

blown too far from a colony are deserted by their parents. We suggest that one advantage Eared Grebes derive from nesting within a gull colony is structural stability derived from attaching their nests to the gull nests.

Franklin's Gulls do not prey on the eggs and chicks of conspecifics or other species (Burger 1974), and thus do not pose a predatory threat to the grebes. Occasionally gulls will gaffer aggressively at the grebes as they slip onto their nests (unpubl. data), but they stop when the grebes are incubating.

We thank G. Huschle, G. Tisher, and D. Bennett for logistical support and advice; J. Boe for helpful comments on the ms; and Virgil, Cathy and Andy Erickson for logistical support, lodging, and companionship while at Agassiz National Wildlife Refuge. This project was part of a cooperative agreement between the U.S. Fish & Wildlife Service and Rutgers University.

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The Condor 97:580-585

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PLASMA CORTICOSTERONE IN BAR-TAILED GODWITS AT A MAJOR STOP-OVER SITE DURING SPRING MIGRATION¹

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Key words: Bar-tailed Godwit; body mass; corticosterone; migration.

Shorebirds that overwinter at mid-latitudes but breed in circumpolar regions in spring must cover vast dis-

tances in remarkably short periods of time (Alerstam and Lindström 1990, Drent and Piersma 1990, Evans and Davidson 1990). Such long-distance migrations involve a suite of behavioral and physiological adjustments to changes in climate and ecology many of which are not thoroughly understood (Ramenofsky 1990, Wingfield et al. 1990, Jenni-Eiermann and Jenni 1991). One of the better known features of long-distance migration is the preparatory phase that involves storage of fuels (particularly fat and protein) prior to

¹ Received 29 June 1994. Accepted 28 November 1994.

TABLE 1. Comparison of body mass and plasma levels of corticosterone among three categories of Bar-tailed Godwits captured in May 1989 in the Dutch Wadden Sea. Values represent mean \pm SD and sample sizes are indicated within parentheses.

Categories	Body mass (g)	Corticosterone (ng/ml)
Arriving adults (females = 8) (males = 10)	265.7 \pm 45.9* (18)	60.3 \pm 11.3** (16)
Departing adults (females = 2) (males = 3)	370.4 \pm 30.2 (5)	59.9 \pm 13.2** (5)
Sedentary juveniles (females = 1) (males = 9)	266.1 \pm 22.5* (9)	17.7 \pm 9.58 (9)

* Differs significantly from departing adults by analysis of variance (ANOVA) followed by Fisher's Protected Least Square Differences tests. ($F = 15.32$, $P = 0.0001$).

** Differs significantly from juveniles by ANOVA ($F = 46.11$, $P = 0.0001$).

departure (Evans and Davidson 1990, Lindström and Piersma 1993). During long-distance flight fat as well as protein including flight muscles are utilized (Piersma and Jukema 1990).

The physiological mechanisms regulating dramatic shifts in body composition are poorly understood. Recently, however, focus has been placed on the adrenal glucocorticosteroid, corticosterone. Plasma levels of corticosterone rise in response to stressful conditions that include starvation and strenuous exercise (Harvey et al. 1984, Rees et al. 1985, Chérel et al. 1988). The elevated levels promote protein and amino acid catabolism and liver gluconeogenesis that effectively augment availability of carbohydrate (Harvey et al. 1984). Increased *in vitro* secretion of the adrenal gland has been identified during migration in a number of migratory species (Peczely 1976).

Although long-distance migrants cover vast distances, the length of any one leg of flight may be short (hence the name "hoppers") or long ("jumpers") as exemplified by the Bar-tailed Godwit (*Limosa lapponica*) (Piersma 1987; Drent and Piersma 1990). Populations of this species winter in West Africa (Banc d'Arguin) and breed in the Siberian Arctic. Adults complete the 8,000 km trip with a mid-way stop-over at the Dutch Wadden Sea (Prokosch 1988; Piersma and Jukema 1990). Covering such distances necessitate deposition of large amounts of fuel that are utilized during flight. Dramatic rates of fat and protein deposition have been documented in adult godwits during the month period of refuelling in spring at the Dutch Wadden Sea site (Piersma and Jukema 1990, Lindström and Piersma 1993). No study, thus far, has investigated the regulatory role of corticosterone during stop-over in a long-distance migratory shorebird species.

