migratory period (Sillett and Holmes 2002), which illustrates the need for research on how birds regulate energy reserves during that critical stage of the annual cycle.

Environmental factors that influence energy stores before, during, and after migration greatly influence an individual's survivorship and reproduction (Marra and Holberton 1998, Marra et al. 1998, Norris et al. 2003). Corticosterone, the primary glucocorticosteroid in birds (Holmes and Phillips 1976, Harvey et al. 1984), has been linked with increased food intake and lipogenesis during the nonmigratory period (Berdanier 1989, Gray et al. 1990, Astheimer et al. 1992, Breuner et al. 1998). Corticosterone has also been identified as a key facilitator of behavioral and physiological responses to real or perceived challenges to an individual's energy demand (Sapolsky 1987, Wingfield 1994). In general, plasma levels of corticosterone are low but can increase rapidly in response to a variety of potential stressors, such as storms or predation risk (Wingfield et al. 1983, Silverin 1998, Scheuerlein et al. 2001). The rapid release in corticosterone from adrenocortical tissue and the hormone's subsequent effects on an individual's behavior, such as increased food searching and intake (Berdanier 1989, Gray et al. 1990, Astheimer et al. 1992, Breuner et al. 1998), help it meet short-term increases in energy demand. In that way, the short-term adrenocortical response can serve as a stress avoidance mechanism by redirecting behaviors away from ongoing activities and toward life-saving ones until conditions abate (Wingfield 1994). However, if poor conditions persist or the change in behavior does not help an individual meet its new energy demand, corticosterone may remain elevated. When lipid stores are depleted, energy in the form of skeletal muscle protein can be mobilized through the process of gluconeogenesis (Cherel et al. 1988, Dallman et al. 1993, Jenni et al. 2000). Longer-term survival through chronic poor conditions may come at the expense of activities and processes, such as reproduction or immune function, that may not be essential for immediate survival (Sapolsky 1987). Baseline corticosterone and the adrenocortical response can be influenced by many factors, such as gender, season, breeding stage, fed state of the individual, habitat quality, and probability of encountering poor conditions (Astheimer et al. 1992, 1994; Wingfield 1994; Wingfield et al. 1994; Romero et al. 1997; Marra and Holberton 1998; Breuner and Wingfield 2000; Holberton and Able 2000; Reneerkens et al. 2002).

In addition to its role in meeting unpredictable challenges, corticosterone has also been linked with behavioral and physiological responses associated with normal and predictable changes in energy demand during different life-history stages, including natal dispersal and migration (John 1966, Peczely 1976, Meier et al. 1965; for overview, see Dufty et al. 2002). Migratory condition in birds is characterized by increased food intake, and energy stores are primarily in the form of high-caloric lipids, allowing birds to meet the energetic demands of flight while being buffered against unpredictable environmental conditions (King and Farner 1965, McWilliams and Karasov 2001, Long and Stouffer 2003). Several field and laboratory studies on a variety of bird species have shown that both baseline corticosterone and the strength of the adrenocortical response can differ significantly, during migration, from patterns seen at other times of the year (Holberton et al. 1996, 1999; Holberton 1999; Romero et al. 1997). Holberton et al. (1996) found that, in autumn, free-living Gray Catbirds (Dumetella carolinensis) that had completed prebasic molt and had begun to fatten, had higher baseline levels of corticosterone and a reduced adrenocortical response compared to cattails sampled earlier in premigratory condition. In the same study, Yellow-rumped Warblers (Dendroica coronata) sampled on stopover during migration showed patterns of corticosterone secretion
similar to that of the catbirds in migratory condition. The migration modulation hypothesis (MMH; Holberton et al. 1996, Holberton 1999) was proposed to explain those patterns in corticosterone secretion in the absence of any known stressor, such as storms. The MMH posits that during migration birds may (1) express elevated baseline corticosterone levels, intermediate to low maintenance levels, and high catabolic levels to facilitate migratory fattening; and (2) show a reduced adrenocortical response, which would protect skeletal muscle from catabolic activities (e.g. gluconeogenesis) that could be stimulated by further elevation of corticosterone above an already elevated baseline. A subsequent laboratory study provided support for the MMH (Holberton 1999). When Yellow-rumped Warblers were brought into migratory condition in captivity through changing photoperiod, baseline corticosterone increased and the adrenocortical response was reduced as the birds fattened. Unfortunately, as in the earlier field study, there was too little variation in individual body condition, corticosterone levels, or both at any given sampling time to investigate relationships between the amount of energy reserves and degree to which baseline corticosterone and the adrenocortical response were modulated (Holberton et al. 1996, Holberton 1999). This aspect is important for determining if baseline corticosterone and the adrenocortical response remain in a modulated state throughout the migratory period, regardless of energetic condition, or if they can be adjusted to meet the changing energetic needs of migrants during different stages of stopover.

