

Daily and Seasonal Variation in Response to Stress in Captive Starlings (*Sturnus vulgaris*): Corticosterone

L. Michael Romero and Luke Ramage-Healey

Department of Biology, Tufts University, Medford, Massachusetts 02155

Accepted March 13, 2000

Captive starlings were used to examine daily and seasonal changes in basal and stress-induced corticosterone levels. Birds were bled at 4 times during the daily cycle and during three different simulated seasons: under a short-day photoperiod (mimicking winter), under a long-day photoperiod (mimicking summer), and while undergoing a prebasic molt. Basal corticosterone samples were assayed from blood collected within 3 min of disturbance and corticosterone increases in response to handling and restraint were monitored in blood taken at 15, 30, and 45 min postdisturbance. Handling and restraint elicited robust increases in corticosterone at all times of the day and during all three seasons. Both basal and stress-induced levels varied with the time of day (with the exception of basal samples during molt). Levels were higher at night, during the bird's inactive period, and decreased during the day. These data indicate that starlings have daily rhythms in both basal corticosterone levels and in their response to stress, with more corticosterone released during the night in response to identical stimuli. Starlings also show pronounced seasonal variation in both basal and stress-induced corticosterone levels. Although birds held on short and long days had equivalent corticosterone levels, both basal and stress-induced levels were lower during molt. This parallels data from free-living birds and provides a laboratory model for studying seasonal corticosterone regulation. © 2000 Academic Press

Key Words: stress; glucocorticoid; molt; seasonality; circadian; circannual.

Glucocorticoid release is considered the hallmark of the vertebrate stress response. Glucocorticoids are released in response to a wide variety of noxious stimuli in both laboratory animals (Dallman *et al.*, 1987; Sapolsky, 1992; Romero and Sapolsky, 1996) and under natural conditions (Wingfield and Romero, 2000). It has become clear, however, that the magnitude of both basal (unstressed) and stress-induced glucocorticoid levels undergo daily fluctuations (e.g., Dallman *et al.*, 1993; Widmaier and Kunz, 1993). Daily fluctuations in basal glucocorticoid levels are believed to regulate the overall metabolism of the animal (Widmaier, 1992; Atkinson and Waddell, 1995), presumably by interacting with insulin to regulate the deposition and storage of energy (Dallman *et al.*, 1993; Santana *et al.*, 1995). Daily variation in basal levels also has a profound effect on the stress-induced elevations in glucocorticoids. Stress-induced corticosterone levels in the rat, for example, peak at approximately 30 $\mu\text{g}/\text{dl}$ even though basal levels cycle between 1 and 20 $\mu\text{g}/\text{dl}$ (Dallman *et al.*, 1993). Clearly, corticosterone responses in the rat are far more sensitive to stress at certain times of the day. This knowledge has been exploited for many years so that stressors are usually applied only when the sensitivity to stressors is at a maximum.

Unfortunately, information about the daily rhythmicity of glucocorticoid release and sensitivity to stressors is generally available only for standard lab-

oratory animal models. Little is known about daily glucocorticoid rhythms in nontraditional species. This information is important since recent studies have used many nontraditional avian species as models for glucocorticoid release under more naturalistic conditions (e.g., Wingfield, 1994; Wingfield and Romero, 2000). When these species are brought into the laboratory as well, it would be important to be able to parallel studies in domesticated species and take advantage of times in the day when their responsiveness to stress is at a maximum.

Furthermore, it is becoming increasingly clear that many wild free-living avian species can seasonally modulate their corticosterone levels (the primary glucocorticoid in birds, Holmes and Phillips, 1976). These species elevate their nonstressed and stressed levels of corticosterone at some times of the year (e.g., Dawson and Howe, 1983; Wingfield *et al.*, 1992; Wingfield, 1994; Romero *et al.*, 1997). There have been a few attempts to replicate these seasonal changes in captive birds under laboratory conditions (Marra *et al.*, 1995; Breuner *et al.*, 1999; Romero and Wingfield, 1999), but they have been largely unsuccessful. Although studies in several avian species (e.g., pigeons, chickens, and white-crowned sparrows) show daily corticosterone rhythms similar to the typical mammalian rhythm (Joseph and Meier, 1973; Lauber *et al.*, 1987; Westerhof *et al.*, 1994; Breuner *et al.*, 1999), changes in photoperiod (to mimic seasonal changes) have not altered these rhythms.

