General and Comparative Endocrinology 119, 60–68 (2000)
doi:10.1006/gcen.2000.7492, available online at http://www.idealibrary.com on IDEAL®

Daily and Seasonal Variation in Response to Stress in Captive Starlings (*Sturnus Vulgaris*): Glucose

Luke Remage-Healey and L. Michael Romero

Department of Biology, Tufts University, Medford, Massachusetts 02155

Accepted March 13, 2000

We investigated the seasonal and daily variation in plasma glucose levels in response to stress in captive wild starlings. Starlings were captured from the wild during the winter, held on short days (11L:13D, mimicking winter), and then shifted to long days (19L:5D, mimicking summer). Birds were maintained on long days until they began a prebasic molt, the energetically costly replacement of feathers. Throughout the daily cycle we took a basal blood sample within 3 min of disturbance and took subsequent blood samples at 15 and 30 min. Birds were kept in cloth bags (restraint) between bleeds. Experiments were repeated during all three seasons (short day, long day, and molt). Starlings showed no sexual difference in circulating glucose levels at any time of the day or in any season. Both basal and stress-induced glucose levels, however, showed a significant effect of season, with birds held on long days exhibiting the highest levels, molting birds showing intermediate levels, and birds held on short days exhibiting the lowest levels. Basal glucose levels also showed a circadiel rhythm in all three seasons. Regardless of season, however, the daily peak in basal levels occurred at midday with nadir in the middle of the scotophase. This trend was paralleled in the overall weights of the birds. Although stress-induced glucose levels showed no circadiel rhythm, the stress-induced elevation of glucose above baseline showed a significant daily rhythm, indicating that stress elevated plasma glucose levels only during the scotophase in all three seasons.

Key Words: circadiel; circannual; stress; corticosterone; molt; energetics.

Glucocorticoids have been widely shown to be associated with the stress response in birds and mammals. Corticosterone (CORT; the most common glucocorticoid in birds; Holmes and Phillips, 1976) effects behavior and alters the physiology of many avian species in such a way that seems to increase chances of survival in stressful situations (Wingfield *et al.*, 1994). Interestingly, some birds have exhibited circadiel (daily) and seasonal rhythms in stressed and nonstressed levels of circulating CORT (Meier and Fivizzani, 1975; Bruener *et al.*, 1999). This suggests that some species show differential sensitivities to stress during different parts of the day and across different seasons. We have recently demonstrated similar results in wild starlings (*Sturnus vulgaris*), which show seasonal and daily rhythms in circulating CORT as well as a robust elevation of CORT during stress (Romero and Remage-Healey, 2000).

With this in mind, we examined *in vivo* one well-known physiological consequence of long-term exposure to glucocorticoids. Glucocorticoids have been classically shown to inhibit glucose uptake into tissues of the gut and periphery (Norris, 1997). This action is primarily through antagonizing the effects of insulin, the primary hormone responsible for in-

0016-6480/00 $35.00

creasing cellular glucose uptake universally throughout the body (Houssay *et al.*, 1954; Malchoff *et al.*, 1982; Strack *et al.*, 1995). The majority of glucose mobilization resulting from glucocorticoid stimulation takes place in hepatocytes (Leung and Munck, 1975). For example, high doses of cortisol, a mammalian glucocorticoid, increased hepatic gluconeogenesis in dogs (Goldstein *et al.*, 1993). Glucocorticoids also act on nonhepatic tissues, including stimulating fatty-acid mobilization from adipose cells (Malchoff *et al.*, 1982; Gregoire *et al.*, 1991; Rudman and DiGirolamo, 1971), initiating muscle breakdown at high doses (Tomas *et al.*, 1979), and inhibiting glucose uptake in skeletal muscle (Leung and Munck, 1975). In sum, research to date suggests that long-term exposure to glucocorticoids serves to mobilize endogenous glucose stores to aid in stressful situations (Munck *et al.*, 1984).

A direct causal link between elevated glucose levels and acute (as compared to chronic) glucocorticoid release, however, has not been firmly established. The effects of acute stress on circulating glucose levels has been studied in laboratory rats (Curi *et al.*, 1990; Brown *et al.*, 1982), golden perch (Carragher and Rees, 1994), and captive bats (Widmaier and Kunz, 1993). Each of these species exhibits a marked hyperglycemic stress response closely associated with, although not unambiguously linked to, stress-induced glucocorticoid release. In the majority of these studies glucose concentrations had not risen significantly above basal levels until approximately 15–30 min after the initial stressor. For this reason our study examined basal, 15-min, and 30-min stress-induced glucose levels to determine the glucose stress response in starlings.

