PATTERNS OF CORTICOSTERONE SECRETION IN MIGRATING SEMIPALMATED SANDPIPERS AT A MAJOR SPRING STOPOVER SITE

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ABSTRACT.—Seasonal changes in corticosterone metabolism may be in part responsible for mediating the changes in nutrient reserves before and during migration. To investigate the role of glucocorticoids in the migratory physiology of Semipalmated Sandpipers (*Calidris pusilla*), we compared plasma levels of corticosterone in response to capture and handling stress during prolonged stopovers in Delaware Bay during spring 1996 and 1997. Although Semipalmated Sandpipers showed significant stress responses to handling in both years, the magnitude of the response was significantly lower in 1997. We found no correlation between energetic condition and initial corticosterone concentration in either year, or between energetic condition and corticosterone concentration in samples collected 30 min after capture in 1996. However, energetic condition was positively correlated with corticosterone concentration in 30 min sample collected in 1997. Between-year differences in regression functions of energetic condition by Julian date suggested that birds were accumulating fat mass more rapidly, or arriving in better energetic condition during 1996 compared to 1997. Those differences were especially evident during the "early" stages (before 26 May) of stopover periods. In 1997, we found that birds sampled early in the season did not show a significant increase in corticosterone 30 min after capture, while birds sampled in early 1996 did. In both years, birds sampled during the "late" stages of stopover periods (after and including 26 May) showed significant stress response. Birds in relatively poor energetic condition, or with low rates of fat-mass gain, were less likely to secrete additional corticosterone in response to acute stress, possibly to protect skeletal muscle needed for migratory flight. Those results suggest that patterns of corticosterone secretion in sandpipers can be modified in response to changes in energy demand during the migratory period. *Received 20 November 1998, accepted 8 August 2000.*

REGULATION OF body composition is critical for the completion of long-distance migration of birds. Changes in body composition can be mediated through behavioral processes such as diet selection (Bairlein 1990, Prop and Deerenberg 1991), and physiological processes such as hyperphagia (see review in Berthold 1996), lipogenesis (Ramenofsky 1990), and muscle hypertrophy (Lindström and Piersma 1993, Jehl 1997). Ramenofsky et al. (1995) and Holberton et al. (1996, 1999) have proposed that corticosterone, the primary glucocorticoid in birds (Holmes and Phillips 1976), may be important in mediating changes in body condition in preparation for and during migration, as first suggested by Meier and his colleagues (Meier and Farner 1964, Meier et al. 1965).

Corticosterone secretion from adrenocortical tissue is controlled by the hypothalamic–pituitary–adrenocortical axis (HPA; Harvey et al. 1984, Greenberg and Wingfield 1987). The HPA axis is sensitive to a variety of endogenous and exogenous sensory information, and a rapid adrenocortical response is believed to help maintain homeostasis (Selye 1971, Holmes and Phillips 1976, Harvey et al. 1984, Munck et al. 1984). Unpredictable events (e.g. storms) often cause a short-term rise in plasma corticosterone concentration (Wingfield et al. 1983, Smith et al. 1994), which is believed to redirect behavior away from ongoing activities such as reproduction and territoriality, and toward immediate lifesaving activities such as increased food searching and hyperphagia (Wingfield 1988, Gray et al. 1990, Astheimer et al. 1992).

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For many species, maximal corticosterone concentrations are typically reached within 30 to 60 min after the initial stressor, and return to predisturbance levels soon after the potentially stressful conditions abate (Wingfield 1994). In addition, elevated plasma corticosterone can result in lipogenesis if an individual can meet its immediate energy demands (Berdanier 1989, Dallman et al. 1993, Breuner et al. 1998). Those behavioral and physiological processes not only serve to enhance survival during short-term emergencies (Wingfield 1994), they are also major components of the migratory condition of birds (see review in Berthold 1996).

Although adrenocortical responses to acute stress may be beneficial in the short-term, chronically high levels of the hormone may be detrimental through its negative effect on growth, development, reproduction, and the immune system (see reviews in Sapolsky 1987, Wingfield 1994). In addition, chronically high levels of plasma corticosterone can result in gluconeogenic activity on muscle protein when sufficient food or energy reserves are unavailable, resulting in significant catabolism of skeletal muscle (Holmes and Phillips 1976, Cherel et al. 1988, Dallman et al. 1993). For migrants, significant loss of flight muscle is likely to reduce flight efficiency, which may affect an individual's ability to reach its destination. Recent studies indicate that in birds, the adrenocortical stress response can be modulated to reduce rates of acute corticosterone secretion when higher levels of the hormone may especially compromise growth (Sims and Holberton 2000), reproduction (Wingfield and Silverin 1986, Wingfield et al. 1992, 1994a, b; Astheimer et al. 1995), and migration (Holberton 1999, Holberton et al. 1996, 1999), and when birds are forced to forage in poor quality habitats (Marra and Holberton 1998).

