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SEASONAL, AGE, AND SEX DIFFERENCES IN WEIGHT, FAT RESERVES, AND PLASMA CORTICOSTERONE IN WESTERN SANDPIPERS

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Abstract. Western Sandpipers (Calidris mauri) were followed throughout their annual cycle along the Pacific Coast of North America. Changes in body condition and corticosterone were tracked at two overwintering sites (Ensenada, Mexico, and San Diego, California), four migration stopover sites (Bodega Bay, California, Grays Harbor and False Bay, Washington, and Hartney Bay, Alaska), and a breeding site (Nome, Alaska). Adult males and females had elevated weight and fat scores during spring migration, breeding, and autumn migration relative to lean levels during winter. Although elevated mass and fat reserves may hinder escape from predators and are not necessary at wintering sites with benign conditions, the cost-benefit trade-offs with weight and agility shift during migration and breeding. Extra fat and muscle are necessary for fueling the long flight to and from the breeding grounds and serve as a hedge against unpredictable food and weather conditions on the breeding grounds. First-year birds weighed less and had lower fat reserves at smaller stopover sites than migrants at a large stopover site. Plasma levels of corticosterone revealed seasonal differences in the adrenocortical response to stress, although initial levels were fairly consistent across seasons. The highest stress response of the annual cycle in males was during autumn migration, in contrast to the lowest levels during early spring migration, breeding, and overwintering. Late-spring migrants and autumn premigrants had intermediate stress responses. An emerging pattern from this and other shorebird studies is that migrants with imminent flights of more than 1000 km have elevated corticosterone levels.

Key words: breeding, Calidris mauri, corticosterone, fat, migration, stress, Western Sandpiper.

Diferencias Estacionales de Edad y Sexo en Peso, Reservas de Grasa y Corticosterona Plasmática en Calidris mauri

Resumen. Se siguieron individuos de Calidris mauri a través de su ciclo anual a lo largo de la costa Pacífica de Norteamérica. Se evaluaron los cambios en la condición corporal y la corticosterona en dos sitios de invernación (Ensenada, México y San Diego, California), cuatro sitios de escala migratoria (Bodega Bay, California, Grays Harbor y False Bay, Washington, y Hartney Bay, Alaska) y un sitio reproductivo (Nome, Alaska). Los machos y hembras adultos tuvieron pesos y niveles de grasa altos durante las épocas de migración de primavera, reproducción y migración de otoño con relación a los niveles magros del invierno. Aunque presentar masa elevada y reservas de grasa puede limitar el escape de los depredadores y no es necesario en los sitios de invernada con condiciones benignas, existe un cambio en la solución de compromiso entre el costo-beneficio del peso y la agilidad de vuelo durante la migración y la reproducción. La grasa y músculos adicionales son necesarios para proveer combustible para los largos vuelos hacia y desde las áreas de reproducción y sirven como protección contra condiciones alimenticias y climáticas impredecibles en las áreas reproductivas. Las aves adultas pesaron menos y tuvieron menos reservas grasas en sitios de escala pequeños que los migrantes en un sitio de escala grande. Los niveles plasmáticos de corticosterona mostraron diferencias estacionales en la respuesta adrenocortica al estrés, aunque los niveles iniciales fueron relativamente consistentes a través de las estaciones. La respuesta al estrés más alta del ciclo anual de los machos se presentó durante la migración de otoño, contrastando con los niveles más bajos durante el inicio de la migración de primavera, la época reproductiva y la época de invernación. Las aves que migraron temprano en la primavera y las premigrantes de otoño presentaron niveles intermedios de respuesta al estrés. Un patrón que emerge de éste y otros estudios sobre aves marinas es que las migratorias que hacen vuelos de más de 1000 km presentan niveles elevados de corticosterona.

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INTRODUCTION

The Western Sandpiper (Calidris mauri) is one of the most abundant coastal migrants along the Pacific flyway of North America. Despite its relative abundance, Western Sandpipers are still at risk because of their dependence on an increasingly limited number of estuarine migration stopover and wintering sites. In an effort to better understand the importance of each site to individuals as they negotiate each life-history stage, we compared intra-annual differences in body condition and the adrenocortical response to stress. This is the first field study to determine a hormonal profile of a shorebird species throughout the entire annual cycle. Our comprehensive approach allowed us to follow transitions of life-history stages from wintering to migrating and breeding, and determine times when these sandpipers may be especially vulnerable to disturbance.