Therefore, we hypothesized that plasma corticosterone would correspond inversely with body mass in adults during spring stop-over with highest levels at arrival that subsequently decline with mass acquisition. Locally summering juveniles (presumably from the European population) (Boere and Smit 1980; Drent and Piersma 1990) were investigated also. These sedentary juveniles neither prepare for nor undergo migration (Drent and Piersma 1990) and thus provided a valuable comparison for migrating adults.

MATERIALS AND METHODS

Birds and field conditions at time of capture. On 5 and 10 May 1989, respectively, three and 15 adult Bar-tailed Godwits were captured in the Paesenserpolder, Friesland (53°21'N, 6°06'E). Later, 30 May 1990, five and nine juvenile birds were captured in the Polder Eendracht, Texel (53°08'N, 4°50'E). Birds were captured individually or in small flocks between 12:00 and 18:00 hr local time.

Both sites are considered traditional spring staging areas for godwits in the Dutch Wadden Sea (Piersma and Jukema 1990). All birds were captured with a wind assisted clap net or "wilsternet" (Koopman and Hulscher 1979). Adults sampled on 30 May belonged to a population which was preparing to depart for the breeding grounds in Siberia. An estimated 6,000 godwits (consisting of 5% juveniles) were present at the high tide roost. On 1 June 1989 all but 200 adults and 300 juveniles had disappeared. Their departure from the Dutch Wadden Sea in an east-northeast direction was recorded both by radar and observers on the ground (R. Drent, pers. comm.). Clearly, only the adults captured in late May were migrants, en route from West Africa to Siberia (Piersma and Jukema 1990).

Birds were aged according to primary wear and plumage characteristics (Hayman et al. 1986) with adults always showing a fairly complete breeding plumage and juveniles with only traces of it. Prominent sexual dimorphism allowed for identification of sex on the basis of bill and wing length (females bigger than males) and plumage characteristics (males with darker rusty-red breeding plumage than females) (Piersma and Jukema 1990). Sex-ratios of categories of godwits examined on different capture dates remained reasonably constant (Table 1).

Quickly after capture, blood (2 ml) was collected from the wing vein into a heparinized syringe. Samples were held on water ice until separated by centrifugation and stored at -30°C then transported to Seattle, Washington, for hormonal analyses. Between capture and bleeding or weighing, birds were kept in a soft-walled dark box. They were weighed on a Pesola spring-balance within 1 hr of capture (see Piersma and Jukema 1990). By using the 'wilsternet' method to snare birds

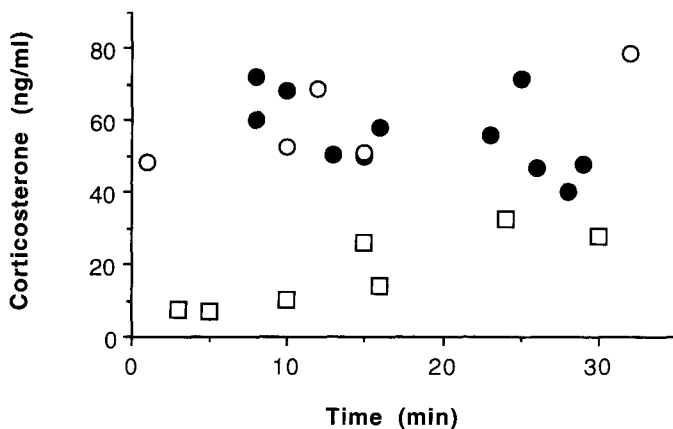


FIGURE 1. Relationship of plasma levels of corticosterone and time required to capture and handle (a) adult godwits (filled circles) that had recently completed the first leg of the migratory journey from West Africa to the traditional stop-over site in the Dutch Wadden Sea ($r = 0.55$, $P = 0.08$, $n = 11$), (b) juvenile godwits (open squares) residing on the traditional summering site in the Dutch Wadden Sea ($r = 0.87$, $P = 0.01$, $n = 7$) or (c) adult godwits (open circles) that were within one to two days of departing for breeding grounds in Siberia ($r = 0.82$, $P = 0.08$, $n = 5$) by Least Squares Regression analysis.

it was not always possible to capture and bleed individuals within a very short time span (5 to 10 min). However, only birds bled within 60 min of capture were included in the analyses.

