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Integrating stress physiology, environmental change, and behavior in free-living sparrows

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Abstract

As weather deteriorates, breeding animals have a diverse array of options to ensure survival. Because of their mobility, birds can easily abandon territories to seek out benign conditions away from the breeding site. The timing of abandonment, however, may have repercussions for territory size, mate quality, reproductive success, and survival. There is a large body of evidence indicating that the adrenocortical response to stress plays a role in mediating the onset and maintenance of this behavioral switch. Here we develop a model describing the interactions of weather, food availability, body condition, and stress physiology in initiating departure from the breeding site. We tested the model using a population of white-crowned sparrows breeding at high elevation in the Sierra Nevada, where severe weather at the beginning of the breeding season often induces temporary abandonment of breeding territories and facultative altitudinal migration to lower elevation refugia. The data show that (1) during inclement weather, exogenous corticosterone delays return to the breeding site after territory abandonment; (2) during good weather, exogenous corticosterone alone does not induce territory abandonment, but does increase activity range around the breeding site; and (3) the magnitude of the corticosteroid response to stress is inversely related to body condition of the sparrow.

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In fluctuating environments, animals attempt to time events in their lives to optimize survival and reproductive success (Lack, 1968; Perrins, 1970; Wingfield, 1983). However, some changes in environmental conditions occur very rapidly and cannot be anticipated; these require flexible adjustments in physiology and behavior on short time scales. For example, unpredictable short-term changes in weather can drastically alter conditions in some habitats, demanding quick, often temporary alterations of physiology and behavior for animals to survive. Such unpredictable events are generally thought to exert their effects through the hypothalamo–pituitary–adrenal (“stress”) axis (Sapolsky, 1987; Sapolsky et al., 2000; Wingfield, 1994; Wingfield et al., 1997).

As some of the most highly mobile organisms on earth, birds have access to diverse options for avoiding problem situations. Seasonal migrations between breeding and wintering sites can permit individuals to use geographic areas that would be unacceptable if they had to remain year-round (Gill, 1990). Smaller-scale movements appear to be induced by short-term modifications in environmental conditions, such as inclement weather, extreme temperatures, or low food availability. Temporary abandonment of the breeding territory is a common response to unpredictable environmental perturbations (Lens, 1995; Wingfield, 1985b). In mountain birds, territory abandonment can involve a facultative altitudinal migration to lower elevation. This behavior provides a temporary mechanism for finding food and refuge until the breeding territory is once again tolerable. Facultative altitudinal migrations represent one example of behavior that is widespread in migratory birds: a tendency to initiate or extend geographic movements flexibly in re-

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sponse to relatively unpredictable changes in environmental conditions. As a dramatic, robust behavioral phenomenon, facultative altitudinal migration may be an excellent model for studying responses to natural environmental stressors.

The factors influencing facultative altitudinal migration are unknown, but available information suggests that interactions among corticosterone (CORT), body condition, food availability, and weather are logical candidates to explore. In free-living songbirds, circulating CORT levels often increase in response to inclement weather (Rogers et al., 1993; Schwabl et al., 1985; Wingfield, 1985a,b; Wingfield and Ramenofsky, 1997). Increased circulating CORT can influence behavioral switches appropriate to adverse conditions, such as inhibition of territoriality and nest attendance (Silverin, 1986; Wingfield, 1985a,b; Wingfield et al., 1982, 1983; Wingfield and Ramenofsky, 1997; Wingfield and Silverin, 1986). In captive birds, behavioral effects of corticosterone depend on food availability. Captive Gambel's white-crowned sparrows (*Zonotrichia leucophrys gambelii*) with CORT implants show little activity if food is available *ad libitum*, but increase activity when food is removed (Astheimer et al., 1992). Food deprivation alone also can increase both activity and endogenous CORT (Lynn et al., in press). Finally, in many species, handling-induced CORT secretion is reduced in individuals with substantial fat deposits compared with leaner individuals (Cherel et al., 1988; Kitaysky et al., 1999; Levin et al., 2000; Schwabl, 1995; Smith et al., 1994; Wingfield, 1994; Wingfield et al., 1994). These relationships suggest that an unpredictable event in the environment, such as a severe storm, might lead to the greatest and most rapid increases in circulating CORT, and the most pronounced behavioral response, in individuals with relatively low energy reserves. Field studies of relationships between glucocorticoid stress physiology and behavior in a tractable mountain-breeding bird therefore hold promise for understanding the mechanistic bases of facultative altitudinal migration.