To address the potential conflict between the anabolic and catabolic actions of corticosterone during migration, Holberton et al. (1996) proposed a general framework for understanding relationships between migratory disposition, energetic condition, and patterns of corticosterone secretion. The Migration Modulation Hypothesis (MMH, Holberton et al. 1996, Holberton 1999) posits that during preparation for migration, birds maintain baseline levels of corticosterone that are intermediate to normal-ly low, nonmigratory levels needed for daily metabolic activities, and high, emergency, catabolic levels. In migratory birds, intermediate levels of corticosterone may promote lipogenesis as has been proposed in mammals (Dallman et al. 1993). However, if baseline corticosterone is maintained at those relatively higher levels during migration, then additional corticosterone secretion in response to acute stress may be reduced, a response that could protect skeletal muscle needed for migratory flight. Several field and laboratory studies, on a variety of bird species, have provided some support for that hypothesis, either by showing that birds maintain elevated baseline levels of corticosterone, or that they exhibit a reduced response to handling stress during migration (Holberton et al. 1996, 1999, Holberton 1999, Piersma and Ramenofsky 1998, Romero et al. 1997, but see Schwabl et al. 1991), or both. Initially, it was suggested that change in the corticosterone stress response was an intrinsic component of migratory condition and not a facultative response to a migrant's changing energy demands during the migration period. However, variation in the extent to which corticosterone secretion is modulated may reflect differences in energy demand during migration periods, or differences in migratory strategies among and within species.

For Arctic-breeding sandpipers, seasonal modifications in nutrient reserves are critical for completion of migration (Kersten and Piersma 1987, Piersma and Jukema 1990, Driedzic et al. 1993). Long-distance flights interspersed with two to three protracted stopovers along the migration route are typical in this group (Morrison 1984, Myers et al. 1987). During stopovers, individuals accumulate large fat reserves to fuel subsequent migratory flights (Myers et al. 1987, Evans and Davidson 1990) and show significant hypertrophy of muscle tissue (Davidson and Evans 1988, Piersma and Jukema 1990, Driedzic et al. 1993).

Migrating sandpipers may experience a physiological "tug-of-war" between corticosterone's catabolic effects on muscle tissue and its anabolic effects on lipid reserves. Sandpipers might balance those costs and benefits by maintaining elevated baseline levels of corticosterone to facilitate feeding and fattening during stopovers, while reducing additional corticosterone secretions in response to acute

stress to conserve skeletal muscle, as predicted by the MMH. However, energy demands can change during prolonged stopovers as sandpipers replenish energy reserves, and modifications in patterns of corticosterone secretion may reflect changes in energetic condition. For example, individuals arriving with low fat reserves might exhibit higher baseline corticosterone concentrations and a reduced response to acute stress. As those individuals accumulate reserves of fat, the need for high corticosterone levels may decline, and concomitantly, the adrenocortical response to stress might be reinstated as energy reserves other than muscle become more available. In contrast, individuals arriving in optimal energetic condition may show lower baseline hormone levels compared with lean birds and more typical adrenocortical responses to stress.

In this study, we examined patterns of corticosterone secretion in Semipalmated Sandpipers (*Calidris pusilla*) during a stopover along the spring migration route to better understand relationships between acute glucocorticoid secretion and changes in energy demand in a long-distance migrant. Specifically, we asked (1) whether variation in the strength of the adrenocortical stress response correlated with fat reserves that Semipalmated Sandpipers accumulate during spring migration stopovers, and (2) does variation in baseline corticosterone levels reflect variation in energy reserves.

METHODS

Study area and species.—We collected blood samples from Semipalmated Sandpipers along the New Jersey coast of Delaware Bay at Thompsons Beach, Cumberland County (39°13′N, 75°00′W), and Dennis Creek Marsh, Cape May County (39°11′N, 75°55′W). Those sites constitute an almost contiguous tidal marsh system that consists of extensive mud flats, tidal creeks, and salt marsh plains thickly vegetated with *Spartina* sp. The Delaware Bay estuary is considered the most important spring stopover site for migrating sandpipers in the eastern United States (Myers et al. 1987). Semipalmated Sandpipers are long-distance migrants that travel between Arctic breeding grounds and nonbreeding residences as far south as coastal Brazil (Gratto-Trevor 1992). During spring migration, this species occurs at high densities in Delaware Bay with peak numbers occurring between 27 May and 5 June (Clark et al. 1993).

Bird capture, plasma collection, and measurements.— Birds were captured with mist nets during daylight hours (0700–1400 EST) between 12 May and 6 June 1996, and 3 May and 5 June 1997. Mist-netting efforts focused on low tides to increase the probability of capturing Semipalmated Sandpipers during daylight hours (D. Mizrahi unpubl. data). Because tidal cycles advance approximately 45–60 min each day, time of day that birds were captured could not be standardized across sampling periods.

Collection of initial blood samples from each individual was completed within 3 to 5 min after capture. Time of capture for each sampled bird was recorded so that a second blood sample could be collected exactly 30 min later to determine the rate of increase in plasma corticosterone over that period. In birds, plasma corticosterone concentrations can rise rapidly in response to many stressors including the stress of capture and handling (Wingfield 1994). The protocol of taking repeated samples from individuals to produce plasma profiles of acute corticosterone secretion is a widely used method for assessing an individual's adrenocortical responsiveness to stress (Wingfield 1994, Astheimer et al. 1995). Corticosterone stress profiles have been demonstrated in a wide variety of bird species (e.g. Dawson and Howe 1983, Wingfield et al. 1992, 1994a, b, 1995; Holberton et al. 1996, Dufty and Belthoff 1997). If taken within the first few minutes after capture, the initial sample can provide an estimate of predisturbance plasma corticosterone concentration. Subsequent samples can provide estimates of the maximum amount of corticosterone secreted by an individual, and also the rate of hormone secretion.