None of these studies, however, has examined corticosterone release in captive birds undergoing a prebasic molt (the costly replacement of all body feathers). In field studies, comparisons between molt and the breeding season have provided the largest differences in nonstressed and stressed corticosterone release (Romero *et al.*, 1998b,c,d). Consequently, the present study compares the corticosterone response to stress in captive starlings during three simulated seasons: (1) with birds held on a short-day photoperiod to mimic winter, (2) with birds held on a long-day photoperiod to mimic summer, and (3) while birds were undergoing a prebasic molt. We chose starlings since they are a relatively common model species used in both laboratory and field studies.

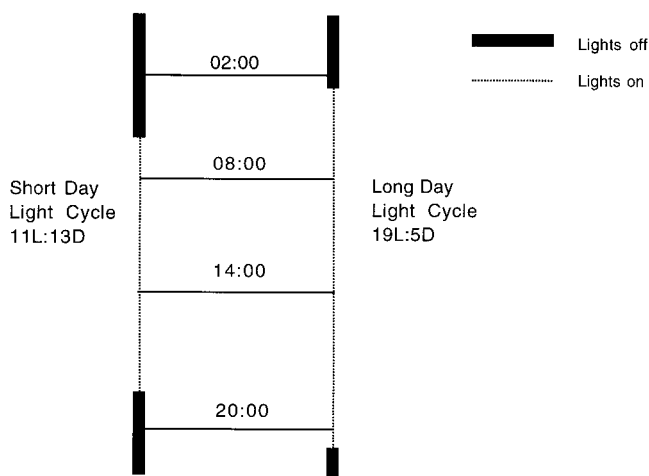


FIG. 1. Diagram of light cycles used to simulated seasons in the laboratory. Sample times are indicated for both photoperiods. Molt-ing birds were maintained on the long-day photoperiod. Each line indicates when the birds were bled during the daily cycle.

MATERIALS AND METHODS

Birds

Wild European starlings (*Sturnus vulgaris*) were captured using mist nets during the late fall (October–December) in eastern Massachusetts. There were no juveniles in this study, but some birds may have been hatch-year or 2nd-year birds (Pyle, 1997). The starlings in this study are, therefore, a mixture of young and adult birds. Birds were housed communally in large indoor flight aviaries for 1–3 months to acclimate to laboratory conditions. Birds were then transferred to individual cages. Light cycles were adjusted throughout the experiment to induce seasonal changes in anatomy and physiology. Birds were initially maintained on an 11L:13D light cycle (short day) to mimic winter conditions at the time of capture. Once all requisite samples were collected, the birds were shifted to a 19L:5D light cycle (long day) to mimic summer and allowed to acclimate for 2 weeks (Fig. 1). Birds were maintained on long days for approximately six weeks, at which time they commenced a prebasic molt (replacing all their flight and body feathers). Sampling was suspended for the first 2 weeks of the molt. The light cycle was maintained at 19L:5D throughout the molt (approximately 90 days, Cabe, 1993). All rooms

were maintained at 25°C with food and water provided *ad libitum*. All experiments were performed according to AALAC guidelines and approved by Tufts University Institutional Animal Care and Use Committee.

Sample sizes included nine males and nine females during each season. Technical difficulties (malfunctioning light cycles) prevented each bird from being sampled in each season, so 25 birds were used during the study.

Stress/Sampling Procedures

Birds were subjected to the stressors of handling and restraint as they were removed from their cages for blood sampling. Samples were taken at 6-h intervals over the 24-h daily cycle (Fig. 1). Blood sampling was limited so that no more than one sampling time (02:00, 08:00, 14:00, or 20:00) was taken within 36 h to allow birds time to replenish blood volumes and recover from the stress of the previous sampling. Thus, sampling over the “daily” cycle was completed over the course of several weeks. Thirty-six hours is sufficient for corticosterone to return to basal levels and hematocrit levels remained unchanged throughout the experiment (unpublished data). All sampling on the 11L:13D light cycle was completed before shifting birds to the 19L:5D light cycle, and subsequent long-day samples were completed before birds commenced their prebasic molt.