Mountain white-crowned sparrows (MWCS; *Zonotrichia leucophrys oriantha*) are perfect subjects for such field studies. These birds are site-faithful migrants that breed in subalpine meadows in the mountains of western North America and spend the winter in Mexico (Cortopassi and Mewaldt, 1965). We have been studying facultative altitudinal migration in a population of *Z. l. oriantha* breeding at Tioga Pass in the Sierra Nevada. Early in May when *Z. l. oriantha* arrive on the breeding grounds, weather conditions are unpredictable and often severe; new snowfall that covers all available foraging areas frequently occurs (Hahn and Morton, 1995; Morton, 2002). Such conditions are potentially devastating to small ground-feeding birds. However, the eastern slope of the Sierra Nevada falls precipitously into the Great Basin. Birds preparing to breed at 3000 m elevation near Tioga Pass can drop 1000 m to the shrub-steppe desert near Mono Lake by flying only 20 km. During severe storms, MWCS frequently make the short flight from Tioga Pass to lower elevation refugia in Lee Vining Canyon

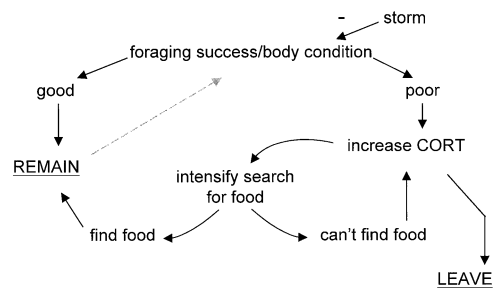


Fig. 1. Possible environmental and physiological factors mediating facultative altitudinal migration

and the Mono Basin, where they may remain for days before returning to the breeding area (Hahn et al., submitted for publication; Hahn and Morton, 1995).

Based on the known correlations among weather, body condition, corticosterone levels, food availability, and behavior presented above, we have formulated hypotheses regarding control of facultative altitudinal migration behavior in birds. These hypotheses are illustrated diagrammatically in Fig. 1. When weather conditions are good and food is readily accessible, foraging success is likely to be high, and good body condition can readily be maintained. Under these conditions, the bird will remain on the breeding ground, but will continue monitoring body condition and foraging success. A storm can disrupt this pattern. Inclement weather negatively affects foraging success (by rendering feeding areas inaccessible) and body condition (by reducing access to food, and/or by imposing increased energy demands). This can lead to an acute stress response, including an increase in circulating CORT. The immediate behavioral effect of elevated CORT is to intensify the search for food in the local area. If this immediate response is effective and foraging success improves, then the bird can remain at the breeding site. If the storm is sufficiently severe, then even intensified foraging may be fruitless, leading to yet further increases in circulating CORT. At this point, the combination of low food availability, poor body condition, and high CORT level causes the bird to change tactics dramatically, initiating a facultative altitudinal migration to lower elevations where foraging opportunities will be superior and the thermal environment will be less challenging.

A number of testable predictions can be drawn from this model regarding the interactions of weather, CORT, and body condition in regulating facultative altitudinal migration:

1. During inclement weather, CORT implants will accelerate departure from the breeding site;
2. During good weather, CORT implants will increase foraging, but will not induce facultative altitudinal migration;
3. Stress-induced CORT secretion will be negatively correlated to body condition.

Since 1997, we have been testing these predictions in the population of white-crowned sparrows breeding at Tioga

Pass using radiotelemetry and CORT implants. The current state of this ongoing research is reported here.