For each sample we collected 50–75 μL of blood in heparinized capillary tubes using a 26-gauge needle to puncture the brachial vein. Blood samples were kept on ice for approximately 2 h until centrifuged. Recovered plasma was kept frozen in microcentrifuge tubes until assayed for corticosterone by radioimmunoassay following procedures described by Wingfield et al. (1992). Between the initial and 30 min sample collection, individuals were housed separately in multicelled holding boxes. During that time each bird was banded with a U.S. Fish and Wildlife Service aluminum band, scored for subcutaneous fat reserves in the furcular and abdominal regions, weighed to the nearest ±0.1 g with a portable pan balance, and measured (wing chord, total head length, culmen, tarsus; nearest ±0.1 mm). We used the following regression model proposed by Skagen et al. (1993) to estimate fat mass (FM) in Semipalmated Sandpipers: FM = 18.248 + 0.957 × (body mass) − 0.184 × (wing chord) − 0.554 × (total head length), and used the proportion of body fat (PBF, fat mass divided by total mass) as a relative index of energetic condition.

Statistical analyses.—We used a one-way analysis of variance (ANOVA, Sokal and Rohlf 1981) to determine whether initial corticosterone levels differed among samples collected 3, 4, and 5 min after cap-

ture. We did that to see how rapidly corticosterone levels rise immediately after capture and to determine whether samples collected within 5 min could be pooled for use in subsequent analyses. Because several species of birds show diel fluctuations in corticosterone secretions (Meier and Fivizzani 1975, Schwabl et al. 1991), we used simple linear regression to examine within-year variation of corticosterone levels explained by time of day samples were collected.

A two-way, repeated measures ANOVA was used to detect differences in corticosterone secretion between years (YEAR) and samples (SAMPLE, i.e. initial and 30 min after capture), and to examine interaction between the two main effects. We used Fisher's protected least significant difference test (PLSD, Kuehl 1994) to make within-year SAMPLE comparisons (two-tailed, paired t-tests), and between-YEAR comparisons (two-tailed, independent t-tests) of corticosterone concentration for initial and 30 min samples. We used regression analysis (Sokal and Rohlf 1981) to examine the energetic condition of birds as a function of Julian date during stopover periods in each year, and correlation analysis to examine relationships between corticosterone levels and energetic condition. Because proportions are known to form binomial rather than normal distributions (Sokal and Rohlf 1981), analyses involving PBF were done on arcsine-transformed values (ASPBF). We used SAS (SAS Institute 1989) to perform all statistical analyses and to test critical assumptions associated with each statistical test. Results of all tests were considered significant for $P \leq 0.05$.

RESULTS

Sample collection and assays.—We collected complete stress-series samples (i.e. initial and 30 min after capture) from 47 individuals in 1996 (11 May to 6 June, Julian dates 132 to 158), and from 74 individuals (12 May to 5 June, Julian dates 132 to 156) in 1997. Analyses of samples were spread across three assays, each containing a representative sample from a plasma pool and a known standard concentration of corticosterone (Sigma Chemical Co.) from which inter- and intra-assay variation were determined. Extraction efficiency of corticosterone from the plasma ranged between 78–88% across the three assays, and the inter- and intra-assay variation was 16.8 and 8.6%, respectively. The sensitivity of each assay was <7.8 pg.

Minutes after capture and time of day effects on initial samples.—Results of the one-way ANOVA revealed no significant differences between
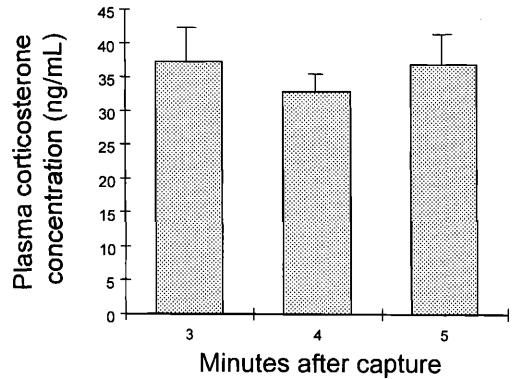

FIG. 1.   Comparison of corticosterone concentrations in samples collected 3, 4, and 5 min after capture. Mean hormone concentrations were not significantly different among groups.

samples collected 3, 4, or 5 min after capture (3 min, $\bar{x} = 37.79 \pm$ SE of 5.49 ng/mL; 4 min, $\bar{x} = 34.74 \pm 4.37$ ng/mL; 5 min, $\bar{x} = 37.04 \pm 5.27$ ng/mL, $F = 0.298$, df = 2 and 68, $P = 0.74$; Fig. 1). Consequently, we pooled all samples collected within 5 min of capture and refer to them as initial in all subsequent statistical analyses. We found no significant relationships between the time of day samples were collected and either initial or 30 min corticosterone levels in 1996 (*initial*, $F = 0.774$, df = 1 and 44, $P = 0.38$; 30 min, $F = 0.025$, df = 1 and 44, $P = 0.88$). In 1997, we found a significant negative relationship between initial corticosterone levels and the time of day samples were collected ($F = 9.370$, df = 1 and 72, $P = 0.003$), and a significant positive relationship between 30 min corticosterone levels and time of day ($F = 6.50$, df = 1 and 72, $P = 0.01$). However, time of day explained a relatively small amount of variation in corticosterone levels (*initial*, $R^2 = 0.10$; 30 min, $R^2 = 0.08$).