All birds were bled within 3 min of entering the room in order to measure basal (unstressed) corticosterone levels. All samples taken within these 3 min were pooled for statistical purposes since corticosterone levels generally do not begin to rise until after approximately 3 min of the initiation of a stressor (Wingfield *et al.*, 1982). Subsequent samples were collected at 15, 30, and 45 min from the initial stressor. Birds were restrained between bleeds in opaque cloth bags. At each time point approximately 60 μ l of blood were collected in heparinized microhematocrit tubes after puncturing the alar vein. Cotton stanchied blood flow. Following the last sample birds were examined for molt progression. Samplings during periods of darkness were completed under blue light since it is less likely to penetrate the skulls of birds and therefore

does not reset circadian or circannual rhythms (Oishi and Lauber, 1973).

Sample Processing and Assays

After collection of blood, microhematocrit tubes were sealed on one end with clay and centrifuged at approximately 400g for 5 min. Plasma was then removed and frozen. Corticosterone assays were performed via radioimmunoassay after extraction in dichloromethane as described previously (Wingfield *et al.*, 1992). All samples were equilibrated with small amounts of tritiated corticosterone to determine the recovery of corticosterone in the assay. Interassay and intraassay coefficients of variation were 15 and 8%, respectively (determined using plasma pools).

Data Analysis

Within each season, differences in corticosterone increases over the 45 min of the sampling period (the stress response) at different times of the day were compared using a repeated-measures ANOVA. For analysis of daily and seasonal changes, we chose to examine (1) basal levels as a measure of how corticosterone levels change in the absence of stress, (2) 30-min samples since many previous studies have used 30 min as an index of maximal stress (e.g., Romero *et al.*, 1998b,c,d; Romero and Wingfield, 1998), and (3) integrated corticosterone levels (e.g., area under the corticosterone response curves from Fig. 2) over the 45-min restraint period to determine the amount of corticosterone available to tissues. Seasonal and sex differences in the basal, 30-min, and integrated corticosterone levels were compared using a three-way factorial ANOVA with time of day, season, and sex as factors. Technical difficulties prevented all birds from being sampled during each season, thus precluding a repeated-measures ANOVA.

RESULTS

Corticosterone levels increased in response to the stress of handling and restraint during all three seasons, regardless of the time of day (Fig. 2; $F = 84.21$,