Two hypotheses related to the pattern of physiological changes during the annual cycle in the Western Sandpiper were examined. The first hypothesis was that individuals adjust their energy stores in anticipation of the demands of the approaching season. To compensate for the most energetically demanding period, migration, individuals undergo hyperphagia, fattening, and increased aerobic capacity of flight muscles (Berthold 1975, Ramenofsky 1990, Piersma 1998). Although breeding individuals do not have the extreme flight costs that migratory individuals face, they do have significant energetic challenges. In particular, Arctic breeders must have sufficient energy reserves as a hedge against storms that may reduce food availability. In contrast, individuals wintering in relatively benign conditions with consistent food availability may be lean. Therefore, we expected individuals to have the greatest stores of energy during the migratory stages, moderate levels during breeding, and low levels on the wintering grounds.

The second hypothesis was that plasma corticosterone at least partially directs seasonal changes in activity of sandpipers. Corticosterone levels increase after application of stressful stimuli, such as capture and handling, in a wide variety of species, including the Western Sandpiper (Wingfield 1994). Elevated levels of corticosterone have been associated with gluconeogenesis (Harvey et al. 1984), increased activity associated with foraging (Astheimer et al. 1992), fat deposition (Devenport et al. 1989, Dulloo et al. 1990, Gray et al. 1990), migratory behavior (Peczely 1976, Silverin et al. 1989, Wingfield et al. 1990), and decreased reproductive behavior (Silverin 1986, Wingfield and Silverin 1986, Harvey and Hall 1990). In light of these potential effects of elevated corticosterone, we predicted that secretion of corticosterone would be highest during migration and lowest during breeding, with intermediate levels during winter. Using the standard capture-stress protocol of obtaining an initial blood sample after capture followed by subsequent samples, we assessed the activity of the hypothalamo-pituitary-adrenal axis (Wingfield et al. 1992, 1998).

Migrants were expected to have higher initial and stress-induced corticosterone levels than breeding or wintering individuals. Because elevated corticosterone levels have been associated with migratory behavior (Ramenofsky et al. 1995, Piersma et al. 2000) and may interfere with reproductive behavior (Silverin 1986, Wingfield et al. 1990), we predicted a suppression of the stress response in breeding individuals. Although briefly elevated levels of corticosterone are unlikely to affect reproduction, repeated spikes of corticosterone in response to unfavorable weather, reduced food availability, predation pressure, or other "labile perturbation factors" (Jacobs 1996), may result in abandonment of the nest and breeding area (Wingfield et al. 1998). Therefore, Arctic breeders, with a limited nesting window, are expected to have a reduced sensitivity to labile perturbation factors, trading a potentially higher survival rate for increased reproduction. Other studies on Arctic-breeding birds have reported a suppression of the stress response (Wingfield et al. 1995, O'Reilly and Wingfield 2001), although there are exceptions to this pattern (Astheimer et al. 1995, Romero et al. 1997).

We investigated these hypotheses by comparing seasonal changes in weight, deposition of fat, and corticosterone levels for adult males. Additional comparisons to females and hatch-year individuals were made during breeding and autumn migration, respectively.

METHODS

STUDY SITES AND THE ANNUAL CYCLE OF WESTERN SANDPIPER

Adult Western Sandpipers were captured at one or more sites during each of the four major sea-
SEASONAL CHANGES IN WESTERN SANDPIPER BODY CONDITION

FIGURE 1. Study sites for the annual cycle of Western Sandpipers. San Diego and Ensenada represent overwintering sites, Nome is the breeding site, and the remaining sites are migration stopover sites.