Materials and methods

Study site and animals

The population of MWCS in this study breeds near Tioga Pass, Mono County, California ($\sim 37.5^\circ\text{N}$ latitude, ~ 3000 m elevation). Sparrows were studied along Lee Vining Creek and neighboring Tioga Pass Meadow. Animals were caught in seed-baited live traps and banded with both a National Biological Service band and a unique combination of three color bands.

Radiotelemetry

Each male was fitted with a radiotransmitter (Advanced Telemetry Systems, Isanti, IL) weighing 1 g. Two loops of elastic thread were attached to the transmitter; each loop fit snugly around a leg of the bird to hold the transmitter securely in place (Rappole and Tipton, 1991). Each transmitter emitted a signal of a different frequency, allowing individual identification of birds. The transmitters can reliably be detected at distances of 2–3 km around Tioga Pass. Birds that moved to lower elevations were located by scanning from the steep hillsides on the western edge of the Mono Basin.

Implants

Fifteen-millimeter lengths of silastic tubing (Dow Corning, Midland, MI; 1.47 mm in diameter) were filled with crystalline CORT (Sigma) and sealed at both ends with silastic sealant (Dow Corning). Just prior to implantation, one end of the implant was cut open to facilitate CORT diffusion from the implant. Blank implants contained nothing but a plug of silastic sealant at one end. Implants were placed subcutaneously on the upper back.

Inclement weather study

1998 had much higher snowpack than usual (the 75-year average April 1 snowpack for Tioga Pass is 170 cm; April 1 snowpack in 1998 was 282 cm). We began trapping birds on May 18. By May 28 we had 10 sparrows wearing radiotransmitters: 4 were given CORT implants, 2 were given blank implants, and 4 had no implants. All 6 implants were given within 7 days of the beginning of the study (2 CORT and 1 blank implant given on May 23, and 2 CORT and 1 blank implant given on May 28). On May 25, a heavy snowstorm dropped 15–30 cm of new snow at the breeding site. The weather then cleared until June 2–3, when it snowed for approximately 36 straight hours. Skies were clear for the rest of the study except for a series of small

snow showers on June 7 and 8. Each day of the study (May 30 through June 8) we arrived at the breeding site before dawn and scanned for the presence/absence of each sparrow every 10–15 min. Scanning time ranged from 2 to 10 h (average \pm SEM 5.3 ± 0.97 h); on June 2 we did not scan because we could not reach the breeding site during the day (road closed by snow). During the afternoons we drove around at low elevation determining the location of the sparrows that had abandoned their territories. After 22:00 every evening we determined roost site for each sparrow, scanning the breeding site for presence/absence, and then locating the animals at their low elevation sites if absent from the breeding site (we were able to reach the breeding site for the June 2 night roost scan). On average, we found 83% of the study animals every night. If a sparrow was not located, we assumed it was at low elevation (Hahn et al., submitted for publication).

Analysis

Over the 10 days of the study, data were collected for each bird regarding location of roost site, time of arrival at the breeding site in the morning (if returning from low elevation), and amount of time present at the breeding site during scanning. We then calculated the percentage of nights (of 11 total) each bird spent at the breeding site, an average time-of-arrival rank for each individual (consisting of data only from days the bird arrived at the breeding site), and the average percentage of time spent at the breeding site (the number of hours each bird was present divided by the total number of hours spent scanning that day ((hours present/total hours spent scanning) \times 100)). Treatment effects were evaluated with Mann–Whitney *U* tests. A family-wise $\alpha = 0.05$ significance level was used for all tests, and the Bonferroni method was used to control for simultaneous testing (time of arrival and percentage of time present).

Good weather study

During both 1997 and 1999 prenesting periods, there were no significant storms. The snowpack was lower than 1998 in both years (211 and 198 cm, respectively). In both years, males were fitted with radiotransmitters, and radio-tracked multiple times per day, between 06:00 and 17:00. In the middle of the study, males were given either a CORT-filled or blank implant. Individuals were not always verified by sight, to avoid influencing behavior. Once an individual was localized by telemetry, it was not tracked again for at least an hour.