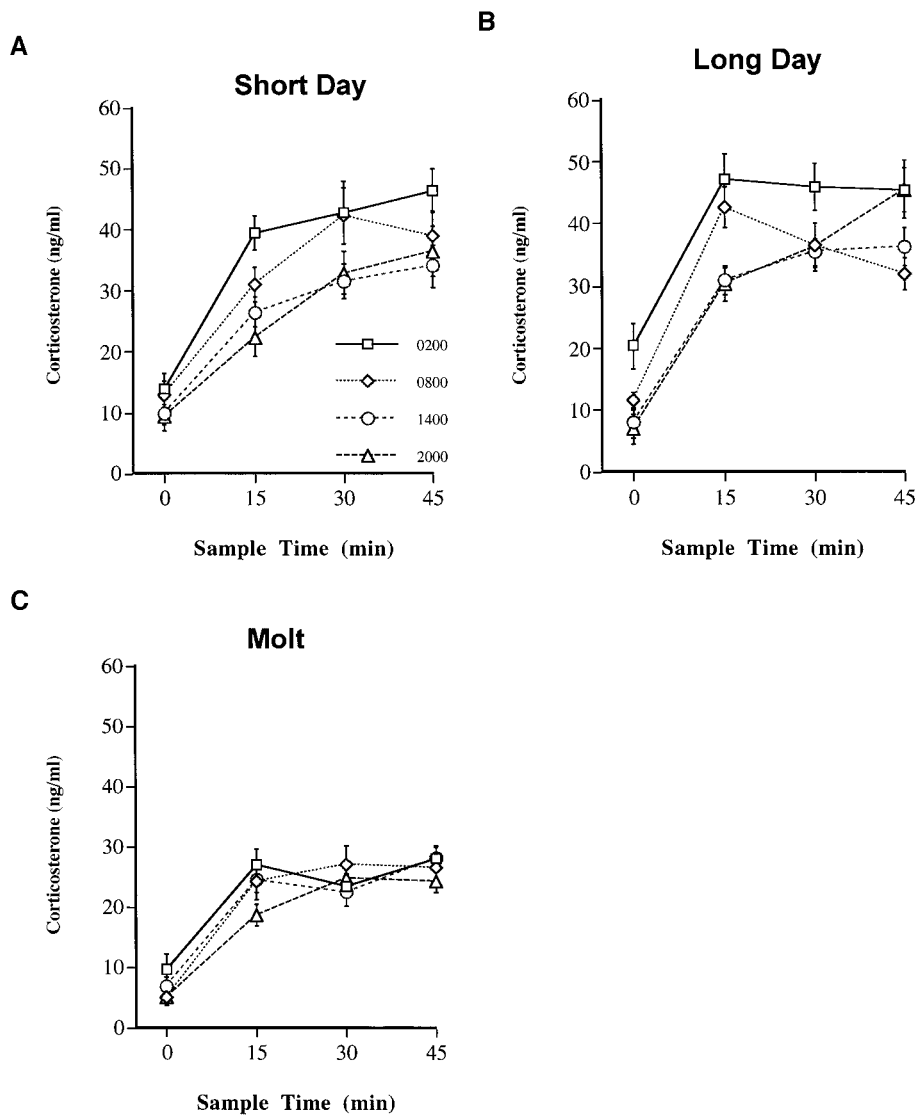


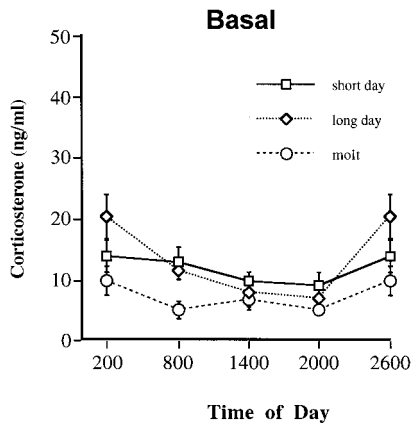
FIG. 2. The increase in corticosterone levels (the stress response) in birds held on a short-day photoperiod (A), a long-day photoperiod (B), and while undergoing a prebasic molt (C). Symbols for the hour of sampling in B and C are identical to A. For each sample $N = 18$ (9 males and 9 females) at each time of day and during each season.

$df = 3$, $P < 0.0001$ during the simulated winter; $F = 90.47$, $df = 3$, $P < 0.0001$ during the simulated summer; and $F = 94.11$, $df = 3$, $P < 0.0001$ during molt).

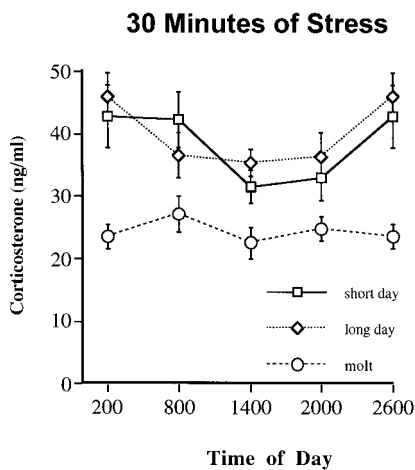
Both basal and 30-min stress-induced levels showed distinct daily and seasonal rhythms (Fig. 3). Basal titers were lowest during the day and highest at night during all three seasons ($F = 7.10$, $df = 3$, $P < 0.0002$), and there was a significant reduction, albeit more pronounced at 08:00, in corticosterone levels during molt ($F = 7.85$, $df = 2$, $P < 0.0006$). These

results were mimicked in the 30-min stress samples. There was a distinct daily rhythm in corticosterone levels during both the simulated winter and summer ($F = 2.9$, $df = 3$, $P < 0.036$), although this rhythm seems to disappear during molt. Furthermore, the reduction in corticosterone levels during molt is more pronounced at 30 min than basally ($F = 19.96$, $df = 2$, $P < 0.0001$). The total amount of corticosterone released also varies daily and seasonally, with less corticosterone released during the day and during

