Rapid Behavioral Response to Corticosterone Varies with Photoperiod and Dose

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The magnitude of the adrenocortical response to stress can be modulated by a variety of environmental and physiological factors, such as daylength and body condition. To determine the consequences of this modulation for the organism, one also needs to investigate behavioral sensitivity to glucocorticoids. We examined the behavioral response of Gambel's white-crowned sparrows (*Zonotrichia leucophrys gambelii*) to elevated glucocorticoids. Using a behavioral assay in which a rapid and transient dose of corticosterone (CORT: the avian glucocorticoid) rapidly increases perch hopping, we first investigated the photoperiodic regulation of this behavioral response. Intermediate levels of CORT (∼24 ng/ml), which increased activity in sparrows exposed to a long-day (breeding) photoperiod, had no behavioral effect in sparrows exposed to a short-day (winter) photoperiod. Hence, the neural mechanisms which regulate the behavioral response to CORT appear to be less sensitive under a winter photoperiod. Using the same behavioral assay, we also measured a dose-response curve for CORT's effects on activity in sparrows exposed to the long-day photoperiod. Intermediate levels (24 and 40 ng/ml) increased activity to threefold background levels, whereas high physiological levels (65 and 97 ng/ml) had no effect. Given that the behavioral response does not increase linearly with CORT, we can no longer assume that modulation of the adrenocortical response to stress will result in linear changes in behavior. © 2000 Academic Press

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In wild vertebrates, environmental perturbations may rapidly increase circulating glucocorticoids. Evidence from several vertebrate classes suggests that glucocorticoid levels secreted in response to a stressor depend on physiological and environmental factors, including body condition, social status, and season (Demas and Nelson, 1996; Dunlap and Wingfield, 1995; Paolucci, Esposito, Di Fiore, and Botte, 1990; Ronchi, Spencer, Krey, and McEwen, 1998; Sapolsky, 1987; Smith, Wingfield, and Veit, 1994; Wingfield, 1994). Early in the day, for example, white-crowned sparrows (*Zonotrichia leucophrys gambelii*) show higher peak plasma corticosterone (CORT) levels in response to handling and restraint than they do in the afternoon and night (Breuner, Wingfield, and Romero, 1999). Similarly, at the beginning of the breeding season, white-crowned sparrows secrete more CORT in response to capture and handling than they do during the winter.

Although the stress-response is increasingly well studied, several critical questions remain unanswered. First, do behavioral and physiological responses to CORT also change with environmental or physiological factors? While the adrenocortical response to stress has been well characterized, it is only one step in the cascade from experience of a stressor to changes in organismal behavior and physiology. There are many downstream factors, such as level of corticosteroid binding globulins, receptor number, and second messenger signaling, which affect the behavioral and physiological outcome of a CORT increase. We hypothesize that these downstream processes are modulated by environmental and physiological factors in a similar manner as CORT secretion.

Second, how do increasing levels of CORT modify physiology and behavior? Work in mice and rats suggests that the dose-response curve for CORT is an inverted-U-shaped curve, with maximal response occurring at intermediate levels of CORT (Diamond, Bennett, Fleshner, and Rose, 1992; Kavaliers, Perrot-Sinal, and Ossenkopp, 1997; Sandi, Venero, and

TABLE 1

CORT Dose and Behavioral Information

Dose No.	Vehicle	CORT in mealworm	Plasma CORT data				Behavioral data[e]	
			Year[b]	No. birds	CORT 7 min after ingestion[c]	ANOVA[d]	Year	No. birds
1	None[a]	No CORT	1995	12	7.45 ± 1.13	a, b	1997	6
2	Peanut oil	No CORT	1995	7	4.65 ± 0.75	a	1997, 1998	9, 7
3	DMSO	No CORT	1995	12	8.42 ± 1.33	a, b	1995, 1996	3, 8
4	Peanut oil	4 μg	1995	7	10.05 ± 1.99	b	1997	6
5	DMSO	4 μg	1995	12	24.38 ± 3.25	c	1995, 1996	3, 8
6	Peanut oil	8 μg	1997	11	38.47 ± 5.55	d	1997, 1998	9, 7
7	Peanut oil	14 μg	1997	6	65.42 ± 10.45	e	1997, 1998	9, 7
8	DMSO	20 μg	1995	8	97.11 ± 9.12	f	1996	9

[a] Uninjected mealworms.
[b] Doses 1, 3, 5, and 8 tested in one group of birds, all other 1995 treatments tested in a second group.
[c] ng/ml; mean ± SEM; doses 2–5 and 8 have been published previously in Breuner *et al.,* 1998.
[d] Factorial ANOVA: $F = 46.81$; $df = 7$, $P < 0.0001$, different letters denote significant differences.
[e] For data and statistics, see Fig. 2.