FIGURE 1

Western Sandpipers have a modest breeding range consisting of western Alaska and northeastern Siberia (Wilson 1994). The breeding population we sampled was located 21 km east of Nome, Alaska, at Safety Sound (64°20'N, 164°56'W; 14 May–4 July 1993). Samples were obtained during three discrete stages of the breeding season: arrival, incubation, and premigration. Arrival was defined as the period prior to the discovery of the first complete nest (samples obtained 14–19 May). Incubation was defined as the period when parents were incubating eggs. The incubation period in this population of Western Sandpipers is 21 days (Sandercock 1998). Samples were obtained from incubating parents within the window of the first complete nest to the date when the majority of eggs had hatched (27 May–14 June). Premigration occurred after all of the study nests had hatched (29 June–4 July). During this period, Western Sandpipers and Semipalmated Sandpipers (Calidris pusilla) gathered into flocks ranging in size from 25–200 individuals, apparently feeding in preparation for autumn migration. Because Western Sandpiper chicks are semiprecocial, parents do not feed young, but rather escort chicks for a period of several days to weeks after hatching (Holmes 1973). The flocks we sampled were composed of individuals largely, if not completely, finished with their parental duties and preparing for migration.

After leaving the breeding grounds, samples were obtained from adults as they passed through Grays Harbor on autumn migration (17–25 July 1993, 24–27 July 1994). Western Sandpipers were not sampled at Hartney Bay during autumn migration because they largely bypass the Copper River Delta on the southbound migration (Senneterre 1977; KMO, pers. obs.). During autumn migration, females typically leave the breeding area before males and juveniles, and

Grays Harbor and the Copper River Delta, of which Hartney Bay is a part, are two of the largest stopover (feeding) sites for this species (Senneterre et al. 1981, Wilson 1991, 1994). Males tend to migrate earlier during spring migration than females, presumably to facilitate territory establishment prior to the arrival of females on the breeding grounds (Holmes 1973). Capture efforts at each site during spring migration were timed to coincide with the first pulse of birds (males); thus females are under-represented in our results.

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thus compose the first pulse of birds heading south (Paulson 1983, Butler et al. 1987). Sampling coincided with the second pulse (adult males) and the third pulse (hatch-year males and females).

Hatch-year Western Sandpipers were captured at two sites during autumn migration: False Bay on San Juan Island, Washington (48°20'N, 123°3'W; 28–30 August 1991), and Bodega Bay (10–12 August 1992).

**SAMPLING PROCEDURE**

At each site, Western Sandpipers were captured with mist nets during daylight hours (06:00–21:00 PST). Several mist nets were set up on mudflats or marshy areas. At most of the sites, sandpipers were attracted to the nets with 30–40 cardboard decoys in the shape of a sandpiper placed nearby in the mud. This method was particularly effective at low tide when sandpipers were dispersed. During the incubation stage at Nome, birds were caught with walk-in nest traps. Each trap was constructed from a 100 × 30 cm piece of hardware cloth bound into a cylinder and covered with fishnet. A small opening allowed the sandpiper to return to the nest.

To assess both the initial plasma levels of corticosterone and the subsequent response of the adrenal cortex to capture and handling stress, we obtained two or more blood samples. The initial sample is an approximation of the level of corticosterone present before capture, but is not the true basal level. Birds were removed immediately from mist nets or traps and bled as quickly and safely as possible. This sampling protocol has been well established in the literature (Wingfield et al. 1998, Romero and Romero 2002).

Within 4 min of capture, and again at 30 min after capture, a 20–200 µL blood sample was obtained by puncturing a wing vein with a 26.5-gauge needle and collecting the blood into heparinized microhematocrit tubes. At Nome and Hartney Bay, additional samples were obtained at 10 min and 60 min after capture. Each sample was stored in a clay-bottomed canister and kept cool until centrifugation. Between samples, individuals were held separately in cloth bags.

Individuals were weighed to the nearest 0.1 g and measured for culmen, tarsus, and wing lengths. Individuals with culmens ≤24.2 mm were classified as males and those with culmens ≥24.8 mm were classified as females (females are the larger sex in this dimorphic species; Page and Fearis 1971, Prater et al. 1977). The few remaining individuals in the overlap range were classified by behavior where possible or omitted from the analyses. After measuring, each individual was visually scored for furcular fat stores on a scale of 0 (no fat visible) to 5 (bulging fat; Wingfield and Farner 1978, Biebach et al. 1986). Since most fat is stored subcutaneously and is easily visible through the skin, the fat score is a good indication of fat content (Connell et al. 1960, Napolitano and Ackman 1990), especially when interobserver variation is eliminated (Krementz and Pendleton 1990). KMO scored each individual to reduce observer error. Capture, handling, and sampling procedures were in compliance with the University of Washington’s Institutional Animal Care and Use Committee guidelines.