1997

This study followed 6 male MWCS over 8 days (June 1–8). To avoid a direct effect of weather, implants were given on 3 separate days (June 3, June 4, and June 6). Five males received CORT implants, and 1 received a blank implant. Males were localized 2–4 times per day for 2–5 days both before and after receiving implants. “Baseline”

blood samples were taken from 3 of the CORT-implanted birds (2 days into the CORT treatment) and 13 nonimplanted birds (taken at the same time and from the same breeding site, but not from birds included in this study) to determine circulating CORT levels.

1999

This study followed 5 male MWCS over 8 days (May 25–June 1). Two CORT and 3 blank implants were given over a 3-day period. Males were localized 2–5 times per day for 3–4 days both before and after receiving implants.

Analysis

Each localization was plotted on a map of the breeding site. For analysis of each bird, the time spent radiotracking was equal before and after implants were given. “Activity range” was calculated from these data using minimum convex polygons (Chandler et al., 1994), a measurement of the area enclosed by tracking locations for each bird during control or CORT treatments (see Fig. 5). This measurement was not considered “home range” because we restricted measurements to where the bird could be found during the day. The complete home ranges of these birds often contains nighttime roost locations that are well outside the area used during the day (Sanders, 1998). Percentage change in activity range ((range after implant – range before implant / range before implant) \times 100) was calculated for each animal, and differences between treatments (blank or CORT implant) were tested using a Kolmogorov–Smirnov non-parametric test. A family-wise $\alpha = 0.05$ significance level was used for all tests. None of the birds from the 1997 study were used in the 1999 study.

Corticosterone response to capture and handling

In 2000, 14 males were caught near the end of the arrival phase (prenesting; June 1–3) and subjected to a standard protocol of capture and handling (Breuner et al., 1999; Wingfield, 1994). A blood sample was obtained within 3 min of finding the bird in the seed-trap, and serial samples were collected at 5, 10, 30, and 60 min. After the 30-min sample was collected, weight and fat score measurements were collected on each individual. Fat score was measured by assigning a score of 0–5 to the abdominal and furcular fat regions (a score of 0 representing no fat, 5 representing a premigratory sparrow, with bulging fat deposits; see Morton, 2002). To obtain the blood sample, the alar vein was punctured with a 26-gauge needle, and 40–60 μ l of blood was collected into heparinized microcapillary tubes. Blood samples were kept on ice until plasma was separated by centrifugation and stored at -20°C .

Plasma corticosterone levels were determined as outlined in Breuner and Orchinik (2001). Briefly, samples were allowed to equilibrate overnight with 2000 cpm of corticosterone for determination of individual recoveries. Each sample was extracted with 4.0 ml of dichloromethane, dried

under nitrogen, and resuspended in phosphate-buffered saline with 1% gelatin. Samples were assayed in duplicate, and assay values were corrected for plasma volume and individual recoveries following extraction. 1997 samples (after CORT implant) and 2000 samples (stress series) were run in separate assays. Results were as follows: 1997: standard curve range, 2000–7.0 pg; detectability, 1.2 ng/ml; intraassay coefficient of variation, 2.2%. 2000: standard curve range, 2000–1.25 pg; detectability, 5.0 ng/ml; intraassay coefficient of variation, 10.7%.

Analysis

Relationships between fat score (abdominal + furcular) and baseline CORT, maximum CORT, and total CORT secreted over the hour were compared using multiple regression. We also produced scatter plots for visual presentation of the data. Maximum CORT represents the highest CORT level measured in each sparrow over the 60 min of capture and handling; total CORT represents the total amount of CORT present in the circulation over the hour of capture and handling. This amount is estimated by calculating the area under the curve.

Results

Inclement weather

During a series of storms beginning May 25, 1998 and continuing sporadically through June 8, all 10 birds (6 control; 4 CORT) in the study left their territories for low elevation. Nine of the 10 birds were found at lower elevation sites (the “off-breeding site” of one control bird was never located), ranging from 2100 to 2750 m elevation. There was no difference in elevational change between CORT and control birds (data not shown). In general, sparrows tended to return to the same low elevation site every time they left their territory at high elevation.