Guaza, 1996). Previous work in the white-crowned sparrow suggested that activity level responds to increasing CORT with an inverted-U-shaped curve as well (Breuner, Greenberg, and Wingfield, 1998), but only two doses of CORT were tested; a more thorough study is needed.

We examined the above questions by experimentally manipulating levels of plasma corticosterone in white-crowned sparrows. In response to elevated CORT, sparrows show a rapid (within 15 min) increase in activity, as measured by perch hopping (Breuner *et al.,* 1998). Using the perch-hopping assay, we (1) quantified the effect of photoperiod (season) on activity following the ingestion of CORT, and (2) quantified activity following ingestion of several different amounts of CORT. Our data suggest that the behavioral response to CORT is down-regulated under winter photoperiods, similar to the regulation of the adrenocortical response to stress, and that CORT affects activity with an inverted-U-shaped curve, where only intermediate levels of CORT increase activity above baseline levels. Together, these data suggest that the response to a stressor is significantly regulated not only at the adrenocortical level, but also downstream, at the neural level.

METHODS

Animals

Gambel's white-crowned sparrows were captured in eastern Washington State during fall migration

(September 15–October 1, 1994, 1995, 1996, and 1997). Sparrows were housed in outdoor aviaries at the University of Washington until January, when they were brought indoors to avoid photostimulation (housed under 8L:16D). During experiments to measure circulating CORT levels, sparrows were housed communally in environmental chambers (2.4 × 1.7 × 2.2-m rooms with temperature (20°C) and light control (8L:16D or 20L:4D)). During the behavioral trials, sparrows were housed in isolation boxes (0.5 × 0.33 × 0.5 m; 20L:4D or 8L:16D). Bird chow, wild bird seed, and water were available *ad libitum*; mealworms were fed only as part of the experiments. Although baseline CORT levels in white-crowned sparrows are static throughout daylight hours (Breuner *et al.,* 1999), behavioral responses to CORT may vary over the 20 h of daylight. Therefore, all experiments were done between 09:00 and 14:00.

Effect of Photoperiod

We recorded changes in perch-hopping activity in response to 0 and 4 μg CORT ingestion (CORT dissolved in DMSO: doses 3 and 5, Table 1) under both long-day (20L:4D) and short-day (8L:16D) photoperiods. The two photoperiods mimic natural photoperiods experienced by sparrows on their breeding and wintering grounds, respectively. To record perch hopping, cages were equipped with two perches, each attached to a microswitch; the microswitches were connected to a computer running LabView (National Instruments Corp.), that recorded hops/minute. Each

bird was tested with each treatment only once. To account for daily variation in behavior, perch hopping was recorded before and after mealworm ingestion. Thirty minutes after a mealworm was placed in a covered dish inside the cage, baseline perch hopping activity was recorded for 15 min. From outside the isolation box, the lid on the mealworm dish was raised, allowing the sparrow access to the mealworm. After the sparrow had eaten the entire mealworm, perch-hopping activity was recorded for the subsequent hour. Trials were excluded if the bird did not consume the entire mealworm within 1 min of initially grabbing it.

To correct for daily variations in activity, total hops from each of the four 15-min periods during the hour after mealworm ingestion (f) were divided by total hops from the initial 15 minutes before mealworm ingestion (i). Data were log-transformed, $\log(1 + f/i)$, and repeated-measures ANOVA was used to compare treatment effects (control vs CORT) under both long- and short-day photoperiods. Tukey's HSD post hoc test identified differences within photoperiod. Relative activity (f/i) was used instead of percentage change (($(f - i)/i * 100$) because transformation of the data was not possible after the percentage change calculation.