After the birds were released, blood samples were centrifuged for 10 min at approximately 400 g. Plasma was drawn off with a Hamilton syringe and frozen at −20°C until assayed.

**CORTICOSTERONE ASSAY**

Corticosterone levels were measured by a direct radioimmunoassay. Aliquots of plasma (10–25 µL) were measured into centrifuge tubes and allowed to equilibrate overnight with 2000 cpm tritiated corticosterone. Corticosterone was extracted in 4 mL of redistilled dichloromethane added to each sample. Extracts were aspirated with Pasteur pipettes and evaporated under nitrogen in a warm-water bath. After evaporation of dichloromethane, samples were dissolved in 550 µL of phosphate-buffered saline with gelatin and allowed to equilibrate overnight at 4°C.

Aliquots of samples were transferred to duplicate test tubes (200 µL each) for radioimmunoassay. In addition, a 100-µL aliquot was placed in a vial for determination of percentage recovery of the initial 2000 cpm. This recovery value was used to adjust final assayed concentrations of corticosterone. Standard curves were set up over the range of 2–500 pg. Samples were refrigerated overnight after addition of equal (100 µL) amounts of labeled corticosterone and antiserum. Dextran-coated charcoal (0.5 mL) was added 12 min prior to centrifugation to separate bound and free fractions. Supernatants were decanted into scintillation vials and counted after addition of 4.5 mL Ultima Gold® scintillation fluid (Packard BioScience, Meriden, Connecticut).
TABLE 1. Seasonal weight and fat score comparisons (means ± SE) of male and female Western Sandpipers. Significant interannual variation was observed at Grays Harbor during spring migration, with 1992 males fatter than 1994 males \((P < 0.05)\), and during autumn migration with 1994 males heavier than 1993 males \((P < 0.01)\).

<table>
<thead>
<tr>
<th>Stage</th>
<th>Site</th>
<th>Dates of study</th>
<th>n</th>
<th>Male</th>
<th>Female</th>
<th>Male</th>
<th>Female</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring migration</td>
<td>Bodega Bay</td>
<td>Apr 1992</td>
<td>27</td>
<td>10</td>
<td>25.6 ± 0.4</td>
<td>28.9 ± 0.4</td>
<td>3.4 ± 0.2</td>
<td>3.8 ± 0.4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Grays Harbor</td>
<td>Apr 1992–1994</td>
<td>82</td>
<td>13</td>
<td>25.5 ± 0.3</td>
<td>27.2 ± 0.8</td>
<td>3.6 ± 0.1</td>
<td>3.3 ± 0.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hartney Bay</td>
<td>May 1992–1993</td>
<td>93</td>
<td>24</td>
<td>25.2 ± 0.2</td>
<td>27.9 ± 0.5</td>
<td>3.2 ± 0.1</td>
<td>3.5 ± 0.2</td>
<td></td>
</tr>
<tr>
<td>Arrival</td>
<td>Nome</td>
<td>May 1993</td>
<td>32</td>
<td>12</td>
<td>25.1 ± 0.3</td>
<td>28.6 ± 1.0</td>
<td>3.4 ± 0.2</td>
<td>3.4 ± 0.3</td>
<td></td>
</tr>
<tr>
<td>Breeding</td>
<td>Nome</td>
<td>Jun 1993</td>
<td>39</td>
<td>34</td>
<td>26.6 ± 0.3</td>
<td>29.1 ± 0.4</td>
<td>3.0 ± 0.1</td>
<td>2.9 ± 0.1</td>
<td></td>
</tr>
<tr>
<td>Premigration</td>
<td>Nome</td>
<td>Jun 1993</td>
<td>46</td>
<td>51</td>
<td>25.6 ± 0.2</td>
<td>29.0 ± 0.3</td>
<td>3.5 ± 0.1</td>
<td>3.7 ± 0.1</td>
<td></td>
</tr>
<tr>
<td>Autumn migration</td>
<td>Grays Harbor</td>
<td>Jul 1993–1994</td>
<td>44</td>
<td>9</td>
<td>25.7 ± 0.5</td>
<td>28.3 ± 1.5</td>
<td>3.4 ± 0.2</td>
<td>3.8 ± 0.4</td>
<td></td>
</tr>
<tr>
<td>Winter</td>
<td>San Diego</td>
<td>Feb 1993</td>
<td>14</td>
<td>0</td>
<td>22.5 ± 0.2*</td>
<td>—</td>
<td>2.6 ± 0.2</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ensenada</td>
<td>Dec 1994</td>
<td>36</td>
<td>4</td>
<td>21.3 ± 0.3*</td>
<td>22.0 ± 0.5*</td>
<td>1.0 ± 0.2*</td>
<td>0.5 ± 0.3*</td>
<td></td>
</tr>
</tbody>
</table>