Our objective here was to sample an annual migrant, the Hermit Thrush (Catharus guttatus), during autumn migration to see if patterns of corticosterone secretion vary with energetic condition within the migratory period and in a manner consistent with the MMH. We obtained baseline as well as 30-min blood samples from Hermit Thrushes to determine the magnitude of adrenocortical response over that period of capture and then related those two aspects of corticosterone secretion to variation in individual energy reserves.

We predicted that patterns of corticosterone secretion (baseline and adrenocortical response) could change to help migrants meet their energetic needs during the migratory period. Specifically, we predicted that if elevated corticosterone is needed to initiate and facilitate migratory fattening, leaner birds with greater need to accumulate energy stores would have higher baseline corticosterone levels than birds with greater energy reserves. Further, if the adrenocortical response can be modulated in such a way that it protects skeletal muscle-protein reserves, the adrenocortical response would be lower in leaner birds, particularly those with elevated baseline corticosterone.

Methods

We captured Hermit Thrushes—6 after-hatching-year (AHY), 10 hatching-year (HY), 2 of unknown age (U)—in mist nets, during daylight hours either on 17 October 1995, in Manomet, Massachusetts (n = 4) or between 27 September and 12 October 1999 at Steuben, Maine (n = 14). Sex cannot be reliably determined in this species in autumn (Pyle 1997). We collected an initial baseline blood sample (referred to as “time 0” in all statistical analyses and figures) within 5 min of the bird’s capture in the net. Blood samples were taken by puncturing the brachial vein with a 27-gauge needle and collecting the blood directly into heparinized capillary tubes. We took a second sample 30 min after the bird was captured (referred to as “time 30” in all statistical analyses and figures) to determine the strength of adrenocortical response over that half-hour period. Between sampling times, birds were placed in the shade in cloth bags. After blood sampling, we weighed the birds to the nearest 0.01 g and banded them with federal aluminum leg bands to prevent sampling the same individual more than once. Because no birds were recaptured or resighted after initial capture during the study period, we considered them to be on migratory stopover at the time of capture. We recorded wing chord (± 0.01 mm) as a measure of body size and scored furcular fat using the method of Helms and Drury (1960), modified as follows: 0 = no visible fat in the fossa, 0.5 = trace of fat at the base of the fossa, 1 = fat lining the furculum but not filling the fossa, 2 = fat completely filling the fossa, and 3 = fat beginning to bulge beyond the fossa.

Blood samples were kept on ice until centrifuged at 6,000 rpm for 10 min. Plasma was removed with a 50-µL Hamilton syringe and frozen in microcentrifuge tubes until later analysis by radioimmunoassay (following Wingfield et al. 1992; described in Cash and Holberton 1999). Intra-assay coefficient of variation, based on sample replicates, was 2.59% and 2.75% for 1995 and 1999, respectively. Because samples were collected more than a year apart, we ran them in two assays, which precluded use of the same batch of solutions usually used to track interassay variation (e.g. a set of tubes containing an aliquot of a single
batch of stored plasma and a set of tubes containing an aliquot of a standard solution containing a known concentration of corticosterone, run across multiple assays). However, interassay variation determined from other corticosterone assays for which aliquots of those two components have been used ranges between 6.0% and 12.5% in our laboratory.

After correcting body mass for structural size, we looked at variation in energetic condition related to baseline corticosterone, 30-min corticosterone levels, and magnitude of the 30-min adrenocortical response within a group comprising birds of potentially different body sizes. The relationship between body mass and wing chord was significant ($F = 23.7, df = 1$ and $15, r^2 = 0.61, P = 0.0002$; body mass was missing for one bird). Following Marra and Holberton (1998), residuals of that regression were used as an index of size-corrected energetic condition as the independent variable in regression analyses against time-0 (baseline) corticosterone, time-30 corticosterone, and the percentage of change in corticosterone over that period: $[(time \ 30 – time \ 0) / time \ 0] \times 100$ (log transformed for analysis). Those residuals are labeled “energetic condition” in the figures, wherein positive values and negative values indicate birds whose body mass is either more or less, respectively, than that predicted from their structural size. We also looked for patterns between fat score and time 0, time 30, and the magnitude of the 30-min adrenocortical response. We used STATVIEW 4.5 (Abacus Concepts, Berkeley, California) for all statistical analyses.