The difference between years may have resulted from differences in the time of day that samples were collected. However, circular statistical analysis (Batschelet 1981) indicated that the time of day samples were collected in each year were not significantly different (1996, $\bar{x} = 1,108$ EST ± 15.2 min; 1997, $\bar{x} = 1,109$ EST ± 12.0 min; Watson-Williams F-test, $F = 0.001$, df = 1 and 118, $P = 0.99$). Because of the equivocal results regarding time-of-day effects, we performed the two-way, repeated measures ANOVA and *post hoc* PLSD tests two ways: (1) while statistically controlling for variance at-
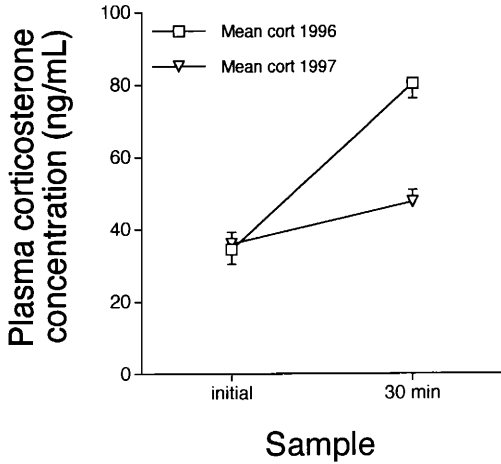
FIG. 2. Adrenocortical response to stress in 1996 and 1997. Semipalmated Sandpipers showed significant increases in plasma corticosterone concentrations 30 min after capture during both years. Initial corticosterone concentrations were not significantly different between years, but concentrations in 30 min samples were significantly higher in 1996 compared with 1997.
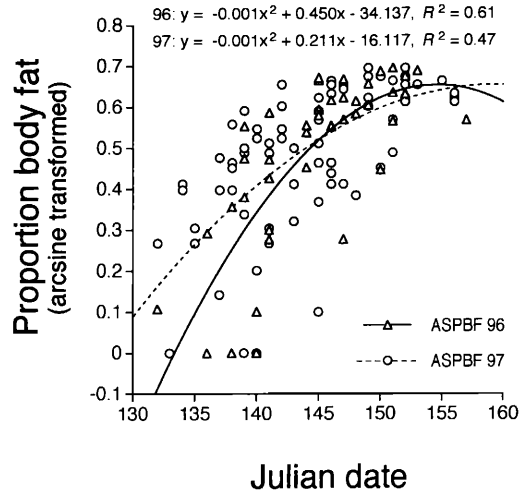

FIG. 3. Quadratic regression functions of proportion body fat (PBF, fat mass divided by total mass) and Julian date during 1996 and 1997. Because proportions are known to exhibit binomial rather than normal distributions, PBF was arcsine transformed. The regression functions were significantly different between years.

tributable to the time of day samples were collected, and (2) without controlling for that effect. We found no differences between the overall relationships revealed by each of the analytic approaches; therefore, we describe the results of our analyses without controlling for the time of day that samples were collected. That permits us to report meaningful least-square means $\pm$ SE for comparisons made between corticosterone levels found for each SAMPLE and YEAR.

Adrenocortical response to stress.—The two-way, repeated measures ANOVA revealed significant YEAR ($F = 19.25$, df = 1 and 119, $P < 0.0001$), and SAMPLE ($F = 51.00$, df = 1 and 119, $P < 0.0001$) effects. We also found a significant YEAR $\times$ SAMPLE interaction ($F = 20.38$, df = 1 and 119, $P < 0.0001$), indicating that either initial, or 30 min corticosterone levels, or both varied between years. Corticosterone concentrations in samples collected 30 min after capture were significantly higher than initial samples in both years (1996, $\bar{x} = 34.42 \pm 4.06$ ng/mL vs. $\bar{x} = 80.26 \pm 4.06$ ng/mL, $t = -7.981$, $n = 121$, $P < 0.0001$; 1997, $\bar{x} = 34.89 \pm 3.24$ ng/mL vs. $\bar{x} = 47.57 \pm 3.24$ ng/mL, $t = -2.771$, $n = 121$, $P = 0.007$; Fig. 2). We found no significant difference between intitial

corticosterone levels in 1996 and 1997 ($t = -0.091$, $n = 121$, $P = 0.93$; Fig. 2), but there was a significant difference between 30 min samples collected in each year ($t = 6.295$, $n = 121$, $P < 0.0001$; Fig. 2).

Energetic condition and corticosterone levels.—Semipalmated Sandpipers showed significant nonlinear (i.e. quadratic) relationships between ASPBF (proportion body fat, arcsine transformed) and Julian date in both years (1996, $F = 34.36$, df = 2 and 44, $P < 0.0001$, $R^2 = 0.61$; 1997, $F = 30.89$, df = 2 and 71, $P < 0.0001$, $R^2 = 0.47$, Fig. 3). However, there was no correlation between ASPBF and initial corticosterone levels in either year (1996, $r = 0.04$, $n = 47$, $P = 0.78$; 1997, $r = 0.16$, $n = 74$, $P = 0.16$; Fig. 4A, B) or in samples collected 30 min after capture in 1996 ($r = 0.18$, $n = 47$, $P = 0.24$; Fig. 4C). In 1997, we found a significant positive correlation between ASPBF and samples collected 30 min after capture ($r = 0.31$, $n = 74$, $P = 0.007$; Fig. 4D).