After sparrows abandoned their territories for low elevation, a general behavioral pattern emerged. In the days following the storm, sparrows would fly back up to the breeding site, usually arriving within a few hours of dawn. They would remain there for a few hours before heading back down to low elevation. Time spent at the breeding site ranged from 1 to 7 h; birds that stayed throughout the afternoon into evening usually roosted at the breeding site that night.

When birds returned to the breeding site on days following a storm, they normally arrived early in the morning. Depending on the day, the time of arrival in control birds (both no-implant and blank-implant birds) ranged from 04:45 to 07:00. Time of arrival for CORT birds ranged from 05:45 to 07:00 (Fig. 2). Control birds (no-implant and blank-implant data were pooled) arrived on average 1 h earlier than CORT birds (control = $5:15 \pm 5$ min, CORT = $6:14 \pm 12$ min; Mann–Whitney U : $Z = -2.558$, $P < 0.01$).

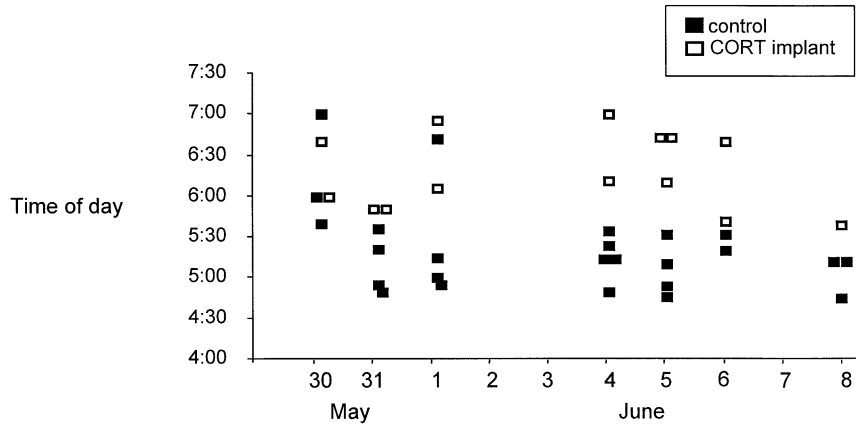


Fig. 2. *Inclement weather*. Time of arrival at the breeding site after roosting at low elevation. On average, CORT birds ($n = 4$; open squares) arrived 59 min later than control birds ($n = 6$; solid squares). If a bird roosted at the breeding site the previous night, it was not included in analysis.

If a bird roosted at the breeding site the night before, it was not included in the arrival data.

Not only did CORT birds arrive later in the morning, but they also left earlier, leading to much less total time spent at the breeding site. Of the total time spent scanning (~ 48 h over 9 days), control birds were present $75.7 \pm 6.3\%$ of the time, whereas CORT birds were only present $23.9 \pm 7.5\%$ of the time (Mann–Whitney U : $Z = -2.558$; $P < 0.01$).

CORT also affected roost site choice (Fig. 3). Over the 10 nights of the study, control birds roosted at the breeding site on average 44% of the nights (proportion of birds at the control site varied over the course of the study), whereas CORT birds never roosted at the breeding site (Mann–Whitney U : $Z = -2.558$; $P < 0.01$).

Good weather

During two seasons of good weather (prenesting during 1997 and 1999), we radiotracked males both before and after implant treatment. In 1997, CORT levels reached 42.83 ± 2.71 ng/ml ($n = 3$) within 2 days of implantation (nonimplanted sparrows measured at the same time had

baseline levels of 22.49 ± 2.74 ng/ml, $n = 13$). None of the sparrows abandoned their breeding territories for lower elevation refugia. However, CORT did affect patterns of space use. Activity range increased in all seven CORT-implanted birds in the study, whereas blank implants had no effect (Fig. 4; difference between treatments (combining years): Mann–Whitney U : $Z = -2.646$; $P < 0.01$).