Dose Response

We recorded changes in perch hopping in response to eight different treatments (doses 1–8, Table 1) in sparrows under long-day photoperiods (20L:4D). Perch hopping was recorded and analyzed as above, but only the first 15 min of postingestion activity is reported here (there were no differences in activity during the last 45 min of recording). The data for these experiments were collected from several individual experiments performed in different years (Table 1). Moreover, some treatments were repeated among individuals and some were not (e.g., doses 2, 6, and 7 were tested in the same 16 animals, whereas doses 3 and 5 were tested in a separate group of 11 animals). Thus, for all potential statistical tests assumptions of independence are violated. However, for the purposes of analysis we treated the data as independent, so that we could analyze the data with a factorial ANOVA (differences between groups were identified with Fisher's PLSD post hoc analysis). This decision is supported by two factors: first, several doses (2, 3, 5, 6, and 7) were tested in multiple years, and for none of them did the behavioral response vary by year; second, a secondary analysis (repeated-measures

ANOVA) of doses tested within the same animals supports the findings of the factorial ANOVA in which independence was assumed.

Corticosterone Delivery

CORT was administered in a noninvasive, nonstressful manner by feeding CORT-injected mealworms to white-crowned sparrows (see Breuner *et al.,* 1998, for a fuller description). CORT (Sigma) was dissolved in peanut oil or dimethyl sulfoxide (DMSO). Data obtained delivering CORT with both vehicles are included in this study because there is no effect of vehicle alone on perch hopping or endogenous levels of circulating CORT (Breuner *et al.,* 1998). CORT administered using either vehicle reaches peak levels in the blood within 7 min of mealworm ingestion and returns to baseline by 60 min.

To determine CORT levels after mealworm ingestion, seven different treatments were injected into mealworms (0–20 μg CORT/mealworm), and circulating CORT levels were measured in the sparrows 7 min after eating the mealworm. For vehicle and dose information, see Table 1. Circulating CORT levels from five of the treatments have been published previously (doses 2–5 and 8; Breuner *et al.,* 1998), but perch-hopping data were only published for three of those doses (doses 3, 5, and 8). To best describe the dose-response curve for this behavior, we tested each of the doses previously determined, and created three more (doses 1, 6, and 7). Sparrows were housed in individual cages in environmental chambers (8L:16D), with 4–10 birds per chamber. Thirty minutes before the trial started, the injected mealworm was placed in a covered dish inside the cage. The mealworm became accessible when we pulled a string attached to the lid of the dish from outside the chamber. Seven minutes after the sparrow consumed the mealworm, we punctured the wing vein with a 26-gauge needle and collected the blood sample into heparinized microcapillary tubes. Each blood sample was obtained within 3 min of the investigators' entering the chamber. Plasma was separated from the blood sample by centrifugation and stored at $-20°$C until assayed.

Levels of circulating CORT were log-transformed ($\log(x + 1)$) to correct for heteroscedasticity (Zar, 1984) and compared statistically with a factorial ANOVA. Differences between groups were identified with Fisher's PLSD post hoc analysis. We had to assume independence of each treatment to complete analysis.

To test whether photoperiod has an effect on circulating CORT levels after mealworm ingestion, we fed

mealworms injected with three different CORT solutions (0, 8, and 14 μg CORT in peanut oil) to sparrows under breeding ($n = 7$) and wintering ($n = 6$) photoperiods (20L:4D and 8L:16D, respectively), and measured circulating CORT levels 7 min after ingestion. Results were analyzed with a repeated-measures ANOVA, treating dose of CORT as a within-factor variable (repeated among individuals), and photoperiod as a between-factor variable (not repeated).

Hormone Assay

We determined plasma levels of CORT by radioimmunoassay (described in detail by Wingfield, Vleck, and Moore, 1992). Plasma samples of 10–20 μl were equilibrated with 2000 cpm of tritiated CORT (for determination of percentage recovery following extraction of each sample) and diluted to 200 μl with distilled water. After equilibration, samples were extracted with 4 ml of redistilled dichloromethane. The dichloromethane was evaporated under nitrogen, and samples were reconstituted in 550 μl PBSG buffer. Samples of 200 μl were assayed in duplicate, with 100 μl of each sample taken to determine recovery after extraction. Bound and free fractions were separated by addition of dextran-coated charcoal. Recoveries after extraction were 75–95% (measured for each sample independently and adjustments to the final assayed concentration made accordingly). Interassay variation was less than 12%.