Between-year differences in adrenocortical responses to stress.—Although our results clearly show that Semipalmated Sandpipers responded to capture stress with significant increases in corticosterone, we were interested in why the magnitude of response was significantly
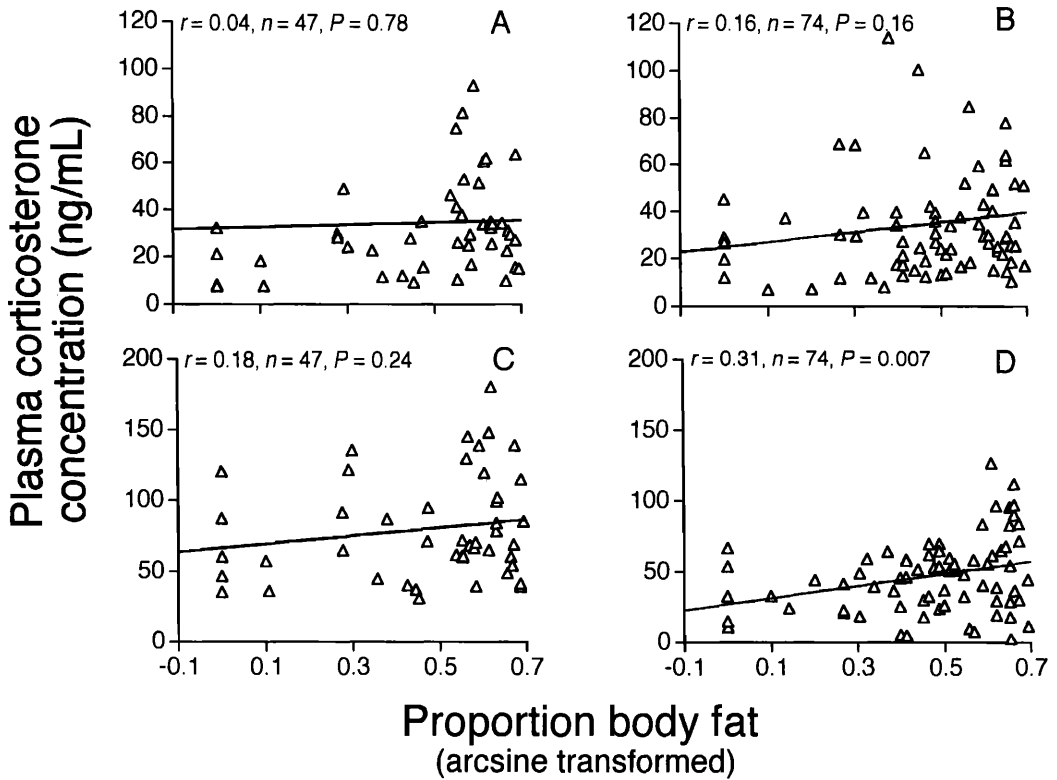
FIG. 4. Correlations between plasma corticosterone concentrations and proportion body fat (arcsine-transformed). Initial samples: (A) 1996, and (B) 1997. Samples collected 30 min after capture: (C) 1996, and (D) 1997. Correlation coefficients for initial samples and proportion body fat were not significant in either year and not significant for 30 min samples in 1996. However, correlation coefficients were significant in 1997.

lower in 1997 compared with 1996 (i.e. significant between-year differences in 30 min samples; Fig. 2). We were also interested in why corticosterone levels in 30 min samples were correlated (i.e. positive) with ASPBF only in 1997 (Fig. 4D). Because seasonal changes in food availability can influence energetic condition during stopovers, we investigated the temporal dynamics of energetic condition in each year as a possible explanation for differences in patterns of corticosterone secretion we observed. We used analysis of covariance (ANCOVA, Sokal and Rohlf 1981) to compare the quadratic regression functions of Julian date on ASPBF in each year. This analysis indicated that the slopes of the functions were significantly different (t = 2.23, n = 121, P = 0.03).

The regression plots suggested that differences in the functions resulted from between-year differences in the energetic condition of birds sampled during the "early" stages of

stopover periods (i.e. before the intersection of the functions; Fig. 3) rather than the latter stages (i.e. "late," after the intersection of the functions; Fig. 3). By setting the equations of the functions equal to each other and solving for x, we identified day 146 as the intersection point along the x-axis. ANCOVA showed that the rate of change in the regression functions was significantly greater in 1996 than in 1997 before day 146 (t = 2.22, n = 67, P = 0.02), whereas the functions greater than or equal to day 146 were not significantly different between years (t = −0.44, n = 54, P = 0.66). Based on those results we divided each year's data into early (Julian date <146) and late (Julian date ≥ 146) stages to investigate whether patterns of corticosterone secretion differed between stages in each year. Data were analyzed using the statistical approaches described previously.