* Measurement is significantly lower than other seasonal measurements within each sex, \(P < 0.05\).

Twelve assays were necessary to measure corticosterone levels in all of the samples. Interassay variation was 15% and intra-assay variation did not exceed 8%. The mean estimate of the standard \((1.0 \text{ ng})\) was 1.09 ng. These procedures have been described in greater detail elsewhere (Wingfield and Farner 1975, Wingfield et al. 1992).

STATISTICAL ANALYSES

Comparisons of weight, fat, and corticosterone by stages in the annual cycle were made by one-way ANOVA, followed by Fisher’s PLSD post hoc test, if necessary, to determine which stages were significantly different. Interannual variation was analyzed by independent, two-tailed Student’s \(t\)-test for stages with two years of data and by one-way ANOVA for stages with three years of data. Within a stage, significant differences between adults and hatch-year individuals were discerned using two-tailed Student’s \(t\)-tests. Gender comparisons of corticosterone profiles at Nome were made using repeated measures ANOVA. Data were tested for conformation to assumptions for parametric tests before statistical analysis. Differences between means \((± \text{ SE})\) were considered significant for \(P < 0.05\). Statistics were performed using Statview 5.0 (SAS Institute 1999).

RESULTS

BODY CONDITION

Gender and seasonal comparisons. Female Western Sandpipers weighed more than males at all stages except the wintering stage in Ensenada \((P < 0.02, \text{Table 1})\). Body weights during winter were significantly lower than those during the rest of the year for both sexes \((\text{males: } F_{8,416} = 27.2, \text{ } P < 0.05; \text{females: } F_{7,55} = 7.2, \text{ } P < 0.05, \text{Table 1})\). Weights remained relatively constant during spring migration, breeding, and autumn migration. A significant interannual variation was detected in males during autumn migration. Males measured in 1994 were significantly heavier than males measured in 1993 \((1993: 24.2 ± 0.5, n = 21, 1994: 27.0 ± 0.7, n = 23, t_{22} = 3.3, P < 0.01)\).

There were no significant differences between males and females in furcular fat score at any stage. Mean fat scores were lowest during the wintering stage in Ensenada \((\text{males: } F_{8,415} = 22.4, \text{ } P < 0.05; \text{females: } F_{7,150} = 8.4, \text{ } P < 0.05, \text{Table 1})\). Males sampled during spring migration at Grays Harbor in 1992 had significantly more
fat stores than males sampled in 1994 (1992: 3.9 ± 0.1, n = 41, 1994: 3.3 ± 0.1, n = 32, F2,79 = 3.5, P < 0.05).

Age comparisons. Hatch-year (HY) individuals were sampled at two sites during autumn migration: False Bay and Bodega Bay. HY males at False Bay and Bodega Bay had significantly less mass and fat than after-hatch-year (AHY) males at Grays Harbor (mass: F2,74 = 8.3, P < 0.001, fat: F2,74 = 16.8, P < 0.001, Fig. 2). The differences between HY and AHY females in fat score mirrored male differences, with AHY females having significantly more fat than HY females at both sites (F2,24 = 6.4, P < 0.01, Fig. 2). However, HY females sampled at False Bay were intermediate in weight between heavier AHY females at Grays Harbor and lighter HY females at Bodega Bay (F2,22 = 2.9, P = 0.03, Fig. 2).

