

MODULATION OF THE ADRENOCORTICAL STRESS RESPONSE IN NEOTROPICAL MIGRANTS DURING AUTUMN MIGRATION

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ABSTRACT.—Seasonal changes in corticosterone metabolism have been implicated in the migratory physiology of passerines. To investigate how this hormone might relate to migratory condition in free-living birds, we compared plasma levels of corticosterone in response to capture and handling stress in premigratory and migrating Gray Catbirds (*Dumetella carolinensis*). Lean, premigratory catbirds exhibited stress responses typical of other nonlipogenic, nonhyperphagic bird species sampled on the breeding or wintering grounds (i.e. low levels of corticosterone at capture followed by significant increases over 1 h). In contrast, fat, migratory catbirds sampled later in the season showed significantly higher baseline levels of corticosterone at capture and no significant increase in hormone levels with handling time. We also sampled a group of migrating Yellow-rumped Warblers (*Dendroica coronata*) at a stopover site. Like catbirds, migrating warblers exhibited an absence of a stress response, with no significant change in corticosterone levels with capture and handling stress. Unlike birds sampled on the breeding grounds, there was no relationship between corticosterone levels at capture and fat scores in premigratory and migratory catbirds, or in the migratory warblers. These results support our Migration-Modulation Hypothesis regarding seasonal changes in corticosterone levels, viz.: (1) an absence of a relationship between fat deposition and baseline corticosterone levels illustrates the permissive nature of the hormone, which remains elevated throughout the migratory period to facilitate hyperphagia and lipogenesis independent of short-term changes in energetic condition; and (2) further elevation of corticosterone in response to acute stress is suppressed during migration to protect skeletal muscle needed for flight. Received 25 April 1995, accepted 14 July 1995.

RECENT RESEARCH ON Neotropical migrants has focused on habitat selection, foraging ecology, and conservation issues related to stopover sites, with less emphasis on physiological adaptations associated with their migration (e.g. Loria and Moore 1990, Martin and Karr 1990, Kuenzi et al. 1991, Hagan and Johnston 1992). Indeed, recent studies on the physiology of passerines during migration have focused primarily on Old World species (Schwabl et al. 1991, Bairlein and Totzke 1992, Gwinner et al. 1992, Jenni and Jenni-Eiermann 1992). Like Old World migrants, many Neotropical migrants interrupt their autumn journey to the wintering grounds to rest and refuel. As food and weather become less predictable, migrants may face energy and time constraints in their ability to replenish fat reserves quickly and efficiently.

Corticosterone is the primary glucocorticoid and hormone of stress in birds (Holmes and

Phillips 1976). It is released rapidly into the bloodstream in response to a variety of stressors (Holmes and Phillips 1976, Siegel 1980, Harvey et al. 1984). A rise in corticosterone in the bloodstream promotes gluconeogenesis to increase glucose substrates, often at the expense of muscle tissue (Holmes and Phillips 1976). These energy substrates help an individual meet additional energetic demands that occur during periods of extreme stress such as storms, attack by predators, or food shortage (Wingfield et al. 1983, Harvey et al. 1984, Chérel et al. 1988, Smith et al. 1994, Wingfield 1994).

An individual's responsiveness to a stressor (i.e. amount and rate of corticosterone release from adrenal tissue) can be measured by repeated blood sampling for a period of time after capture and handling, activities assumed to be stressful to free-living birds (e.g. Wingfield et al. 1992). The protocol of repeated sampling after capture has become the accepted paradigm for measuring the sensitivity of an individual's

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hormonal response to stress. In general, birds sampled during benign weather conditions on the breeding or wintering grounds exhibit a stress response to capture and handling characterized by low baseline levels at the time of capture followed by a significant increase in corticosterone over a 30- to 60-min period (Wingfield et al. 1992; Holberton and Wingfield 1994; Smith et al. 1994; Wingfield et al. 1994a, b; Holberton et al. 1996). An increase in foraging activity (i.e. hyperphagia and searching for food) and lipogenesis are among the short-term effects of higher levels of corticosterone (Wingfield and Silverin 1986, Berdanier 1989, Gray et al. 1990, Astheimer et al. 1992). Among its chronic or long-term effects is catabolic activity on skeletal muscle as a glucose/energy source, often a last resort if adequate food does not become available (Holmes and Phillips 1976, Siegel 1980, Wingfield and Silverin 1986, Chel et al. 1988, Gray et al. 1990).