    Between-stage differences in corticosterone secretion.—In each stage, we found significant YEAR
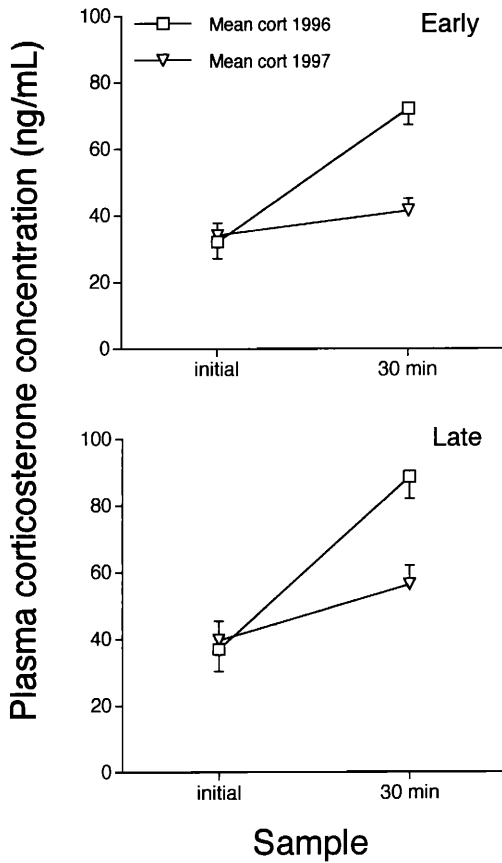
FIG. 5. Adrenocortical response to stress during early and late stages in 1996 and 1997. Semipalmated Sandpipers showed significant increases in plasma corticosterone concentrations 30 min after capture during early 1996, but not during early 1997. Significant increases in corticosterone concentrations 30 min after capture were evident during late stages in both years. Initial corticosterone concentrations were not significantly different between years during either stage, but concentrations in 30 min samples were significantly higher (*) in 1996 compared with 1997 during both stages.

TABLE 1. Mean plasma corticosterone concentrations (ng / mL ± SE) for initial and 30 min samples collected during early (before 26 May) and late (after and including 26 May) stages of 1996 and 1997 stopover periods. Comparisons of means were made using Fisher's protected least significant difference tests ($\alpha = 0.05$).

Year	Stage	Initial[a]	30 min
1996	Early	32.01 ± 4.95	72.17 ± 4.95[b]
1997	Early	31.45 ± 3.70	41.29 ± 3.70[d]
1996	Late	36.94 ± 6.64	88.70 ± 6.64[b]
1997	Late	39.65 ± 5.72	56.28 ± 5.72[b,c,d]

[a] No significant differences between initial samples in any year or period.
[b] = Significantly greater than paired initial samples.
[c] = Significant difference between samples of preceding period.
[d] = Significant difference between samples in corresponding period from preceding year.

cantly different from initial samples in early 1997 ($t = -1.88$, $n = 43$, $P = 0.07$; Table 1, Fig. 5). During the late stage, concentrations in samples 30 min after capture were significantly higher than initial samples in both years (1996, $t = -5.51$, $n = 23$, $P < 0.0001$; 1997, $t = -2.06$, $n = 31$, $P = 0.04$; Table 1, Fig. 5).

We found no significant between-year differences in initial corticosterone levels during early ($t = -0.089$, $n = 65$, $P = 0.93$; Table 1), or late ($t = -0.310$, $n = 52$, $P = 0.76$; Table 1, Fig. 5) stages. In contrast, corticosterone concentrations in samples collected 30 min after capture were significantly lower in 1997 compared with 1996 during both stages (early, $t = 4.99$, $n = 65$, $P < 0.0001$; late, $t = 5.18$, $n = 52$, $P = 0.0005$; Table 1, Fig. 5).

Energetic condition within and between years.— A two-way ANOVA (main effects, YEAR, and STAGE) indicated that ASPBF was not significantly different between years ($F = 0.26$, df = 1 and 119, $P = 0.61$), but that STAGE had a significant effect on energetic condition ($F = 55.88$, df = 1 and 119, $P < 0.0001$). Lack of significant interaction between main effects ($F = 0.41$, df = 1 and 119, $P = 0.52$) suggested that between-stage differences in energetic condition were consistent between years. *Post hoc* Fisher's PLSD tests showed that ASPBF was significantly lower during early compared with late stages in each year (1996, $t = -5.21$, $n = 47$, $P < 0.0001$; 1997, $t = -5.43$, $n = 74$, $P < 0.0001$). However, we found no significant between-year differences in mean ASPBF during either early ($t = -0.85$, $n = 67$, $P = 0.40$) or late ($t = 0.09$, $n = 54$, $P = 0.93$) stages.

(early, $F = 12.92$, df = 1 and 65, $P = 0.0006$; late, $F = 5.74$, df = 1 and 52, $P = 0.02$) and SAMPLE (early, $F = 24.37$, df = 1 and 65, $P < 0.0001$; late, $F = 26.57$, df = 1 and 52, $P < 0.0001$) effects, and significant YEAR × SAMPLE interactions (early, $F = 12.02$, df = 1 and 65, $P = 0.0009$; late, $F = 8.03$, df = 1 and 52, $P = 0.007$). Corticosterone concentrations in samples collected 30 min after capture were significantly higher than initial samples in early 1996 ($t = -5.73$, $n = 24$, $P < 0.0001$; Fig. 5), but were not signifi-

Energetic condition and corticosterone levels within stages.—In both years, we found no significant correlations between ASPBF and initial corticosterone levels during early stages (1996, $r = -0.02$, $n = 24$, $P = 0.92$; 1997, $r = 0.13$, $n = 43$, $P = 0.40$) or late stages (1996, $r = -0.01$, $n = 23$, $P = 0.96$; 1997, $r = 0.04$, $n = 31$, $P = 0.83$). Although there was no significant correlation between ASPBF and corticosterone concentrations in 30 min samples during early 1996 ($r = 0.02$, $n = 24$, $P = 0.93$), 30 min corticosterone concentrations were positively correlated with ASPBF in early 1997 ($r = 0.30$, $n = 43$, $P = 0.05$). Corticosterone concentrations collected 30 min after capture were not correlated with ASPBF during late stages in either year (1996, $r = 0.15$, $n = 23$, $P = 0.50$; 1997, $r = 0.15$, $n = 31$, $P = 0.43$).