CORTICOSTERONE

Gender comparisons during the breeding season. Corticosterone samples were obtained from a subset of individuals captured at each stage due to the difficulty in collecting samples immediately after capture. Further, sample sizes from females at most sites were too small to merit statistical analyses and are not presented for migration and wintering sites. Full stress series (<4 min, 10 min, 30 min, and 60 min after capture) were obtained from males and females during the breeding season at Nome. Males and females did not differ significantly in corticosterone levels at any point during arrival or pre-migration at Nome (P > 0.05). However, males exhibited a significantly reduced stress response relative to females during incubation at 30 min and 60 min after capture (30 min: t18 = 2.4, P = 0.03; 60 min: t18 = 2.1, P < 0.05; Fig. 3).

Seasonal comparisons of males. Seasonal differences in corticosterone were only analyzed for AHY males due to the small sample sizes for AHY females and HY individuals. Although 1992 and 1993 stress series from Hartney Bay were very similar (Fig. 4), only 1992 data are presented for seasonal comparisons (Fig. 5) since only a single initial sample was obtained in 1993.

Initial samples of birds were taken between 0 and 4 min after capture. There was no relationship between time after capture and initial corticosterone level (r² = 0.04, n = 64, P = 0.12), implying that measurements up to 4 min after capture do approximate basal levels. Sites did not differ in the distribution of initial sampling times (F6,57 = 1.2, P = 0.34, respectively). Initial samples were fairly uniform, with two exceptions. Spring migrants at Grays Harbor had significantly lower initial levels than spring migrants at Hartney Bay (P < 0.02), Grays Harbor autumn migrants (P < 0.02), and overwintering individuals at Ensenada (P = 0.001, Fig. 5). Also, the Ensenada samples were elevated over Nome premigratory individuals (P < 0.02).

Samples obtained at 30 min after capture revealed a different pattern (Fig. 5). Autumn Grays Harbor birds had markedly elevated 30-min corticosterone levels, significantly higher than all other periods (P ≤ 0.02), except Hartney...
Bay spring migrants. As the second highest group, Hartney Bay spring migrants had a significantly greater 30-min mean than spring migrants at Grays Harbor and incubators at Nome ($P < 0.02$).

DISCUSSION

BODY CONDITION

**Sex and seasonal comparisons.** Previous studies of shorebirds have shown a strong correlation between weight and fat content, as observed in the present study (Page and Middleton 1972, Mercier 1985, White and Mitchell 1990). The most striking result of this study is the exceptionally low mean weight during winter. Several studies of Dunlin (*Calidris alpina*) and Grey Plover (*Pluvialis squatarola*) have found elevated masses during the winter months relative to the rest of the year (Mascher 1966, Dugan et al. 1981). In contrast to Western Sandpipers, these Dunlin and plover populations spend the winter on the British Isles (latitude 55°N) and are exposed to severe weather (low temperatures and high winds). Higher fat stores during winter may help these populations survive in a less hospitable and unpredictable environment, allowing for an immediate departure should conditions degrade further. Dunlin populations wintering farther south have lower masses during winter (Pienkowski et al. 1979, Buchanan et al. 1985, Warnock and Gill 1996). Western Sandpipers winter in relatively mild to tropical regions. Wintering Western Sandpipers in Texas (latitude 30°N) and Columbia (latitude 5°N) have lower weights relative to migrating individuals (White and Mitchell 1990, Naranjo et al. 1994). Since excess weight is energetically expensive to carry and may reduce an individual's ability to escape predators (Videler, Groenewegen, et al. 1988, Videler, Vossebelt, et al. 1988, Lima and Dill 1990, Kullberg et al. 1996), a lean body is adaptive in an environment with a mild climate and predictable resources.

Elevated mass and fat levels have long been associated with migration, especially in long-distance migrants such as shorebirds (McNeil and Cadieux 1972, Berthold 1975, Evans and Davidson 1990). Fat and protein stores fuel the long flight (Piersma and Jukema 1990). Weight and fat scores during migrations were not higher than during breeding, but this is likely due to the mixed migratory stages of individuals sampled at each stopover site. Determining the actual stopover status of each individual along the coastal flyway is virtually impossible without radio-transmitters.