Corticosterone radioimmunoassay. All samples were thawed and 20 μ l were aliquoted into glass centrifuge tubes to which 300 μ l distilled water was added. A total of 2,000 cpm (3 H)-corticosterone (New England Nuclear) was placed in each sample and allowed to equilibrate overnight at 4°C. The lipid fraction in each sample was extracted with 5 ml of distilled dichloromethane. The organic phase was collected and dried under nitrogen gas at 40°C. The dried extracts were resuspended in 550 μ l phosphate-buffered saline with 0.1% gelatin. Aliquots of 200 μ l were placed in duplicate assay tubes to be run through the radioimmunoassay. The remaining 100 μ l were pipetted into a glass vial to which 4.5 ml scintillation fluid was added (4 g Omnifluor New England Nuclear in 1 L toluene). CPM from each vial were corrected for dilution and provided an estimate of percent recovery of steroid following extraction for each sample. Concentration of corticosterone was determined by specific radioimmunoassay (RIA) according to the procedures described by Wingfield and Farner (1975) with the more recent modification of Ball and Wingfield (1987). Values of each sample were determined from a standard curve that ranged from 7.8–1,000 pg. All samples were adjusted for percentage of recovery. Recovery values ranged from 92–100%. Measurements of least apparent steroid were 8.65 ± 0.85 (mean ng/ml \pm SE) and range of percent binding was 90–99% in ligand-free samples. Final concentrations were calculated in units of nanograms per milliliter of plasma.

RESULTS

Plasma levels of corticosterone are a well-known marker for adrenocortical responses to stress associated with

capture and handling in birds (Harvey et al. 1984, Asheimer et al. 1994). In many species, plasma levels of corticosterone peaked within 5–30 min of capture (Smith et al. 1994, Wingfield et al. 1994). If corticosterone levels rise in response to a stressful episode, it is necessary to correct the values in relation to time required for capture in order to compare baseline values of hormone across individuals. Adults captured soon after arrival at the Dutch Wadden Sea (5 and 10 May) showed no relationship between plasma corticosterone and maximum capture interval of 30 min ($P = 0.08$) (Fig. 1). Later in the month (30 May) sedentary juveniles revealed a positive and significant relationship between plasma corticosterone and a maximum capture interval of 30 min ($P = 0.01$). However, adults captured during preparation for departure appeared to show a positive trend but without significance ($P = 0.08$). The sample size admittedly is small.

In order to compare hormone levels between age categories, given the disparity in responses to capture stress, the values were not corrected for capture time and thus considered maximal. Corticosterone levels of adults captured at arrival did not differ from those prior to departure ($P > 0.05$) (Table 1). Yet, the levels measured in either group of adults were more than three times higher than juveniles ($P = 0.0001$). Body mass of the adults preparing to depart exceeded both that of adults captured soon after arrival and juveniles ($P = 0.0001$).

Plasma levels of corticosterone in adults of either sex captured within 10 days after arrival (5 and 10 May) were negatively correlated with body mass. This correlation became statistically significant when both sexes were plotted on the same graph with body mass expressed as a percentage of the final departure mass ($P = 0.003$) (Fig. 2). Plasma levels of corticosterone in the small number of adults captured on 30 May failed to show the same negative relationship with body mass ($r = 0.66$, $P = 0.22$, $n = 7$).