The associations among corticosterone, hyperphagia, and lipogenesis are highly relevant to bird migration physiology. Indeed, the latter two characteristics are used to define migratory condition in captive birds. In spite of the potential benefit of a typical corticosterone stress response, however, actively migrating birds may be faced with a conflict between the hormone's lipogenic activity and its catabolic action on muscle. If migrating birds maintain elevated corticosterone levels to facilitate foraging and lipogenesis, they may, unlike non-lipogenic birds, suppress additional increases in the hormone (e.g. in response to stress) to protect muscle needed for long-distance flight. Several studies have shown that corticosterone secretion in response to handling stress can be suppressed, but these data come from studies of amphibians (Paolucci et al. 1990), reptiles (Bradshaw 1975), and birds (Wingfield et al. 1983, Wingfield et al. 1992, Holberton and Wingfield unpubl. data) during the breeding season, when hormone levels typically are low already.

We investigated the seasonal nature of corticosterone secretion in two species of free-living Neotropical migrants, the Gray Catbird (*Dumetella carolinensis*) and the Yellow-rumped Warbler (*Dendroica coronata*), at an autumn stop-over site in coastal New England. We tested two hypotheses, collectively referred to as the Migration-Modulation Hypothesis. Given corticosterone's effect on lipogenesis and hyperphagia and its catabolic activity on muscle, we

predicted that: (1) birds in migratory condition would exhibit higher levels of the hormone than those in premigratory condition, and (2) actively migrating birds would suppress the stress response by showing no significant increase in the hormone following capture (which presumably involves stress).

STUDY SITE AND METHODS

Study site.—In autumn 1993 we collected blood from Gray Catbirds and Yellow-rumped Warblers on Block Island (41°N, 71°E), which is a 2,900-ha landmass located 19 km south of the coast of Rhode Island. Birds were captured on Clayhead Preserve at the northern tip of the island, where many migrants congregate (Able 1977). The habitat where birds were netted consisted primarily of early successional coastal shrubland dominated by northern arrowwood (*Viburnum recognitum*), black chokeberry (*Pyrus melanocarpa*), northern bayberry (*Myrica pennsylvanica*), shadbush (*Amelanchier* spp.), and poison ivy (*Rhus radicans*).

Bird capture, plasma collection, and weather.—Birds were captured in mist nets throughout the daylight hours. From a vantage point away from the nets, we recorded the exact time when each bird was captured. Immediately after capture, birds were extracted from the net and a blood sample taken by puncturing the wing vein with a 27-gauge needle. The time of completion of the first blood sample was recorded for each bird. All samples included in this study were obtained within 2 min of capture, which represents as closely as possible the pre-disturbance level of hormone and is referred to as baseline (i.e. time = 0) in our analyses. To complete the stress series for each individual, the time of each subsequent sampling was based on the time of capture for that individual. Smaller migrants (all warblers) were bled at 5, 20, and 60 min after capture, whereas larger migrants (all catbirds) were bled at 5, 10, 30, and 60 min after capture. At each sampling time we collected 50 to 100 μ L of blood in a heparinized capillary tube. This procedure took less than one minute. Blood samples were kept on ice in a small cooler until centrifuged 2 to 4 h later. Plasma was then recovered from each sample with a 50- μ L Hamilton syringe and kept frozen in microcentrifuge tubes until assayed for corticosterone by radioimmunoassay as described in Wingfield et al. (1992).

Birds were kept individually in small cloth bags between sampling times. After each stress series was completed, birds were banded with a U.S. Fish and Wildlife Service aluminum band and processed for body mass (\pm 0.1 g), fat score (scale 0–5; see Helms and Drury 1960), and presence of molt. Although the sex of the warblers could be determined by plumage and wing measurements, and hormone levels may differ between the sexes (Wingfield 1994), we pooled

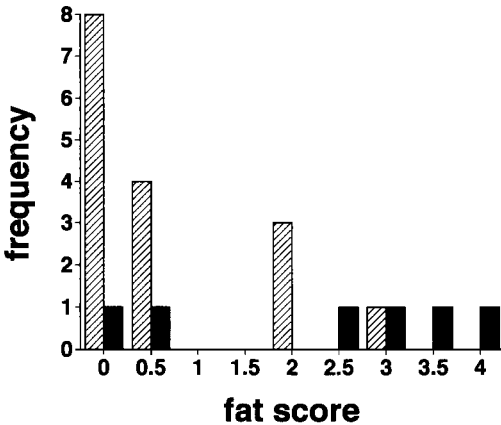


FIG. 1. Fat scores of premigratory (hatched bars) and migratory (solid bars) Gray Catbirds captured at Block Island, Rhode Island, autumn 1993.