Spring and autumn migrants had similar weights and fat scores. This result differs from an earlier study of Western Sandpipers conducted by Butler et al. (1987) at a major stopover site north of Grays Harbor, the Fraser River Delta in British Columbia. Spring migrants at the Fraser River Delta were heavier than autumn migrants. Patterns of use and location of feeding areas during migration partially explain weight differences between the two sites. Spring migrants leaving Grays Harbor can still stop to feed at the Fraser River Delta, a short flight away (240 km). However, the next major feed-
temperatures, fueling elevated metabolism should the conditions warrant.

**Age differences.** Studies on shorebirds and passerines suggest that young birds are less experienced at finding food, which translates into lower weight and fat stores in HY individuals relative to AHY individuals (Page and Middleton 1972, Swanson et al. 1999, but see Butler et al. 1987 for reverse pattern). Younger individuals may be less adept at either finding or competing for food at the larger stopover sites. Smaller sites, such as False Bay and Bodega Bay, may serve as “fill-ins” for individuals in poorer condition who are less able to make non-stop long-distance flights between major stopover sites. Although the smaller sites may have acceptable food availability, other factors may make them less desirable as a stopover site. Small sites are more enclosed, affording concealment of predators such as Peregrine Falcons (Falco peregrinus), Merlins (F. columbarius), and Bald Eagles (Haliaeetus leucocephalus; Ydenberg et al. 2002). An alternative interpretation by Ydenberg et al. (2002) is that slimmer migrants preferentially select the small stopover sites since they are better able to evade predators than fat migrants and their fattening rate is greater at the small site. Apparently the reduced competition compensates for the increased predation pressure. Further data are needed to tease apart the interrelationship of age, body condition, food availability, predation pressure, and site selection. In either scenario, these results illustrate the importance of smaller estuaries during migration as foraging sites for both Western Sandpipers and their predators.

**CORTICOSTERONE**

The annual pattern of corticosterone observed in Western Sandpipers differed from the predicted pattern of high levels during migration, low levels during breeding, and moderate levels during winter. Although plasma corticosterone levels at Grays Harbor were highest during autumn migration, circulating concentrations during spring migration were as low as during breeding. Other studies have also found elevated levels of corticosterone in autumn migrants, including Garden Warbler (Sylvia borin; Schwabl et al. 1991, Gwinner et al. 1992) and Willow Tit (Parus montanus; Silverin et al. 1989), but not in spring migrants (European Blackbird [Turdus merula]; Schwabl et al. 1984).
A major difference between spring and autumn migration is that spring migrants are preparing for reproduction, with gonadal recrudescence and concomitant elevation of reproductive hormones, whereas autumn migrants have regressed gonads and quiescent levels of reproductive hormones (reviewed in O'Reilly and Wingfield 1995). Chronically elevated corticosterone is known to interfere with reproductive behavior and secretion of reproductive hormones (reviewed in Sapolsky 1987, Wingfield 1994). Although the capture stress protocol detects only acute increases of corticosterone, repetitive exposure to stressful stimuli and elevated adrenocortical responses may cause a chronic elevation of corticosterone (Wingfield et al. 1998). Suppression of the stress response during spring migration and breeding may enable individuals to reduce the risk of reproductively debilitating chronic stress.

One problem with this interpretation is the unexplained elevated stress response in spring migrants at Hartney Bay, the last stop before the breeding grounds for many individuals. The interannual consistency of the magnitude of the stress response at Hartney Bay suggests the elevated stress response is not an unusual occurrence. In reviewing the entire annual cycle, an emerging common feature of the sampling periods with elevated corticosterone is the high probability of a long (>1000 km) nonstop flight. Piersma et al. (2000) observed a similar pattern in endogenous corticosterone secretion in captive Red Knots (Calidris canutus) and proposed that corticosterone elevation in fatter individuals is an important mechanism enabling the trans-
tion to a migratory state. Ramenofsky et al. (1995) also report elevated levels of corticosterone in migratory Bar-tailed Godwits (Limosa lapponica) just prior to a 5000-km flight to their breeding grounds relative to sedentary juveniles. In a subsequent study of Bar-tailed Godwits at the same location, the Wadden Sea, The Netherlands, Landys et al. (2002) reported increases in corticosterone associated with new arrivals and birds sampled just prior to departure. Elevated levels of corticosterone during spring and autumn migration in Semipalmated Sandpipers (Tsipoura et al. 1999) further support the hypothesis of Piersma et al.