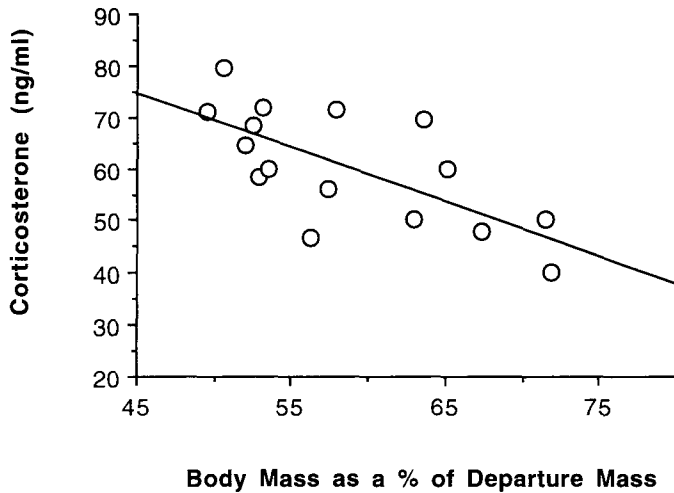


FIGURE 2. Relationship of plasma corticosterone and body mass in adult Bar-tailed Godwits during the early stages of arrival at the Dutch Wadden Sea during spring migration. Body mass is represented as a proportion of average departure mass reached by the sampled individual (i.e., 404 g in males and 495 g in females, fig. 9 in Piersma and Jukema 1990). However, since body mass increases linearly over time (Piersma and Jukema 1990), the x-axis can also be read as a seasonal axis ($r = 0.69$, $P = 0.003$, $n = 16$) by Least Squares Regression analysis.

DISCUSSION

Bar-tailed Godwits cover great distances during each leg of their migratory journey. To successfully complete a leg, vast stores of fat and protein are deposited prior to take-off. These fuels provide energy necessary to sustain high levels of muscular performance. When flight is suspended during periods of rest and refeeding, fuel stores are replenished for use during the next leg of flight. The metabolic processes engaged in energy delivery during flight appear to be regulated, in part, by corticosterone. This adrenal steroid regulates gluconeogenesis that provides a continuous supply of energy to the CNS and working flight muscles to sustain prolonged flight. Utilization of fat during flight is regulated by hormones other than corticosterone including catecholamines, growth hormone, glucagon and thyroid hormones (Goodridge and Ball 1965, John et al. 1988). However, these hormones go beyond the scope of this brief communication.

In light of our hypothesis, these preliminary results and those of others suggest that corticosterone may vary inversely with body mass during stop-over. Upon arrival at the Wadden Sea site, plasma corticosterone was elevated but declined as body mass increased with refeeding. Furthermore, plasma levels of corticosterone of racing pigeons (*Columba livia*) were increased at the conclusion of prolonged flights (> 180 km) (Haase et al. 1986). From these data, we infer that corticosterone rises with flight and energy expenditure however nocturnal samples collected from European migrants as they crossed the Alps en route to southern wintering sites are contradictory (Gwinner et al. 1992). The only individual to exhibit elevated levels of corticosterone possessed no visible stores of fat with elevated concentrations of uric acid. Unlike all others captured, this

bird was in negative energy balance. The others may not have traveled far or long enough to approach a critically depleted state or this may reflect a basic difference between "hoppers" versus "jumpers."

Others have identified negative relationships of corticosterone and body condition (Schwabl et al. 1991, Smith et al. 1994, Wingfield et al. 1994). These examples offer further support that corticosterone may be directly involved with glucoregulatory activities when endogenous stores of fuel reach critically low levels. Adult godwits arrived at the Wadden Sea were in a depleted state since body fat and muscle protein were diminished to nearly 50% in both sexes (Piersma and Jukema 1990). Such a condition appeared comparable to the final phase (III) of body mass loss in fasting King Penguins (*Aptenodytes patagonica*) (Cherel et al. 1988) when body levels of body fat were low but plasma corticosterone high and protein catabolism extensive. Once godwits were able to commence refeeding, the negative energy balance was reversed. Body mass increased linearly during the month-long staging period at a rate of 5.6 g/day for males and 7.5 g/day for females (Piersma and Jukema 1990) and plasma corticosterone declined. Near the time of take-off, as birds attained greater than 80% of their departure mass, the relationship of corticosterone with mass disappeared even though the mean levels of corticosterone of arriving and departing birds did not differ. This result was somewhat confusing but may be due to the small sample size of the departing birds. Nevertheless, the lack of relationship with body mass suggests that as birds attained positive energy balance the importance of the corticosterone-directed glucoregulatory mechanisms subsided.