Plasma glucose levels have also been demonstrated to exhibit seasonal and daily rhythms in a number of species. A small mammal native to the Andes range, *Abrothrix andinus*, shows a seasonal rhythm in glucose uptake when faced with harsh winter conditions (Bozinovic and Iturri, 1990). *Abrothrix andinus* shows a dramatic increase in intestinal uptake of glucose in winter as compared to summer seasons. A circadiel rhythm in circulating glucose has been observed in white rock chickens, and this rhythm is closely associated with metabolic fluctuations through a 48-h period (Siegel *et al.*, 1976).

With this in mind, our study focuses on three questions: (1) What is the response of glucose to stress? (2) Is there seasonal variation in circulating glucose levels in both stressed and nonstressed animals? (3) Is there daily variation in both basal and stress-induced circulating glucose levels?

MATERIALS AND METHODS

Animals

Wild European starlings (*Sturnus vulgaris*) were captured with mist nets in late December in eastern Massachusetts. It is difficult to age birds at this time of year (Pyle, 1997) so it was likely a mixture of hatch-year and older birds. The birds were housed communally in large, indoor flight aviaries on a 11L:13D light cycle. All rooms were climate-controlled and maintained at 25°C. Upon initiation of the experiment, five male and six female starlings were transferred to individual cages. Light cycles were adjusted throughout the experiment to induce seasonal changes in the anatomy and physiology of the birds. To mimic winter, starlings were maintained on the short-day light cycle (11L:13D) they were experiencing in the wild at time of capture. Once all short-day samples had been taken the birds were switched to a long-day light cycle (19L:5D) and allowed to acclimate to this change for 2 weeks before sampling (Fig. 1). This long-day period (mimicking summer) lasted for approximately 6 weeks at which time the starlings began their prebasic molt, which replaces all flight and body feathers. Sampling was again suspended for the first 2 weeks of molt. The light cycle was maintained at 19L:5D throughout the molting period (approximately 90 days; Cabe, 1993). Food and water were provided *ad libitum*. All experiments were performed according to AALAC guidelines and approved by the Institutional Animal Care and Use Committee at Tufts University.

Stress/Sampling Protocols

Birds were subjected to the stress of handling and restraint as they were taken out of their cages for blood sampling. Samples were taken at 3-h intervals

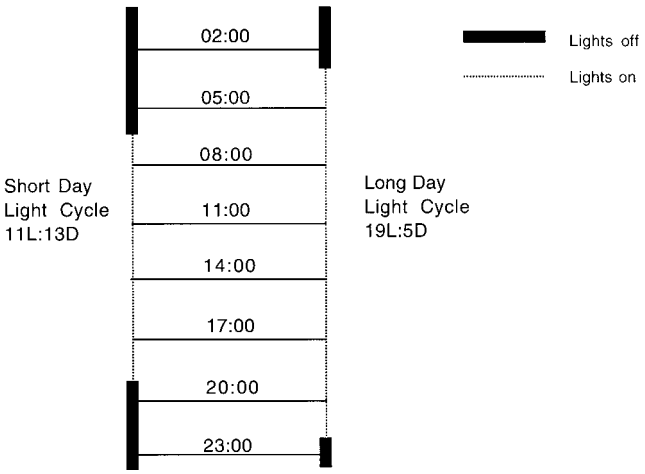


FIG. 1. Seasonal light cycles shown with sampling times. The prebasic molting light cycle is a continuation of the long-day light cycle.

over the 24-h daily cycle (Fig. 1). Blood sampling was limited so that no more than one sampling time (02:00, 05:00, 08:00, 11:00, etc.) was taken in a 36-h period to allow the birds time to replenish blood volumes and recover from the stress of the previous sampling (hematocrit levels remained unchanged throughout the experiment; unpublished data). Within 3 min of entering the room all birds were sampled to yield a basal glucose level, since it has been shown that a significant increase in corticosterone release into the bloodstream does not occur until approximately 3 min after the initial stressor (Romero *et al.,* 1998) and that stress-induced hyperglycemia is not significant until 15–30 min following acute stress (Curi *et al.,* 1990; Brown *et al.,* 1982; Carragher and Rees, 1994; Widmaier and Kunz, 1993). Subsequent samples were taken at 15 and 30 min from the initial stressor. This established a time course in order to compare stressed levels with basal levels of glucose. Birds were restrained between bleeds in opaque cloth bags. At each time point the alar vein was punctured and approximately 60 μl of blood collected into microhematocrit capillary tubes. Cotton was applied to stop blood flow. At the end of sampling birds were weighed and, during the molting season, examined for molt progression. At sampling times during lights-off a light bulb screened for blue light was used to aid experimentation. Since blue light is less likely to penetrate the skull of birds (Oishi and Lauber, 1973), we could sufficiently illuminate the room to take blood samples without stimulating photoreceptors and thereby avoid altering the light cycle of the starlings.