A



B



C

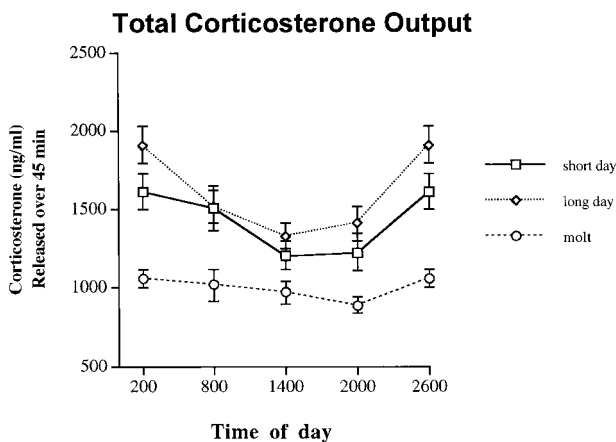


FIG. 3. Seasonal and daily differences in basal corticosterone levels (A), 30-min corticosterone levels (B), and the total corticosterone released over 45 min (C). Values for basal and 30-min corticosterone levels were taken from the data shown in Fig. 2, and total cortico-

molt ($F = 8.08$, $df = 3$, $P < 0.0001$ and $F = 32.52$, $df = 2$, $P < 0.0001$ for daily and seasonal effects, respectively).

Males and females did not differ in their corticosterone responses at basal levels or at 30 min ($F = 0.0001$, $df = 1$, $P = 0.99$ and $F = 2.27$, $df = 1$, $P = 0.13$ for basal and 30-min corticosterone levels, respectively). However, there was a significant difference in the total amount of corticosterone released, with males releasing more total corticosterone than females ($F = 8.65$, $df = 1$, $P < 0.004$).

DISCUSSION

Sex Differences

Differences in the stress response between sexes seem to depend upon the time of year animals are sampled. In free-living birds, several studies have found differences between males and females during breeding (e.g., Wingfield, 1985a,b; Wingfield *et al.*, 1994; O'Reilly, 1995), but other studies have failed to find these differences early in the breeding season or at other times of the year (e.g., Astheimer *et al.*, 1995; Romero *et al.*, 1997, 1998a). It appears, therefore that the stress response in free-living males and females vary only while birds are actively breeding. Since captive birds rarely breed (and didn't do so in this study), a sexual difference should not be anticipated and was not found in this study in either basal or stress-induced corticosterone levels at 30 min, nor was a difference found in other studies examining daily rhythms in captive birds (Marra *et al.*, 1995; Breuner *et al.*, 1999). Furthermore, starlings may not show a sex difference at any season since baseline levels in wild-caught birds do not vary by sex (Dawson and Howe, 1983). There was a difference in this study, however, between the total amount of corticosterone secreted by

sterone released was computed by integrating corticosterone stress responses from the data shown in Fig. 2. $N = 18$ (9 males and 9 females) for each time of day and during each season. Samples taken at 2:00 are double-plotted at 26:00 in order to show the complete 24-h rhythm.

males and females. This is primarily a result of male and female differences in corticosterone levels at 15 and 45 min of the stress response, although it is puzzling as to why males and females should have different corticosterone levels at 15 and 45 min, but not at 30 min.

Daily Rhythms

Captive starlings appear to have a distinct daily rhythm in basal and stress-induced corticosterone levels, as well as in total corticosterone released, throughout most of the year. Only basal levels during molt do not vary over the course of the day. Other studies have also found daily rhythms of basal corticosterone in captive western screech owls (Dufty and Belthoff, 1997), pigeons (Joseph and Meier, 1973), white-throated sparrows (Dusseau and Meier, 1971), and white-crowned sparrows (Breuner *et al.*, 1999). Another study, however, did not find a daily rhythm in white-crowned sparrows (Marra *et al.*, 1995).