the sexes because of small sample sizes. To reduce measurement error, all fat scores were taken by the same two people throughout the study. We assigned half-values (e.g. 0.5, 1.5, 2.5) to birds that could not be placed into fat classes unambiguously. Because corticosterone levels can be affected by weather conditions (Wingfield et al. 1983, Smith et al. 1994), we obtained local data on precipitation, dry air temperature ($\pm 1^\circ\text{C}$), and wind speed and direction. Data were compiled on the day before and the day of sampling to look for possible effects on hormone levels.

RESULTS

Gray Catbirds.—Catbirds are summer residents on Block Island. Of the 16 catbirds captured in early autumn (24–25 September), 15 were undergoing heavy molt. As a group, these birds were lean, with 50% of them having no visible fat (median fat score = 0.25, range 0 to 3; Fig. 1). Based on molt and the absence of fat deposition, we classified these individuals as premigratory. Five of six catbirds captured two weeks later (10–17 October) had completed molt. These birds had significantly greater fat reserves than those captured during the earlier sampling period (median fat score = 2.75, range 0 to 4; Mann-Whitney U -test, $P < 0.05$), with four of them having fat scores of 2.5 or higher (Fig. 1). We considered this latter group to be in migratory condition. No catbirds captured during the premigratory sampling period were recaptured during the migratory sampling period.

We were able to obtain complete stress series

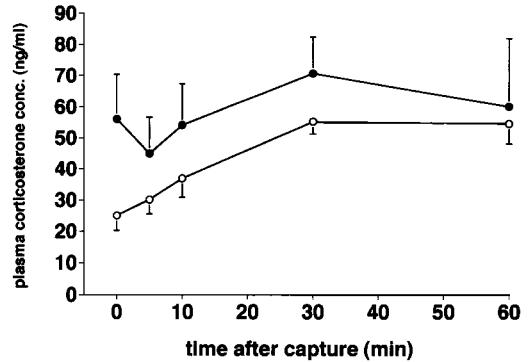


FIG. 2. Plasma corticosterone concentration (mean \pm SE) as a function of handling time after capture for premigratory (open circles; $n = 16$) and migratory (solid circles; $n = 6$) Gray Catbirds sampled for the stress response in autumn.

for only 14 of the 22 catbirds owing to problems with clotting or too little plasma for reliable analyses. Therefore, in lieu of a repeated measures ANOVA, we used a two-factor ANOVA (with $\log [X + 1]$ transformation) to compare corticosterone levels relative to capture and handling stress between the two groups of catbirds (see Keppel [1982] and Zar [1984]). Migratory status explained a significant amount of variation in corticosterone release in catbirds ($F = 9.28$, $df = 1$ and 84 , $P = 0.003$; Fig. 2). There also was a significant overall effect of sampling time after capture on plasma corticosterone levels ($F = 4.41$, $df = 4$ and 84 , $P = 0.003$) for all catbirds. The pattern of hormone release did not differ between the two groups, because the interaction between migratory status and hormone levels at sampling time after capture was not significant ($F = 1.55$, $df = 4$ and 84 , $P = 0.194$).

Differences between catbirds in premigratory and migratory condition were evident in corticosterone levels at the time of capture. Catbirds in migratory condition had higher levels of corticosterone at the time of capture ($\bar{x} = 56.16 \pm \text{SE of } 14.26$ ng/ml) than did premigratory catbirds sampled earlier in the season ($\bar{x} = 25.02 \pm 4.74$ ng/ml; Mann-Whitney U -test, $P < 0.05$; Fig. 2). In addition, premigratory catbirds showed a significant increase in hormone levels between capture ($\bar{x} = 25.02 \pm 4.74$ ng/ml) and 30 min after capture ($\bar{x} = 55.33 \pm 3.98$ ng/ml; paired t -test, $P = 0.0001$; Fig. 2). In migratory catbirds, there was no difference in corticosterone levels at capture ($\bar{x} = 56.16 \pm 14.26$