Results

There was no effect of capture site or age on body mass, wing chord, time-0 and time-30 corticosterone, or percentage of change in corticosterone (Mann-Whitney U-test, $P > 0.05$, for all comparisons). Thus, data are pooled for all analyses. Patterns of corticosterone secretion varied among individuals during autumn migration (Fig. 1). Mean time-0 corticosterone (mean ± SE) was 37.22 ± 7.70 ng mL$^{-1}$ and was followed by a mean time-30 corticosterone of 54.52 ± 6.01 ng mL$^{-1}$. Thirteen of the 18 birds sampled (72%) exhibited time-0 values less than the mean. Time-0 corticosterone was a reliable predictor of the strength of an individual’s adrenocortical response (energetic condition vs. percentage of change from baseline; $F = 2.92, df = 1$ and $16, r^2 = 0.16, P = 0.11$) as it was for each of its components, time 0 and time 30, the energetic condition index was positively correlated with percentage of change from baseline ($r_s = 0.40, n = 17, P = 0.02$; Fig. 3). Leaner birds, which were more likely to have elevated levels of baseline corticosterone, exhibited a lower adrenocortical response than birds in better condition (Fig. 3).

No birds with a fat score >2 were captured, and only 5 of the 18 birds (28%) had more than a trace of fat (i.e. score >0.5). That lack of variation in fat score as a categorical variable resulted in our finding no correlation between fat score and time-0 corticosterone ($r_s = 0.02, n = 17, P > 0.05$), fat score and time-30 corticosterone ($r_s = 0.11, n = 17, P > 0.05$), and fat score and the magnitude

Fig. 1. Variation in individual patterns of corticosterone secretion (baseline at time 0 and adrenocortical response over the 30-min interval) among 18 Hermit Thrushes sampled during autumn migration. Birds with baseline (time 0) at or below the group mean (37.22 ± 7.70 [SE] ng mL$^{-1}$; large solid circle and heavy line) were more likely to show an adrenocortical response over the 30-min interval.
Knowledge of the link between changes in corticosterone secretion and energy reserves in migratory birds is essential to our understanding of how birds cope with weather, suitable habitat and food availability, and predation pressure during that critical period in the annual cycle (Silleiz and Holmes 2002). The results of the present study suggest that baseline corticosterone and the strength of the adrenocortical response do not remain constant during migration and that the pattern of corticosterone secretion is closely associated with changes in energy reserves within the migratory period (but see Piersma et al. 2000). It is clear from the present study and others that the changes in corticosterone secretion (baseline and adrenocortical response) vary with energetic condition within the migratory period and less so with change in migratory state (migratory vs. premigratory). That question was first raised when the MMH was developed, but the lack of variation between corticosterone and energetic condition precluded uncovering those patterns (see Holberton et al. 1996).

Collectively, our data support both components of the MMH. Baseline corticosterone is higher in lean birds, which have a greater need to maximize migratory feeding and fattening rate. However, as energy stores are replenished, the need for elevated corticosterone declines. Although lean birds on stopover may benefit from elevated baseline corticosterone, they can avoid potentially damaging effects (e.g. immunosuppression, catabolism of skeletal muscle needed for flight, preparation for breeding; Sapolsky 1987, Dallman et al. 1993, Holberton et al. 1999) by minimizing the secretion of additional corticosterone above its already elevated level. The present results are congruent with several other studies on songbirds during autumn migration, wherein energetic condition was negatively correlated with baseline corticosterone concentration, or strength of the adrenocortical response was lower in birds in poorer condition, or both (Schwabl et al. 1991, Jenni-Eiermann and Jenni 1996, Holberton et al. 1999, Jenni et al. 2000). It is not known how ubiquitous the pattern may be, but species sampled in those studies comprise short- and long-distance migrants. In long-distance migratory Bar-tailed Godwits (Limosa lapponica), however, Landys-Ciannelli et
al. (2002) found no relationship between physical condition and the magnitude of the adrenocortical response. Those authors suggested that the lean birds in their study were recent arrivals at the stopover site that were carrying residual fat reserves and were not energetically compromised. Therefore, godwits in poor condition may not have been included in their study (Landys-Ciannelli et al. 2002).