DISCUSSION

Adrenocortical response to stress.—We found that in most cases, migrating Semipalmated Sandpipers on stopover in Delaware Bay can secrete corticosterone in response to handling stress above initial levels. That result is similar to those reported for conspecifics (Tsipoura et al. 1999), and congeneric Western Sandpipers (*C. mauri*) (O'Reilly and Wingfield 1995) sampled during spring and fall migrations. However, caution should be exercised when comparing our results with the results of those two studies. In the former study, samples were collected on four days during the late stage of the stopover period (25 May to 3 June), when most individuals would have been in relatively good energetic condition. In fact, the authors did not find significant differences in body mass among individuals sampled during the first two days of the sampling period and the last two. In our study, Semipalmated Sandpipers sampled throughout the entire stopover period showed significant increases in fat reserves. Additionally, based on the reported degrees of freedom, it is unclear how many individuals in the sample pool Tsipoura et al. (1999) subjected to the repeated sampling protocol they describe. In the latter study, only single samples were collected from individuals at varying times after capture, and samples collected during both spring and autumn migration were pooled. That does not mean that the results reported in those studies are not relevant to the

question of corticosterone secretion during migration. However, using samples collected during only one portion of the stopover period, incomplete stress profiles from individuals, or samples pooled across seasons could preclude clear interpretation of corticosterone secretion patterns in sandpipers during migration stopovers.

Our results also suggest that the adrenocortical response can be modulated in relation to changes in energy reserves, or energy demand during migratory periods. That pattern has been reported for several passerine species sampled under different environmental conditions during migration (Holberton et al. 1996, 1999; Romero et al. 1997), and on the wintering grounds (Wingfield et al. 1994b, Marra and Holberton 1998). Semipalmated Sandpipers sampled during our study showed a reduced response to stress in 1997, with corticosterone levels 30 min after capture only 36% greater than initial levels, compared with 133% above initial levels in 1996. Although mean fat reserves were not significantly different between years, population-level rates of fat mass change in birds sampled across the entire stopover period were significantly lower in 1997 compared to 1996, and lower during early 1997 than in early 1996.

Between-year differences in population-level rates of fat mass change may have been related to differences in food availability in Delaware Bay. Horseshoe crab (*Limulus polyphemus*) eggs, a primary food resource for sandpipers staging in Delaware Bay in spring (Myers 1986), were scarce along the New Jersey coast in 1997 compared with other years, especially during the early stage (M. Botton pers. comm.). Interestingly, sandpipers sampled during early 1997 did not show a significant increase in corticosterone after 30 min of captivity. Between-year differences in rates of fat-mass gain also could have resulted if cohorts arriving in Delaware Bay on successive days during 1996 were in better energetic condition compared with 1997, giving the appearance that birds were accumulating fat more quickly. Whether sandpipers in 1996 were in better energetic condition upon arrival or had greater potential for accumulating fat reserves, they appeared to retain a greater responsiveness of the HPA axis compared with 1997. In contrast, sandpipers sampled in 1997 exhibited a reduced adrenocortical

response, possibly to avoid the risk of catabolizing skeletal muscle during bouts of acute stress because other energy sources were not available.

Because we chose to measure corticosterone only up to 30 min after capture, we do not know the maximal corticosterone concentrations that could have been released by sandpipers in response to acute stress. However, our results demonstrate the initial rate of corticosterone secretion in Semipalmated Sandpipers, and thus, an indicator of how rapidly an individual responds to environmental stressors (Wingfield 1994). That may be more relevant than maximal concentrations when considering the purpose of the stress response; that is, to redirect behavior and physiology away from ongoing activities and toward life saving ones. Heath and Dufty (1998) found that American Kestrels (*Falco sparverius*) on food-restricted diets had significantly slower adrenocortical responses to stress than birds fed *ad libitum,* but that maximum levels attained by each group were not significantly different.

Energetic condition and corticosterone levels.— Initial corticosterone levels in Semipalmated Sandpipers that we sampled were not correlated with energetic condition during stopover periods in either year or during any stage. Those results are similar to those reported for free-living Yellow-rumped Warblers (*Dendroica coronata*) sampled under optimal weather conditions during fall migration (Holberton et al. 1996), and for captive warblers sampled during migratory periods (Holberton 1999). Similarly, captive Red Knots (*Calidris canutus*) failed to show a correlation between initial corticosterone concentration and energetic condition during the spring migration period (Piersma and Ramenofsky 1998). In contrast, Schwabl et al. (1991) reported a negative correlation between fat stores and initial corticosterone levels in autumn migrating Garden Warblers (*Sylvia borin*). Lean warblers (Holberton et al. 1999) and Common Storm Petrels (*Pelecanoides urinatrix*) (Smith et al. 1994) sampled during or immediately after storms also showed higher than normal initial corticosterone levels.