Corticosterone and body condition

Corticosterone levels were measured within 3 min of removal from the seed trap, and then at 5, 10, 30, and 60 min (see Fig. 5). Baseline CORT levels were 9.8 ± 1.5 ng/ml; maximum CORT levels were 56.4 ± 4.3 ng/ml; and total CORT levels were 2426.9 ± 159 ng/ml/h. Fat scores ranged from 0 to 3 (of a possible 10). There was no relationship between baseline CORT and fat score (Fig. 6a). However, total CORT secreted over the hour and maximum CORT level were negatively correlated with fat score (Fig. 6b and 6c; multiple regression: baseline CORT: $t = -0.22$, $P = 0.83$; total CORT: $t = -2.59$, $P < 0.03$; maximum CORT: $t = -2.31$, $P < 0.04$).

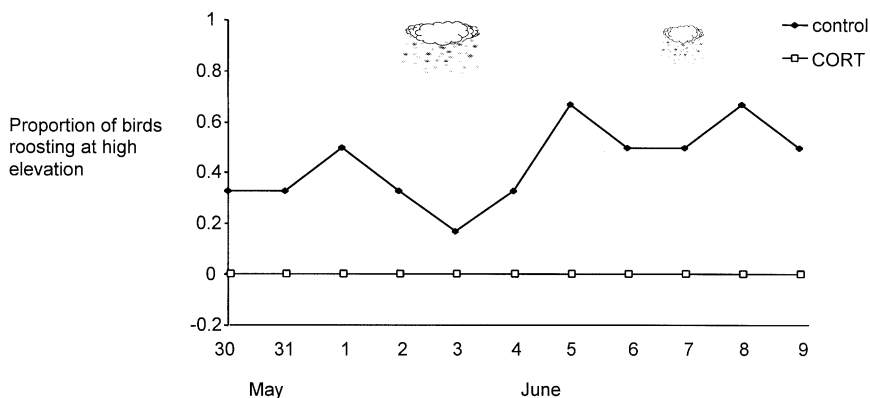


Fig. 3. *Inclement weather*. Roost site choice for control ($n = 6$; solid squares) and CORT ($n = 4$; open squares) birds over the 11 nights of the study. Roost site choice was determined every evening after dark ($>21:30$). Clouds represent approximate periods of snowfall.

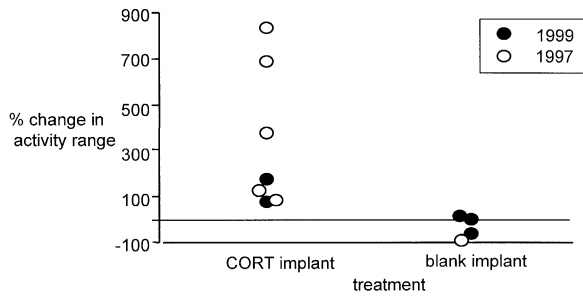


Fig. 4. *Good weather*. CORT implants increase activity range. Data were collected in both 1997 and 1999.

Discussion

In response to severe storms, birds often abandon their territories for a more suitable, but temporary, habitat. We are working toward understanding the interaction of environment, body condition, and stress physiology mediating these behavioral responses to unpredictable environmental events. During inclement weather, exogenous CORT alters the “return behavior” after birds leave the breeding site for low elevation. During good weather, exogenous CORT does not initiate abandonment of the breeding territory, but does increase movement around the breeding site. Finally, the magnitude of the CORT response to a standardized stressor is related to the body condition of the animal.

Inclement weather

Based on the model presented in Fig. 1, we predicted that increasing circulating CORT levels would increase the likelihood of departure from the breeding site. We have not been able to obtain any departure data during this study, primarily because the radiotracking of individuals was done manually, and we could not get up to the breeding site at critical times during the worst weather. However, we were able to measure return rates and roost site choices of the birds after the initial storm had passed. In the days following a snowstorm, birds would return to the breeding site around or after dawn, stay for a few hours, and then return to low elevation. This behavior was usually repeated for a few days before the sparrows remained at the breeding site all day to roost there at night. In other years, this pattern of behavior may be more or less protracted depending on the severity of the storm, or the snowpack at the breeding site (Hahn et al., submitted for publication).