The leanest birds in our study had baseline corticosterone concentrations in ranges well above the average levels for the group. Their inability to exhibit higher corticosterone in response to the stress of capture and handling suggests that the birds were already secreting maximal levels of baseline corticosterone at time of capture, perhaps because lipid reserves were nearly depleted and utilization of muscle protein had begun (Cherel et al. 1988, Dallman et al. 1993, Jenni et al. 2000). In support of that hypothesis, earlier studies have shown the same pattern. Captured birds with extremely high baseline corticosterone levels are usually characterized by marked pectoral-muscle catabolism (Schwabl et al. 1991, Gwinner et al. 1992, Holberton et al. 1999, Jenni et al. 2000, Lindström et al. 2000). If a migrant is meeting its energy demand and is able to put on fat stores via moderately elevated baseline corticosterone, it may be able to protect skeletal muscle by reducing the adrenocortical response (Holberton et al. 1996, 1999; Jenni-Eiermann and Jenni 1996; Jenni et al. 2000). But, if energy demand cannot be met, muscle protein may become an important energy source, requiring lifting the inhibition of the adrenocortical response to begin protein catabolism (Cherel et al. 1988, Dallman et al. 1993). Consistent with that model (Holberton 1999), Jenni-Eiermann and Jenni (1996) found that migrants become more efficient at sparing skeletal muscle protein during the migratory period, and Jenni et al. (2000) suggested that a reduced adrenocortical response may be the mechanism through which that is accomplished. Collectively, the patterns found to date in songbirds and shorebirds are congruent with that model, but more studies, encompassing a wider array of migration strategies, are needed.

Migration is a series of stages characterized by increased energy intake and storage, energy use during flight, and rest and recovery on stopover, with those stages repeated until a bird reaches its destination (Moore and Kerlinger 1987, Moore and Simons 1992). To increase the resolution of our understanding of energy dependent changes in hormone responses, it would be useful to monitor free-living individuals throughout the various stages of migration. However, many studies, including the present one, have had to rely on single observations from individual birds to create a composite of the changes they undergo during migration (Ramenofsky et al. 1995, Tsipoura et al. 1999, Mizrahi et al. 2001, Landys-Ciannelli et al. 2002). For example, on a broad time scale, Piersma et al. (2000) found seasonal peaks of baseline corticosterone during the period of high but stable body-mass change during the migratory period in captive Red Knots (Calidris canutus). In the field, recently arrived Bar-tailed Godwits had lower size-corrected body-mass and higher baseline corticosterone than refueling birds (Landys-Ciannelli et al. 2002). But, interestingly, corticosterone was positively correlated with size-corrected body-mass during the refueling phase (Landys-Ciannelli et al. 2002). To explain that pattern, Piersma et al. (2000) proposed that baseline corticosterone levels may undergo a U-shaped pattern during stopover; initially high at arrival to initiate refueling, declining as energetic condition improves, and increasing again to heighten sensory mechanisms when birds prepare to depart. A recent study of a North American songbird, the Red-eyed Vireo (Vireo olivaceus), provides some support for this hypothesis. Elevated baseline corticosterone at departure was found only in those vireos that appeared ready to depart the stopover site with sufficient fat reserves and were expressing the appropriate orientation direction for crossing the Gulf of Mexico in autumn (Lõhmus et al. 2003), which suggests that corticosterone can play multiple roles shaping migratory behavior in birds, and that elevated corticosterone does not always indicate a compromised condition (Holberton et al. 1996, 1999; Holberton 1999; Piersma et al. 2000).

Ensuring that the initial sample is a reliable representation of predisturbance plasma levels of corticosterone is critical for interpreting initial values of the hormone. Earlier studies have raised concerns about the possible change in plasma corticosterone during the time needed to obtain the initial sample (e.g. Romero and Romero 2002). In the present study, most of the baseline
samples were collected within 2–3 min after the birds hit the net, but a few were collected within 4–5 minutes, which raises some concern that the latter samples may not accurately represent true baseline values. However, at least 9 of the 18 thrushes showed no increase or showed a decline in corticosterone over the 30-min sample period, which suggests that any change in corticosterone in the birds between 3 and 5 min after capture may have been negligible.

Finally, an index of energetic condition based on body mass and corrected for body size may provide more information about an individual’s energy reserves than a categorical variable based solely on fat deposition. An index, such as that used in the present study, takes into account important nonlipid energy sources, such as muscle. The Hermit Thrush, in general, is considered a short-distance migrant, and it is not surprising that in the present study 72% of the birds had little or no fat. Ability to regulate protein use may be particularly important for species, like the Hermit Thrush, that rely heavily on low-protein fruit resources during migration (Long and Stouffer 2003). Birds arriving at a stopover site with emaciated flight muscles may not survive if poor conditions persist and, if they encounter good conditions, may take longer to rebuild energy stores (Moore and Kerlinger 1987). Plasma metabolites of fat and protein use may help us understand how lipid and nonlipid sources of energy are used with respect to different body-mass trajectories (e.g., mass gain or loss, or stable mass) and different migration strategies (see Jenni et al. 2000, Piersma et al. 2000), to help us better understand how migrants with different energy needs meet the demands of migration.

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Literature Cited


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