Glucose Assay

Hematocrit tubes were centrifuged within 12 h of sampling at approximately 400*g* for 5 min to allow separation of erythrocytes from blood plasma. Samples were refrigerated prior to centrifugation. After separation, plasma was aliquotted into Eppendorf tubes and frozen. Levels of glucose were determined using a hexokinase/NAD assay combined with spectrophotometer absorbance reading (Glucose HK Assay Kit, SIGMA Chemical, St. Louis, MO). Interassay variability was 5.3%.

Statistics

Glucose data were analyzed using a repeated-measures ANOVA for the effects of season, time of day, and sex on basal and stress-induced glucose levels in blood plasma. Circadiel changes in glucose levels and weight during each season were analyzed separately, with a Bonferonni correction used to adjust α levels from the ANOVA. Seasonal weights were measured using a repeated-measures ANOVA.

RESULTS

Sex Differences

Male and female starlings showed no difference in baseline glucose levels ($F = 0.91$, $df = 1$, $P = 0.25$) or in stress-induced glucose levels ($F = 1.02$, $df = 1$, $P = 0.161$) across all three seasons. There was also no interaction of sex with season in circulating glucose levels ($F = 0.83$, $df = 1$, $P = 0.23$; data not shown). Data from males and females were consequently combined for all subsequent analyses.

Weight Fluctuations

There were significant circadiel rhythms in birds held on short days (Fig. 2; $F = 6.139$, $df = 7$, $P <$

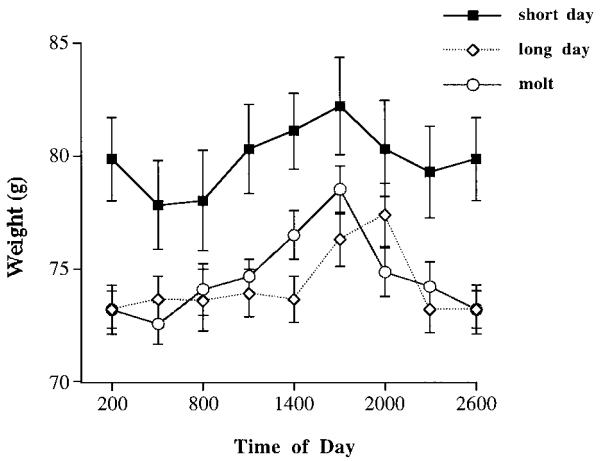


FIG. 2. Seasonal and circadiel changes in body weight in captive starlings held on short days and long days and undergoing molt. Samples taken at 02:00 are double-plotted at 26:00 to show a complete daily rhythm ($n = 11$ for each time point).

0.0001), long days (Fig. 2; $F = 5.452$, $df = 7$, $P < 0.0001$), and while undergoing molt (Fig. 2; $F = 9.863$, $df = 7$. $P < 0.0001$). All three seasons showed a peak in weight measurements late in the photophase, preceding lights-off. There was also a seasonal difference in weight measurements (Fig. 2; $F = 5.265$, $df = 2$, $P = 0.011$) with birds held on short days elevated significantly above both birds held on long days and undergoing molt.