In all of the above studies where corticosterone varied daily, basal corticosterone levels were highest during the inactive period and lowest during the active period. The results from this study support these earlier results and furthermore indicate that the rhythm is independent of photoperiod. Furthermore, together with results from Breuner *et al.* (1999), it is clear that levels are low throughout the active period. This pattern is in contrast to the typical mammalian rhythm where glucocorticoid levels peak at the beginning of the active period and remain elevated for several hours (Dallman *et al.*, 1993). Since the daily rhythm in basal glucocorticoids is believed to regulate energy utilization (Dallman *et al.*, 1993), this suggests that birds and mammals may differ in glucocorticoid function and substrate mobilization during the first few hours of the active period.

Few avian studies have examined whether stress elevates corticosterone differently depending upon the time of day. In rats, plasma corticosterone rises to the same level whether basal levels are at their peak or trough (Dallman *et al.*, 1993). This response appears to be different in birds. Both we and Breuner *et al.* (1999) found a distinct daily rhythm in both peak stress-induced corticosterone levels and the total amount of corticosterone released. It is clear that captive starlings

show a robust stress response to handling and restraint at all times of the day and throughout the year, but when examining both the 30-min (Fig. 3B) and the total amount of corticosterone released in response to these stressors (Fig. 3C), the stress response is significantly higher at night than it is during the day. Although it is currently unknown whether corticosteroid binding proteins in the blood also vary in a daily manner in these species (thereby providing a possible buffer when corticosterone levels are higher), these results suggest that tissues are exposed to higher levels of stress-induced corticosterone during the inactive period. If so, birds may require more corticosterone when inactive than when active to successfully cope with the stressful stimulus (e.g., the need to increase glucose mobilization and redirect behavior).

Seasonal Changes

A multitude of studies, using a variety of free-living avian species, have found seasonal changes in corticosterone release (for a review, see Wingfield, 1994). The most dramatic differences appear to be between breeding and the prebasic molt. In a variety of arctic passerines, for example, both basal and stress-induced corticosterone levels are dramatically elevated during breeding when compared to the prebasic molt (Romero *et al.*, 1998b,c,d), and free-living starlings also had their lowest baseline corticosterone levels during molt (Dawson and Howe, 1983).

It has proven difficult, however, to duplicate these seasonal differences in captive birds. For example, Breuner *et al.* (1999) did not find any differences in corticosterone response in white-crowned sparrows held on short- and long-day photoperiods, and corticosterone levels in American kestrels failed to change during a prebasic molt (Rehder *et al.*, 1986). White-throated sparrows held in outdoor aviaries did show seasonal variations in corticosterone levels, with the lowest seasonal values during the prebasic molt (Dusseau and Meier, 1971), but white-crowned sparrows held in outdoor aviaries failed to show any seasonal rhythms (Romero and Wingfield, 1999). Although starlings in this study held on short- and long-day photoperiods did not show differences in basal, stress-induced levels after 30 min, or total corticosterone

output, each of these measures was significantly lower during a prebasic molt.

One potential problem is that the seasonal order of bleeding was the same for all birds. Molting starlings may have lower corticosterone levels because they had already been through the experimental procedure several times before and no longer recognized the handling procedure as a stressor. Evidence from other studies showing a reduced response during molt (e.g., Romero *et al.*, 1998c), however, makes this suggestion unlikely.

Nonetheless, for the first time it appears that we can now reliably duplicate at least part of the seasonal cycle in corticosterone levels in the laboratory. This will provide us the opportunity to explore why corticosterone levels vary seasonally. Several current hypotheses, for example, might explain why corticosterone levels are regulated seasonally [such as regulating gonadal regression and recrudescence (Chaturvedi and Suresh, 1990) or preventing corticosterone from having a deleterious effect on feather deposition during the molt] and these can now be tested.

ACKNOWLEDGMENTS

We thank Alison Chumnavech and Michael Reed for help in bleeding animals. This work was supported by a grant from Tufts University (to L.M.R.), Grant No. IBN-9612534 from the National Science Foundation (to L.M.R.), and an undergraduate fellowship from the Howard Hughes Medical Foundation (to L.R.H.).

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