RESULTS

Effect of Photoperiod

The behavioral response to CORT is not consistent between summer and winter photoperiods (Fig. 1). Whereas 4 μg of CORT significantly increased activity in birds exposed to the long-day photoperiod, the same dose of CORT had no effect in sparrows exposed to the short-day photoperiod. Under the long-day photoperiod, CORT increased activity significantly within the first 15 min (repeated-measures ANOVA: $F = 6.111$, $df = 1$, $P < 0.04$; Tukey's HSD post hoc analysis), and activity levels fell back to background by the end of the hour. Under the short-day photoperiod, CORT had no effect on activity throughout the duration of the hour of recording ($F = 0.965$, $df = 3$, $P = 0.428$).
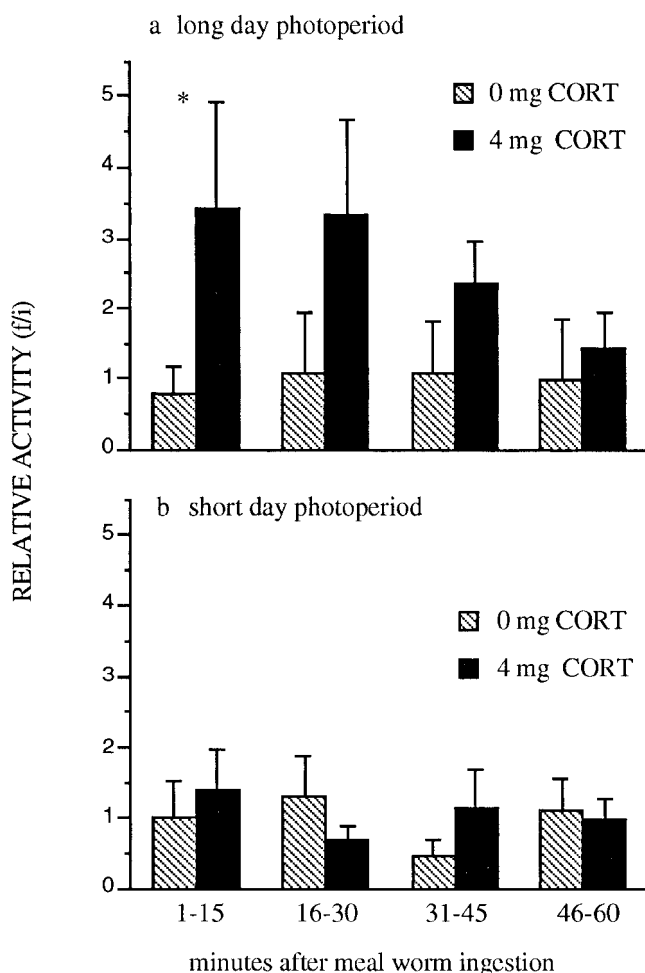

FIG. 1. Behavioral response to CORT varies with photoperiod. Relative activity (*f/i*) due to mealworm ingestion in long-day (a, $n = 11$) and short-day (b, $n = 8$) sparrows. 1, no change in activity in response to hormonal treatment. Figures show mean $\pm$ SEM. *$P < 0.05$.