The CORT-implanted birds showed significant differences in return behavior. CORT birds arrived at the breeding site on average significantly later than the control birds. We do not know from these data if birds were leaving the low elevation sites later in the morning or if it took them longer in transit (distances from low elevation roosting sites to the breeding grounds did not differ between groups). CORT-implanted birds also spent less time overall at the

breeding site. In general, these data suggest that the motivation to be at the breeding site is lower in the CORT-implanted males. This may be because they (a) have a higher threshold for acceptable environmental conditions at the breeding site (as predicted by the model in Fig. 1), (b) have lower testosterone levels due to the CORT implant (assuming that testosterone increases motivation to be on territory), and/or (c) are in poorer body condition (although there were no apparent differences in body condition between CORT and control birds in this study). While these hypotheses are not mutually exclusive, we can test them in future years.

What environmental conditions are the birds assessing to decide whether to stay at the breeding site? Hahn et al. (submitted for publication) found that the high temperature reached during the day is a good predictor of the proportion of birds roosting at the breeding site that night. The sparrows may also be assessing food availability and/or snow cover at the breeding site.

Good weather

In the absence of inclement weather, CORT-implanted birds do not go to lower elevations. However, CORT implants increased activity range in each sparrow and significantly increased activity range in the group as a whole. The increase in activity range after implantation with CORT is consistent with the hypothesis presented in Fig. 1. That is, increased CORT levels may have led to an increase in foraging activity (searching for food over a broader area). In the absence of high snow cover and/or inclement weather, however, there was food available, so the birds did not abandon their territories. Alternatively, it is possible that the birds with higher CORT are not foraging more, but are in a more “eruptive” state and are more easily driven away from their territory by conspecifics or predators for short periods of time. Further study will be required to determine whether the increase in activity range results from wider foraging or from some other mechanism.

The results from the fair weather experiment show that high CORT alone is not a sufficient signal to induce altitudinal migration. However, this interpretation neglects a potentially critical role for corticosteroid binding globulin

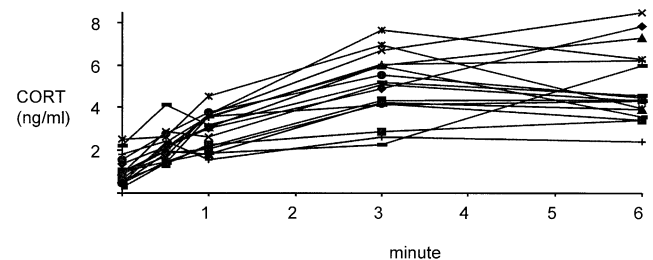


Fig. 5. CORT increase in response to 60 min of capture and handling stress. Data collected in 16 prenesting males in June, 2001.

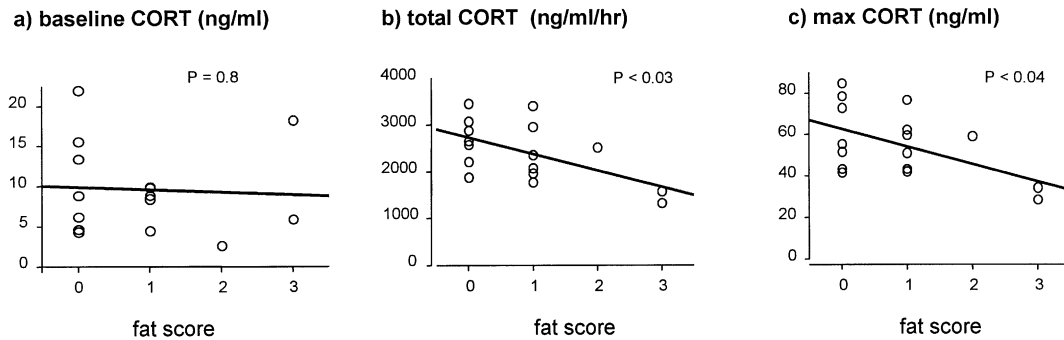


Fig. 6. Relationship of fat score and CORT secretion. Data were regressed against fat score and tested with a multiple regression. Baseline levels (a, the 0- to 3-min blood sample) were not related to fat score. Total CORT (b, area under the curve for each individual) and maximum CORT (c, highest CORT level recorded for each individual) are inversely related to fat score, so that animals with higher fat reserves secrete less CORT in response to a stressor.