The shorebird results described above are not consistent with results from several passerine studies of corticosterone levels during migration. White-crowned Sparrows (Zonotrichia leucophrys) exhibit intermediate stress-induced levels of corticosterone during spring migration and the lowest levels of the year during autumn migration (Romero et al. 1997). Gray Catbirds (Dumetella carolinensis) and Yellow-rumped Warblers (Dendroica coronata) failed to show a stress response at all during autumn migration, but had elevated initial levels of corticosterone (Holberton et al. 1996, Holberton 1999). These passerines have a different migratory strategy than most shorebirds in that they can stop at a variety of plentiful feeding sites en route, whereas shorebirds dependent on estuaries for feeding have limited stopover sites, necessitating long flights between some sites (Piersma 1987, O'Reilly and Wingfield 1995, Butler et al. 1996). The magnified stress-induced levels of corticosterone prior to major flights in migrant shorebirds may be indicative of this difference in strategies.

Upon arrival on the breeding grounds of Nome, Western Sandpipers had substantially lower stress responses, although they still showed an elevation of corticosterone after capture and handling. As the breeding season progressed to the stage where both sexes were incubating eggs, the sensitivity to stress diverged, with males having a lower stress response than females. Because Western Sandpipers are socially and genetically monogamous birds with biparental care, we did not expect intersexual differences in the stress response. In species with unequal parental care, the more parental sex typically has a lower stress response, whereas stress responses are similar in species with equal parental care (Wingfield et al. 1995, Romero et al. 1998, O'Reilly and Wingfield 2001). Experimentally elevated levels of corticosterone reduce territorial defense and parental behavior in male Pied Flycatchers (Ficedula hypoleuca; Silverin 1986) and male Song Sparrows (Melospiza melodia; Wingfield and Silverin 1986). This may partially explain why male Western Sandpipers, which are more responsible for territorial defense and incubation than females (Holmes 1973, Erckmann 1981), had lower corticosterone levels during the breeding season than females. During the autumn premigratory stage, when both sexes were finished with their parental duties, corticosterone levels were indistinguishable between the sexes.

The corticosterone profile observed during winter in Ensenada was intermediate between the extreme high of Grays Harbor autumn migrants and relative low of Nome incubators. In a similar study of White-crowned Sparrows during the annual cycle, Romero et al. (1997) concluded that the corticosterone profile during winter and other nonbreeding life-history stages was the dominant annual profile, with the elevated breeding corticosterone response representing an unusual circumstance. The moderate winter profile in Western Sandpipers is consistent with a "default" concept, with the reduced breeding levels and elevated autumn migration levels representing unusual responses. The difference between stress-induced corticosterone levels during autumn migration in White-crowned Sparrows (lowest of the year, Romero et al. 1997) and Western Sandpipers (highest of the year) may be partially attributable to the difference in molt schedules. As in many passerines, White-crowned Sparrows undergo molt before leaving the breeding grounds and exhibit a reduction in the stress response at this time (Astheimer et al. 1994; also Lapland Longspurs [Calcanus lapponicus], Astheimer et al. 1995). Because Western Sandpipers wait until arrival on the wintering grounds to molt flight feathers and many of their body feathers (Wilson 1994), their stress response during autumn migration is not affected by molt.

These results emphasize the importance of studying a species throughout the annual cycle. Using this method, we were able to detect differences between a shorebird species and many passerine species in their stress response patterns not only between stages, but within stages. However, due to the complexity of the question
and scope of this study, some issues remain unresolved. The annual cycle of female and hatch-year Western Sandpipers was only partially examined here. Females winter farther south than males: how does the increased migratory distance affect their stress response and patterns of fat and weight gain? Further study is also warranted to determine if corticosterone levels, body condition, and site selection are correlated within each sex and age class.

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