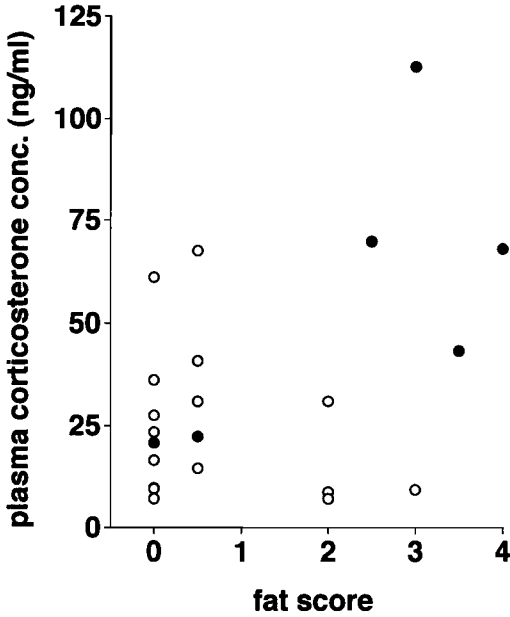


FIG. 3. Plasma corticosterone concentration at the time of capture as a function of fat score in pre-migratory (open circles) and migratory (solid circles) Gray Catbirds.

ng/ml) vs. 30 min after capture ($\bar{x} = 70.78 \pm 11.75$ ng/ml; paired t -test, $P = 0.267$; Fig. 2).

We found no evidence that weather accounted for the above differences. During the earlier sampling period (24–25 September), nighttime temperatures reached a low of 10°C, and daytime temperatures ranged from 18–21°C. Winds were light throughout the period. During the later sampling period (10–17 October), daytime temperatures were similar to those recorded earlier, ranging from 12–21°C, and winds again were light. Nighttime temperatures fell to 7–10°C during this period. No precipitation occurred during either sampling period.

Neither group of catbirds showed a significant correlation between corticosterone level at the time of capture and fat score (pre-migratory: $n = 16$, Kendall's $Z = -0.54$, $P = 0.587$; migratory: $n = 6$, $Z = 1.32$, $P = 0.188$; Fig. 3). However, Figure 3 illustrates the trend between the lower hormone values measured in the earlier group of lean birds and the higher hormone values measured in the later, fatter birds (groups pooled, $n = 22$, $Z = 1.66$, $P = 0.097$).

Yellow-rumped Warblers.—In the absence of a complete series of samples for all individuals, we used single-factor ANOVA to look for the

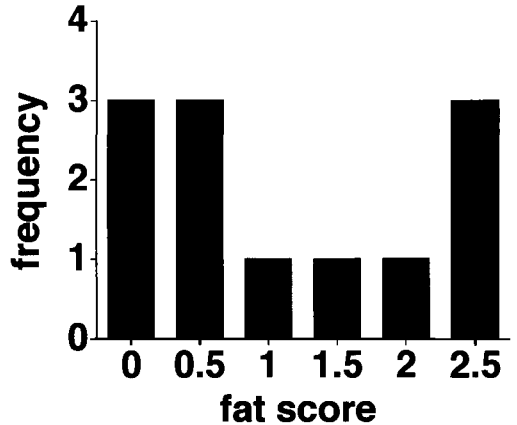


FIG. 4. Fat scores of 12 Yellow-rumped Warblers captured on stopover during migration at Block Island, Rhode Island, autumn 1993.

stress response in 12 Yellow-rumped Warblers captured during the later sampling period (10–17 October). Based on calendar date, we considered these warblers to be actively migrating through the site. Although Yellow-rumped Warblers do not deposit large amounts of fat during fall migration (Holberton pers. obs.), we detected stored fat in 75% of the individuals captured (Fig. 4). Like catbirds in migratory condition, this group of warblers failed to show a significant change in corticosterone levels with time after capture ($F = 0.33$, $df = 3$ and 42, $P = 0.806$; Fig. 5). Because there was little variation in hormone levels at the time of capture (see Fig. 5), there was no correlation between corticosterone levels and fat scores ($n = 9$, Kendall's $Z = -1.01$, $P = 0.312$).