However, recapture rates of individuals during stopovers are low, so observing variation in corticosterone levels within individuals as they accumulate energy reserves is nearly impossible, and that was also the case in our study. We

also had no knowledge of how long individuals were present at our study sites before we captured them. If recently arrived, sandpipers may have higher initial corticosterone levels, possibly associated with prolonged flight (Rees et al. 1985) rather than energetic condition. Given that, we would expect flight-dependent corticosterone levels to decline over the stopover period, despite energetic condition, a condition we did not observe. If our samples were biased toward recent arrivals, then our analyses could incorrectly have shown an absence of correlation between energetic condition and initial corticosterone levels. Although sampling bias might have been possible during early stages as birds begin to arrive in Delaware Bay, it would have been less likely during late stages when most birds would already be present at our study sites. In this study, we collected 49 and 42% of samples during the late stage in 1996 and 1997, respectively, making sampling bias an unlikely explanation for the patterns of corticosterone secretion we observed.

During migration, variation in patterns of corticosterone secretion within species relative to energetic condition may be related to differences in the timing of passage between age and sex classes. Unfortunately, we were only able to reliably assign first-spring status to 8 individuals in both years combined, precluding any meaningful analyses. Using exposed culmen length to classify males and females (Prater et al. 1977), we could only assign gender to 32 individuals (6 males, 26 females) in 1996 and 39 individuals (10 males and 29 females) in 1997. Although our samples were biased toward females, we did not find significant differences in energetic condition between sexes in either year (Student's *t*-tests, all $P > 0.50$), or differences in initial or 30 min corticosterone levels (Student's *t*-tests, all $P > 0.15$).

Migration Modulation Hypothesis.—Without premigratory and postmigratory samples of corticosterone, we were unable to test the first prediction of the MMH that initial levels are elevated during the migratory period compared with nonmigratory periods. However, initial corticosterone levels we measured in Semipalmated Sandpipers during migration were an order of magnitude greater ($\bar{x} = 35.65$ ng/mL) than levels reported by Gratto-Trevor et al. (1991) for the same species sampled during the breeding season near Churchill, Manitoba ($\bar{x} = $

3.35 ng/mL). Although that result should be viewed with caution given the possibility that birds staging in Delaware Bay may belong to a different population than birds breeding in Manitoba, the pattern suggests the first component of the MMH. The constancy of corticosterone concentration we found in initial samples, despite variation in energetic condition, also suggests that there may be an intrinsic switch in corticosterone metabolism during migration. Clearly, more controlled studies are needed to establish the presence of a "switch" in corticosterone secretion as a way in which sandpipers meet the energetic demands of migration.

Our results do provide evidence that the strength of the corticosterone stress response can be regulated to help meet energetic needs during migration. In most years, food resources during stopovers in Delaware Bay may not be limiting to Semipalmated Sandpipers (Botton et al. 1994), so modulation of the adrenocortical response to stress might be unnecessary. However, when food resources are less abundant, as in 1997, that endocrine response can be modulated, possibly to help birds protect protein reserves until food-resource availability improves. Facultative modulation of corticosterone metabolism in response to unpredictable or deleterious environmental conditions has been reported in a variety of avian taxa (Wingfield and Ramenofsky 1997, Marra and Holberton 1998).

Variation in patterns of corticosterone secretion among species studied thus far may be related to differences in migration strategies and the amount of energy reserves a bird needs to reach its destination. Migration strategies span a continuum, from species that accumulate extensive fat reserves in preparation for long-distance flight over ecological barriers (e.g. deserts, large bodies of water), to species that store relatively small amounts of fat and make a series of short-distance flights (see review in Alerstam 1990). Data from more than 20 species of Neotropical passerines engaging in relatively long-distance migration suggest that they are more likely to exhibit elevated initial corticosterone levels and a reduced stress response during migratory periods (Holberton et al. 1996, 1999; Holberton 1999). That pattern appears to be similar to the one we observed in Semipalmated Sandpipers, a species that

spends prolonged periods at migratory stopover sites refueling in preparation for bouts of nonstop, long-distance flight (Morrison et al. 1984).

For many species of birds, spring migration generally proceeds more rapidly than autumn migration, and the energetic demands associated with preparation for breeding may impose markedly different physiological constraints. Relatively short-distance migrants such as the migratory race of White-crowned Sparrows (Zonotrichia leucophrys gambelii) put on less fat in autumn, and have lower baseline corticosterone levels compared with spring (Romero et al. 1997). The greater variation in corticosterone metabolism observed in trans-Gulf migrants in spring compared with autumn may be related to the effect weather and food availability can have on gonadal development during migration (Holberton et al. 1999). Interestingly, Garden Warblers, an Old World long-distance migrant, do not appear to show any modulation during migration other than a loss of the diel pattern in initial corticosterone secretion (Schwabl et al. 1991). Collectively, those studies illustrate the flexibility of glucocorticoid secretion in relation to migration strategies found within and between seasons and species. That variation must be considered when investigating the complex relationships between ecological, behavioral, and physiological aspects of bird migration.

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