Dose Response

All circulating levels of CORT measured in this study fell within the range of CORT measured in free-living sparrows in response to capture and handling (Astheimer, Buttemer, and Wingfield, 1994; Romero, Ramenofsky, and Wingfield, 1997). As shown in Fig. 2, relative activity was not significantly affected by the act of eating a mealworm (dose 1), nor by eating mealworms injected with peanut oil or DMSO alone (doses 2 and 3). In addition, 4 μg of CORT in peanut oil, which did not significantly elevate circulating CORT, did not affect activity. Doses 5 and 6, which increased plasma CORT to 24 and 38 ng/ml, respectively, significantly increased activity. At higher levels
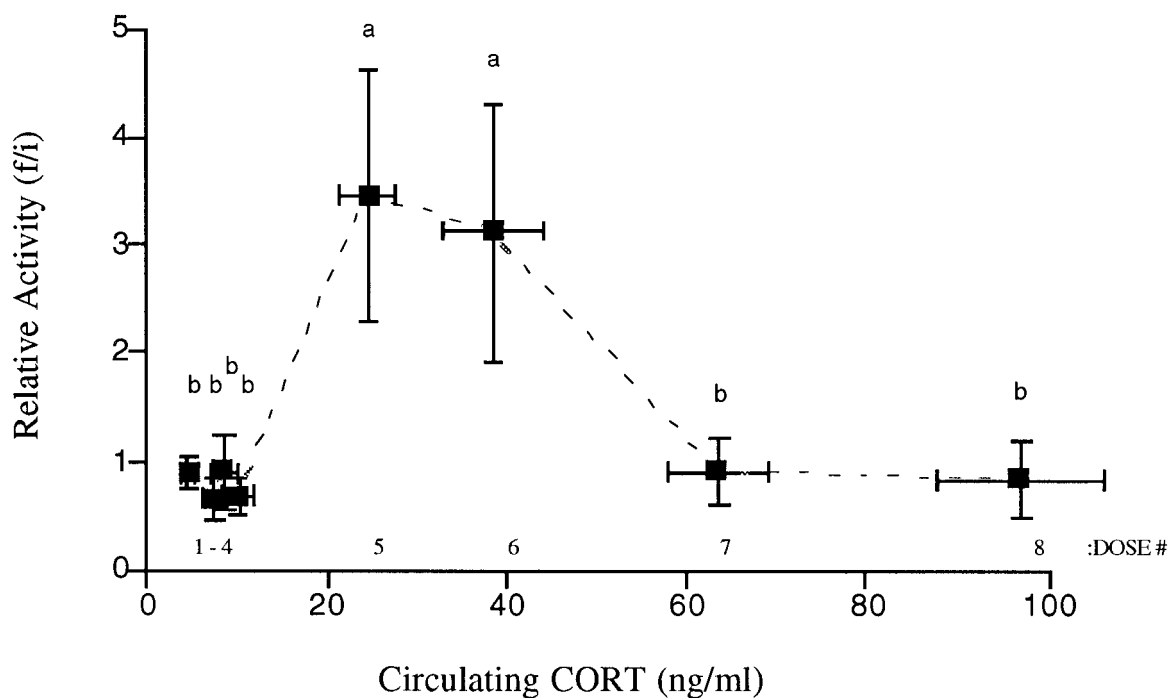
FIG. 2. CORT increases relative activity only at intermediate doses of CORT. Relative activity (*f/i*) within 15 min after mealworm ingestion, as a function of circulating CORT levels at 7 min after mealworm ingestion. 1, no change in activity in response to hormonal treatment. Mean ± SEM is presented for both axes. Different letters denote significant differences in relative activity. Behavioral response to doses 3, 5, and 8 have been published previously in Breuner *et al.,* 1998.

(65 and 97 ng/ml), activity was not significantly different from hopping by control birds (all points compared with a factorial ANOVA: $F = 3.191$, $df = 7$, $P < 0.005$). Thus, perch-hopping activity was significantly elevated only at intermediate levels of circulating CORT.

Plasma Titers of CORT

The vehicle used to deliver CORT had no effect on endogenous CORT levels. Baseline CORT in captive white-crowned sparrows range from 4 to 10 ng/ml (Breuner *et al.,* 1999); CORT levels after ingestion of an uninjected mealworm (dose 1), a mealworm containing peanut oil (dose 2), or DMSO (dose 3) all fall within that range. Vehicle does, however, effect the efficacy of CORT uptake from the gut after mealworm ingestion; 4 μg CORT dissolved in DMSO increased plasma levels of CORT to 24 ng/ml, whereas the same dose of CORT in peanut oil did not significantly increase CORT above baseline levels (10 ng/ml). DMSO is used in veterinary medicine to carry drugs across epithelia, so this difference is not surprising. Given this difference in efficacy of CORT transfer, we

graphed the behavioral changes as a function of the circulating level of CORT, instead of the amount of CORT in the mealworm. Except for the lowest peanut oil CORT dose (dose 4), all other CORT doses raised CORT to levels that were significantly different from baseline and from each other. For a summary, see Table 1.

Photoperiod had no effect on plasma CORT level after mealworm ingestion (Fig. 3). Repeated-measures ANOVA indicated that while different doses of CORT in the mealworm significantly altered plasma CORT ($F = 16.190$, $df = 2$, $P < 0.0001$), there was no effect of daylength on circulating CORT level ($F = 0.052$, $df = 1$, $P = 0.824$).