(CBG). CBG binds CORT in the plasma with high affinity, and is thought to regulate bioavailability and clearance rates of CORT (Hammond, 1995). In the white-crowned sparrow, approximately 95% of CORT is bound to CBG (even when CORT reaches stress-induced levels; C. Breuner, unpublished data). However, food deprivation appears to decrease CBG levels (Lynn et al., in press; Tinnikov, 1999), thereby increasing the amount of free CORT in the plasma. It is possible that when food is abundant, CBG is at its unstressed level; under these conditions, most of the exogenous CORT from the implant would be bound to CBG, and unavailable to tissues. High levels of CORT may only affect altitudinal migration behavior when food availability is low, decreasing CBG levels and causing a dramatic increase in free CORT.

CORT and body condition

Stress-series data taken from prenesting birds in May 2000 suggest that CORT secretion in response to a stressor is related to body condition. In support of the hypothesis presented in Fig. 1, animals with lower fat scores showed higher maximum CORT levels and higher total CORT secreted over the hour (while there was no effect of fat score on baseline levels of CORT). This relationship suggests that animals in poor body condition may have a more pronounced stress response to deteriorating environmental conditions, possibly accelerating their departure from the breeding site. However, the significant relationship of CORT secretion and body condition is dependent on the two individuals with the highest fat score, suggesting that collection of data from more individuals with higher fat scores would be beneficial.

We believe that one of the central components driving behavioral decisions during inclement weather is the balance between food availability in the environment, energetic stores of the organism, and energetic requirements based on metabolic needs. One mechanism by which phys-

iology may alter behavioral choices during stressors is through enhanced secretion of CORT when energy reserves are low. In fact, this relationship between body condition and stress-induced CORT secretion has been demonstrated in many vertebrate species. Wingfield (e.g., Wingfield and Ramenofsky, 1999) created theoretical models predicting when CORT levels will rise and alter behavioral patterns based on energy available in the environment, energy reserves of the organism, and changing energy requirements throughout the breeding season. One interesting direction for research on the Tioga Pass population includes obtaining direct measures of each of these components (weather-induced changes in metabolic expenditure via doubly labeled water; energy availability in the environment via assessment of insect, seed, bud, and shoot availability; and internal energy reserves via mass vs body size residual analysis and estimates of energy available in fat and muscle stores). These data would allow for a better understanding of the role of energy balance in stress physiology and behavioral decisions.

It is important to note that in some circumstances the relationship among corticosterone, behavior, and body condition could be opposite that proposed above. Belthoff and Dufty (1998) hypothesize that in screech owls corticosterone will increase, and promote juvenile dispersal, only when body condition is good. It is intriguing to consider that integration of environmental and physiological cues regulating hormones and behavior could be specific to the particular life history stage of the animal.

In summary, during the first weeks after arrival near the breeding ground, MWCS make facultative altitudinal migrations between their intended breeding sites at Tioga Pass and arid shrubsteppe habitat about 1000 m lower. Some storms are sufficiently severe to force all individuals to abandon the breeding area, but milder storms induce few or none of the birds to leave. Exogenous corticosterone given during a storm decreases the time a sparrow spends at the breeding site during the day, as well as the probability that it will remain there to roost at night. Exogenous corticosterone given during fair weather does not induce altitudinal

migration, but increases the activity range of a sparrow at the breeding site. Endogenous corticosterone secretion is inversely correlated to body condition under stressful conditions.

Taken together, these data support a role for CORT in mediating facultative altitudinal migration, possibly incorporating changes in body condition to alter the severity of the response. To tie these ideas together more solidly with regard to our hypothesis, we need to investigate the role of food availability and energy balance in hormonal and behavioral responses to storms, the role of corticosterone in regulating foraging activity, the role of CBG in mediating the availability of CORT to tissues, and repercussions of this facultative altitudinal migration behavior for survival and reproductive success.

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