Basal Glucose

Daily variations during both long-day (Fig. 3; $F = 8.11$, $df = 7$, $P < 0.0001$) and molting (Fig. 3; $F = 2.74$, $df = 7$, $P = 0.013$) seasons showed statistically significant rhythms in nonstressed, basal glucose. Furthermore in birds held on short days, the circadiel rhythm in basal glucose was nearly statistically significant (Fig. 3; $F = 2.47$, $df = 7$, $P = 0.024$; after Bonferonni correction the required P value was 0.017). Basal glucose levels peaked at midday in birds held on both short days and while undergoing molt. Glucose levels in birds held on long days peaked just after lights on and remained high throughout the day. Glucose levels in all three seasons gradually declined during lights-off to a trough in the middle of the scotophase. As well as a daily effect there was also a seasonal effect on basal levels of plasma glucose (Fig. 3; $F = 33.33$, $df = 2$, $P < 0.0001$). The birds held on short days exhibited the lowest overall basal glucose levels, significantly lower than both the molting and long-day seasons. Glucose levels in molting birds, while exhibiting a mid-range glucose secretion, were still lower than the basal glucose levels in birds held on long days. Finally, birds held on long days showed the most extreme daily changes in basal glucose levels.

Stress-Induced Glucose

Stress-induced glucose levels (from samples taken 30 min after entering the room) showed no significant circadiel variation during short days (Fig. 4; $F = 0.324$, $df = 7$, $P = 0.941$), long days (Fig. 4; $F = 1.083$, $df = 7$, $P = 0.382$), or molt (Fig. 4; $F = 2.133$, $df = 7$, $P = 0.05$; the Bonferonni corrected P value was 0.017). However, a significant seasonal effect was seen in stress-induced glucose levels that mimicked the seasonal difference in basal values (Fig. 4; $F = 23.57$, $df = 2$, $P < 0.0001$). Short-day values were again the lowest, followed by molting, while long-day birds exhibited the highest stress-induced levels of circulating glucose.

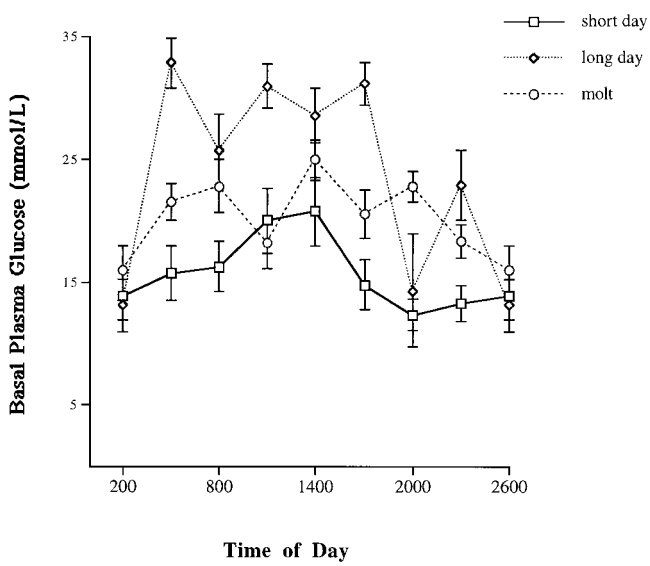


FIG. 3. Basal long-day, short-day, and molt glucose levels vs time of day. Samples taken at 02:00 are double-plotted at 26:00 to show a complete daily rhythm ($n = 11$ for each time point).

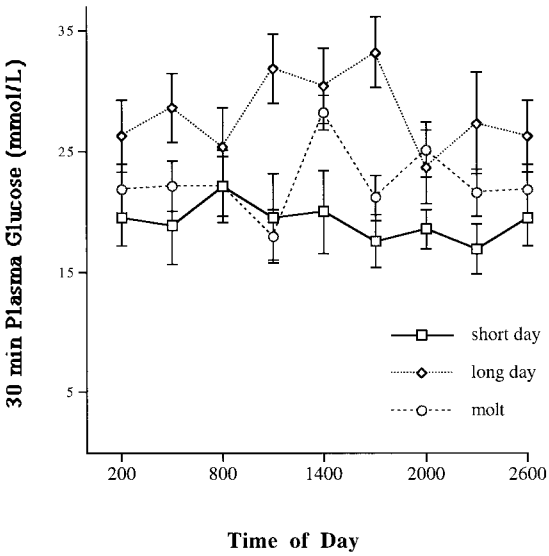


FIG. 4. Stress-induced glucose levels across all three seasons. Samples taken at 02:00 are double-plotted at 26:00 to show a complete daily rhythm ($n = 11$ for each time point).