DISCUSSION

Effect of Photoperiod

Our data show that long-day and short-day sparrows receiving the same amount of CORT (4 μg) showed different behavioral responses: perch hopping increased in long-day birds but not in short-day birds.
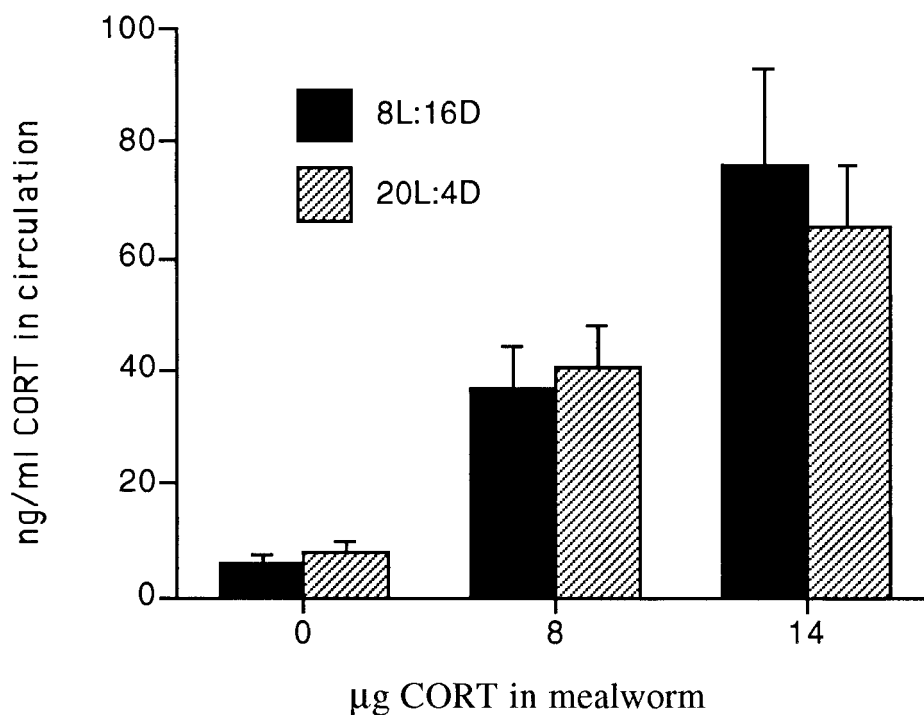
FIG. 3. Photoperiod does not affect CORT levels after mealworm ingestion. CORT levels 7 min after mealworm ingestion are similar under both photoperiods (breeding: 20L:4D, and wintering: 8L:16D).

Several authors have demonstrated that the sensitivity of the hypothalamo-pituitary-adrenal (HPA) axis to stress is modulated seasonally in the white-crowned sparrow (Astheimer *et al.,* 1994; Romero *et al.,* 1997): wintering birds subjected to a standardized protocol of capture and handling had lower levels of circulating CORT than breeding birds—suggesting that the HPA axis is less sensitive to stress in the winter. Our data suggest that white-crowned sparrows modulate their sensitivity to stress at a second level in the cascade from stressor to behavioral change, and thus conclusions regarding the seasonal modulation of the stress response cannot be drawn from hormonal data alone. Not only is the adrenocortical response to stress down-regulated during winter as compared to the breeding season, but the behavioral response to CORT appears to also be less sensitive during winter photoperiods. The functional significance of this regulation is unknown. Several other species regulate the adrenocortical response to stress in the opposite manner, secreting less CORT in response to a stressor during the breeding season than in winter (Wingfield, O'Reilly, and Astheimer, 1995; Wingfield *et al.,* 1992). This is thought to decrease the likelihood of abandoning the nest before absolutely necessary. Much of the work in Gambel's white-crowned sparrow was com-

pleted near the beginning of the breeding season, when weather is still unpredictable on the arctic tundra (the breeding grounds for Gambel's white-crowned sparrow). Sparrows may be in a more opportunistic, irruptive state at this time, ready to abandon their territories if bad weather should arrive. This pattern is seen in the mountain white-crowned sparrow (*Zonotrichia leucophrys oriantha*), which often abandon their breeding territories early in the season under stormy weather conditions (Hahn and Morton, 1995). In the Southwestern United States, where Gambel's white-crowned sparrows spend the winter, the weather is not as severe, and a robust stress response may not be as important.