DISCUSSION

The results from this preliminary study support both aspects of the Migration-Modulation Hypothesis. First, catbirds in migratory condition had higher levels of corticosterone at the time of capture than did catbirds that were actively molting and had little or no stored fat. This suggests that catbirds sampled later in the season had increased plasma corticosterone levels concomitant with, or as a consequence of, coming into migratory condition. Indeed, corticosterone's positive effect on behaviors such as hyperphagia and searching activities, in conjunction with its lipogenic activities (Wingfield and Silverin 1986, Gray et al. 1990), would be

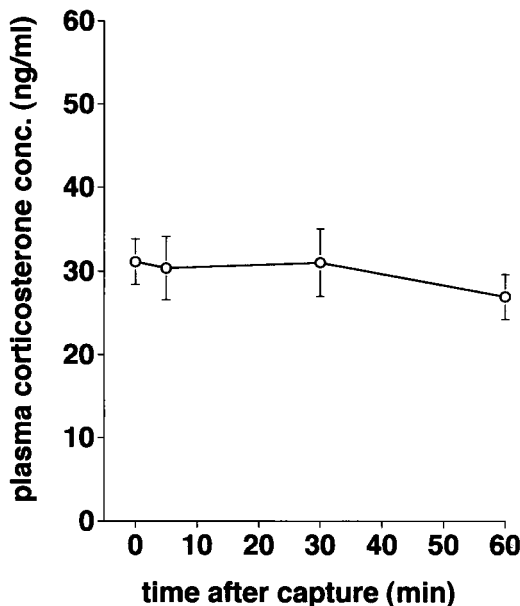


FIG. 5. Plasma corticosterone concentration (mean \pm SE) as a function of handling time after capture for 12 Yellow-rumped Warblers sampled for the stress response during autumn migration.

beneficial to migrants as they prepare to meet the increased energy demand of migratory flight. The second aspect of the Migration-Modulation Hypothesis refers to the apparent conflict that these elevated levels of hormone may impose on migrants. Unlike the premigratory catbirds in this study (and other birds in non-migratory condition; Wingfield et al. 1992, 1994a, b; Smith et al. 1994; Holberton and Wingfield unpubl. data), catbirds in migratory condition appeared to suppress the typical stress response. These birds failed to show a significant increase beyond elevated levels at the time of capture and those measured 30 min later, a time when most birds express maximal levels of corticosterone in this type of sampling paradigm (Wingfield et al. 1992; Holberton and Wingfield 1994; Smith et al. 1994; Wingfield et al. 1994a, b). Moreover, although we were unable to obtain comparable samples from Yellow-rumped Warblers before they came into migratory condition, they, too, failed to show a significant change in corticosterone levels with handling time, a pattern now known in many other species of passerines during migration (Holberton and Moore unpubl. data).

Although weather can influence plasma levels of corticosterone (Wingfield et al. 1983, Rog-

ers et al. 1993, Smith et al. 1994), weather is not believed to have been a factor in the temporal difference in hormone levels or the stress response in our study. Weather conditions were mild and similar both before and during each sampling period. Therefore, differences in the patterns of hormone release between premigratory and migratory catbirds probably reflected an intrinsic change in migratory status. These results support an earlier model proposed by Meier and Farrer (1964), where seasonal changes in daily patterns of corticosterone, in conjunction with prolactin, could explain the onset and termination of migratory behavior (but see Vleck et al. 1980).

If corticosterone facilitates fattening during migration, one might expect leaner birds (i.e. with a greater need to deposit fat) to have higher baseline levels of the hormone than fatter birds that are ready to resume migration. Our results are equivocal for migratory catbirds regarding this point, perhaps because of small sample sizes. However, the Yellow-rumped Warblers did not show the variation in baseline corticosterone levels that would be needed to find such a relationship between fat reserves and corticosterone levels. This suggests that elevated hormone levels, in conjunction with suppression of the stress response, are maintained throughout the migration period regardless of short-term fluctuations in energetic condition (Schwabl et al. 1991; but see Ramenofsky et al. 1995). Clearly, further study is needed to discern the exact relationships between corticosterone levels and energetic condition during stopover.

An important assumption of our Migration-Modulation Hypothesis is that our capture and handling paradigm was stressful enough to elicit maximal amounts of corticosterone release. If birds during the nonmigratory season respond to storms with elevated levels of corticosterone that increase foraging behavior and lipogenesis (Wingfield et al. 1983, Wingfield and Silverin 1986, Gray et al. 1990, Astheimer et al. 1992), then how do migrants that apparently suppress this response respond to such stressors? In an attempt to reach the wintering grounds quickly to compete for wintering sites (Alerstam and Lindström 1990, Holmes and Sherry 1992, Stutchbury 1994), migrants may already be foraging at their maximum potential during stopovers, and additional corticosterone will have no further effect on behavior. It may only be

during periods of extreme stress (which were not present in our study) that fat reserves are exhausted and skeletal muscle mobilized, at which time migrants might exhibit dramatic increases in corticosterone levels (see Gwinner et al. 1992).

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