Glucose Stress Response

Changes in glucose levels in response to stress are defined as the difference between basal and 30-min glucose levels (Fig. 5). The elevation of glucose levels in response to stress exhibited significant variation over the course of the day. Stress-induced elevations of glucose levels generally occurred during lights-off (scotophase) in all three seasons, but responses during the photophase varied seasonally. In birds maintained on short days, where lights-on occurred at 07:00 and lights-off at 18:00 (Fig. 1), glucose levels only increased in response to stress during early and late photophase as well as during the entire scotophase (Fig. 5A). There was no significant glucose response to stress during middle of the photophase during this season. Consequently, a clear daily rhythm in stress elevations of glucose is present in birds maintained on short days ($F = 2.72$, $df = 7$, $P < 0.0099$).

In birds maintained on long days stress elevated glucose at the end of both photophase and scotophase (lights-on at 03:00; lights-off at 22:00, Fig. 1), but the response attenuated rapidly just after lights-on and remained low through most of the photophase ($F = 2.78$, $df = 7$, $P = 0.0083$; Fig. 5B). A similar trend occurred in molting birds (housed under the long-day light regimen, Fig. 1). The peak in the glucose response occurred during the brief scotophase (Fig. 5C), followed by a decrease during early lights-on with little response for the entire photophase ($F = 2.50$, $df = 7$, $P < 0.0182$).

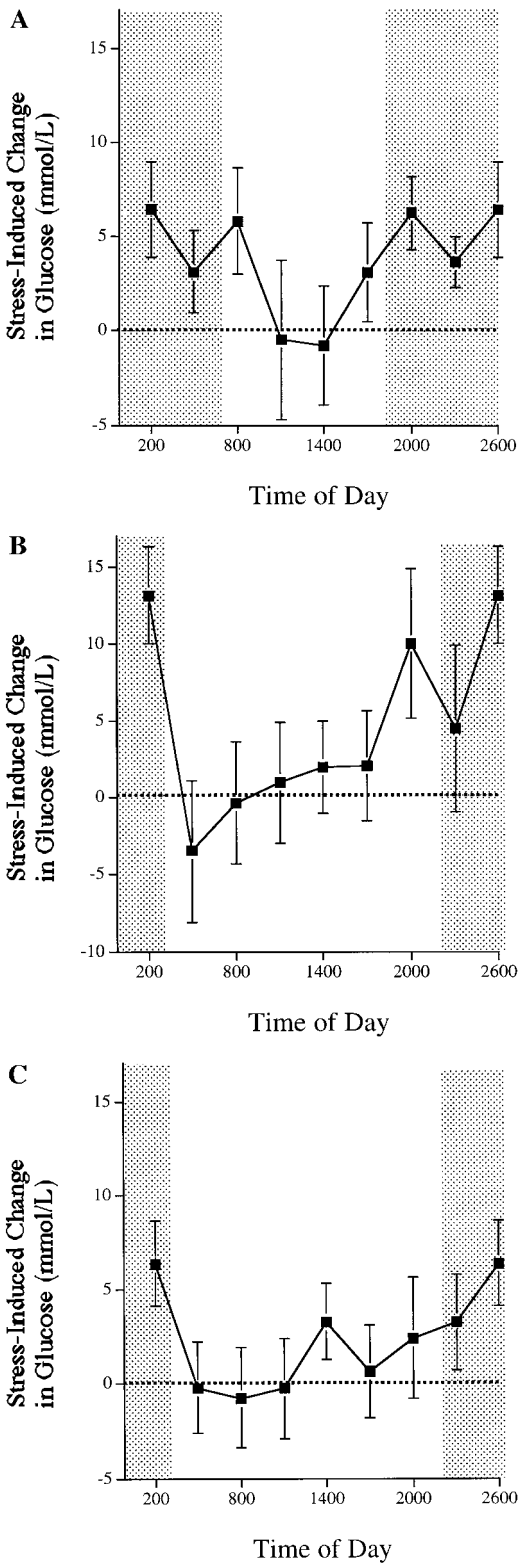
DISCUSSION

Sexual Differences

Starlings are sexually monomorphic, yet may exhibit some sexual differences in circulating CORT levels (Romero and Remage-Healey, 2000). However, as shown here, there is no sexual difference in glucose levels in captive starlings. There is also no interaction of sex difference with season, suggesting that male and female birds do not differ in metabolic glucose needs across winter and summer or while undergoing molt. Interestingly, to our knowledge no previous studies have examined sexual differences in circulating glucose in an avian species, so the comparative aspects of these data remain unclear.