Several mechanisms may account for this seasonal change in behavior. Increased neural levels of 11β-hydroxysteroid dehydrogenase during winter months, for example, could decrease the amount of CORT available to activate receptors. Alternatively, CORT receptor number may be lower in wintering birds. Since this membrane receptor has not yet been cloned, molecular studies quantifying protein and mRNA levels are not yet possible, but equilibrium saturation-binding experiments and autoradiography studies should be able to identify seasonal changes in quantity and localization of receptors. A third possi-

bility is that increased levels of circulating corticosteroid-binding globulin (CBG) could alter the level of free CORT available to cross the blood-brain barrier. However, there are several reasons why this is probably not the explanation for the behavioral differences documented in this paper. First, there is a seasonal difference in CBG levels in free-living sparrows (Romero and Wingfield, 1998), but it is in the opposite direction than would be predicted from this experiment. A increase in circulating CBG in wintering sparrows would be necessary to reduce the behavioral response to CORT. Wintering sparrows in the wild actually have lower levels of CBG than breeding sparrows (Romero and Wingfield, 1998). Second, preliminary experiments on captive white-crowned sparrows show no significant seasonal difference in CBG levels (Breuner and Wingfield, unpublished data). Hence, the change in behavioral sensitivity seen in short-day sparrows is probably not due to an increase in CBG.

Dose Response

As CORT dose increases, perch hopping does not increase linearly. Rather, only intermediate levels of CORT activate behavior, and high levels have no effect. This inverted-U relationship has been described in other systems, such as CORT's effects on hippocampal neuron firing rate (Diamond et al., 1992), serotonin levels, and passive-avoidance behavior (Kovacs, Telegdy, and Lissak, 1977). There has been a well-described inverted-U relationship between stress and learning since 1908 (Yerkes and Dodson, 1908). These dose-response curves may result from the two intracellular corticosteroid receptors being differentially occupied at increasing levels of circulating CORT (Diamond et al., 1992).

Traditionally, glucocorticoids were thought to play a role in the delayed response to stress (hours to days after the onset of the perturbation). Over the past decade, evidence from multiple classes of vertebrates has demonstrated rapid behavioral effects of glucocorticoids (Breuner et al., 1998; Orchinik, Murray, and Moore, 1991; Sandi et al., 1996), suggesting that these hormones may be involved in the early stages of the stress response, within minutes of activation of the HPA axis. It is probable that in white-crowned sparrows, CORT acts through a membrane-mediated mechanism to rapidly increase locomotor activity. At present, there is no known mechanism for a membrane receptor which only effects a change at intermediate levels. Interestingly, this inverted-U-shaped dose response curve is not only evident in long-term

experiments, as mentioned above, but also appears in recent experiments examining rapid effects of CORT in mammals. CORT rapidly increases locomotor activity in the rat, but only at intermediate doses (Sandi et al., 1996). In the mouse, intermediate doses of CORT decrease preference for the scent of an estrous female in a Y maze, 10 min after injection with CORT (Kavaliers et al., 1997); high and low levels did not decrease preference for an estrous female. When considering the mechanisms behind behavioral responses that occur within 15 min of hormone application, one needs to look beyond the classical genomic effect of the intracellular receptors.

What is the functional significance of this inverted-U-shaped dose-response curve for an organism in its natural environment? Environmental perturbations can vary from trivial to severe. A predator attack that kills a mate, for example, may not activate the HPA axis to the same extent as a severe storm that decimates food resources. It would be beneficial for an animal to be able to initiate behavioral responses appropriate for the severity of the stressor. Poor weather conditions may decrease food availability, and slightly increase circulating levels of CORT. This in turn may cause increased foraging. Alternatively, a severe storm may increase CORT to a much higher level. An increase in activity and foraging may be delayed until the storm decreases in severity and CORT decreases to intermediate levels; then the animal can initiate food-searching behaviors. It would be interesting to measure CORT levels in sparrows under different environmental conditions. It is known that CORT levels in white-crowned sparrows increase in response to inclement weather (Wingfield, Moore, and Farner, 1983), but a more detailed analysis of CORT levels, weather conditions, and the resulting behavioral responses is needed. This dose-response curve may provide a mechanism through which stressors of different severity can result in different behavioral responses.

ACKNOWLEDGMENTS

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