Additional evidence that corticosterone may play a regulatory role during migration was found with the

striking disparity between adults sampled in the midst of migration and sedentary juveniles. Plasma levels of corticosterone in adults were three to four fold higher emphasizing that dramatic energetic demands of migration may heighten the "adrenal potential" (Astheimer et al. 1994) as observed in other migrating species (Peczely 1976, Ramenofsky et al. 1990, Schwabl et al. 1991). Alternatively, potentiation of the adrenal function may be involved with reproduction since only the migrating adults were preparing to breed. Further investigations are needed to distinguish between these possibilities.

Finally, adult godwits failed to show an acute response to stress of capture and handling that was observed in juveniles. This failure to respond or "resistance" to acute stress (Smith et al. 1994, Wingfield et al. 1994) may be adaptive at such times in the annual cycle as migration. Disruption or diversion from activities associated with migration (feeding and flying) may prove disastrous so that an adrenocortical response to stress is dampened. Free-living Garden Warblers (*Sylvia borin*) captured during fall migration in the Algerian Sahara (Schwabl et al. 1991) showed highly variable responses to capture stress. Although this represents only two species of migrating birds, alterations in the stress response may be more prevalent than previously appreciated. Further and more complete studies are needed to test these preliminary observations.

We are grateful to It Fryske Gea and Piet Postma (Staatsbosbeheer-Texel) for allowing us to catch Bar-tailed Godwits on the protected nature reserves under their management. Cor Dijkstra made a portable centrifuge available, and the Laboratory for Animal Physiology of the University of Groningen kindly allowed us to use pieces of their equipment. Financial support for hormone analyses were provided by the University of Washington Graduate School Research Fellowship to M.R.

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The Condor 97:585-587

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OBSERVATIONS ON THE NESTING AND BREEDING BEHAVIOR OF THE ROCK WREN¹

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Key words: *Salpinctes obsoletus*; Rock Wren; nest construction; breeding biology; stone-carrying; incubation; territory takeover; extra-pair copulation.

The Rock Wren *Salpinctes obsoletus* is a common bird in the rocky, arid habitats which characterize its range in western North and Central America from Canada to Costa Rica (AOU 1983). Rock Wrens generally nest in holes or crevices in boulders, rocky slopes or cliffs. They are known for their curious habit of constructing a foundation of small, flat stones upon which the nest is built; often a "pavement" or collection of stones is placed at the entrance to the nest as well (Bailey 1904, Ray 1904, Smith 1904, Bent 1948). Other than descriptions of completed nests, however, relatively little is known of the basic breeding biology of this species (e.g., Harrison 1979, Ehrlich et al. 1988, Terres 1991). The one exception is a study of nest temperature and parental feeding rates by Wolf et al. (1985).

I observed the nesting and breeding behavior of six pairs of color-banded Rock Wrens in Rinconada Canyon just west of Albuquerque, New Mexico, from March through August, 1992. The sloping walls of the canyon are covered by large volcanic rocks; the grassland floor at 1,558 m rises 88 m to the top of the mesa. Birds were captured with mist nets, fitted with a U.S. Fish and Wildlife Service aluminum band on the right leg

and a unique combination of plastic color bands (A. C. Hughes) on the left leg for individual identification. Birds were sexed by the presence of a brood patch or cloacal protuberance; these determinations were later confirmed through behavioral observations (e.g., copulations).

Mated pairs were well established on their territories by the first of March, and Rock Wrens were seen carrying nesting material as early as 6 March. Mated pairs remained together throughout the breeding season; two pairs remained on the site for the duration of the study, each producing three broods. One of these pairs remained on their territory following a nest predation event and subsequently raised their third brood. Of the four other banded pairs, predation on nests by either snakes or mammalian predators resulted in either one of both members of the pair abandoning the territory.

Over the course of the study, I made observations of nine active Rock Wren nests. I followed two broods of two different pairs of Rock Wrens from egg-laying through fledging. In both cases the clutch consisted of five eggs which were laid at the rate of one per day. Incubation was by the female only. Incubation was measured as starting from the first time the female was observed incubating until the hatching of the first egg. In both cases the female was first observed incubating early in the morning with a complete clutch of eggs; whether the female may have begun incubating the night before the final egg was laid or just that morning is not known. Incubation time was 12 days in one case, 14 days in the other. The male occasionally fed the

¹ Received 30 June 1994. Accepted 19 October 1994.