Weight Fluctuations

Daily rhythms in body weight peaked close to the end of the photoperiod in each of the three seasons. This suggests that starlings are increasing food intake later in the day to anticipate the overnight fast. Such rhythms have been found in breeding redpolls (Romero *et al.*, 1997) as well as in captive house sparrows (unpublished data) and have been closely associated with overall fat scores in one of those (redpolls). At all points in the daily cycle body weights in birds held on short days were elevated compared to body weights in both birds held on long days and during the prebasic molt. During the simulated winter (short days) the birds are not required to prepare for the breeding season (long days) nor are they sustaining a costly molt (Cabe, 1993), and so this season may be a time of energy caching into fat and muscle deposits for use in more demanding months of the year.



Seasonal Glucose

Both basal and stress-induced glucose levels were highest when starlings were exposed to a simulated summer (long days). This suggests the birds have elevated metabolic demands during the summer months of the year. In the wild, elevated glucose levels during the summer breeding season may be required for a variety of behaviors including territory defense, nest building, egg laying, feeding offspring, and other breeding / nesting activity (Cabe, 1993; Feare, 1984). In the laboratory, under the influence of a longer photoperiod, the birds may be preparing for the energetic demands of the breeding season without actually breeding in captive conditions. Alternatively, a longer photoperiod gives the birds a more lengthy active period and so elevated glucose levels may reflect increased energy demands during the longer days of the year.

During their prebasic molt starlings maintained plasma glucose levels at an intermediate range (below levels during long days but above levels during short days). Molt can be the most expensive time of the year in terms of energy usage (even in comparison with reproductive energy requirements) in species that undergo rapid full-scale prebasic molts (Murphy and King, 1992), so it is interesting to note that glucose levels during molt are below levels of birds held on long days.

Glucose was at a seasonal minimum during the simulated winter (short-day), possibly indicating that energetic needs are reduced during the winter season. The birds are not breeding during this season, nor are they sustaining a costly molt (Cabe, 1993), so winter glucose levels may be reduced because energy expenditures are at their yearly low. Also, though the starlings held on short days are experiencing a winter light regimen, the experimental rooms are climate-controlled so increased metabolic thermogenesis during this simulated winter is not required. Therefore, while adjusting to the shortened active period, with-

FIG. 5. Circadiel rhythms in the difference between basal and stress-induced plasma glucose levels in captive starlings held on short days (A), long days (B), and during a prebasic molt (C). Samples taken at 02:00 are double-plotted at 26:00 to show a complete daily rhythm ($n = 11$ for each time point).

out a concurrent decrease in temperature, the birds may experience lower energetic demands in comparison with the summer (breeding) and molting seasons.

Circadiel Rhythms in Basal Glucose

A clear circadiel rhythm in basal glucose suggests that starlings exhibit varying metabolic demands over the course of the day. In all three seasons glucose peaked during the day, when the birds are eating and most active. Such rhythms have been reported in bird and mammal species alike, the majority being associated with rhythms in feeding patterns and food availability (Widmaier and Kunz, 1993; Siegel *et al.,* 1976). Clearly, the existence of these rhythms shows that energy stores are mobilized at times during the day when the animals need them most and stored during more restful periods. Even birds held in captivity, provided with food *ad libitum,* are rationing their endogenous glucose stores during the 24-h cycle.

It has been proposed that a major function of the CORT rhythm is to cue important physiological changes in order to maintain a daily rhythm in systems that glucocorticoids affect (Bruener *et al.,* 1999). Long-term elevations in CORT are clearly involved in mobilization of glucose stores (Norris, 1997), so a simultaneous examination of the two daily rhythms, CORT and glucose, may elucidate any rhythmic association between the two. Dallman *et al.* (1993), for instance, theorize that metabolic needs and energy mobilization are being partially driven by the rhythm in basal corticosterone. Our data support this hypothesis. CORT rhythms in previously examined avian species peak during the inactive night period just before the onset of daylight and decrease during the daylight hours (Breuner *et al.,* 1999; Meier and Fivizzani, 1975). A suggestion of a similar rhythm occurs in fish (Pavlidis *et al.,* 1999). Our examination of starling CORT patterns are consistent with these earlier studies (Romero and Remage-Healey, 2000). When basal glucose rhythms are compared to the basal CORT rhythm, however, it appears that daily CORT and glucose variations are out of phase (see Fig. 6 for example in birds held on long days). CORT is elevated during scotophase while glucose is at nadir, and CORT is at its trough during the day when glucose is at its peak. This disparity between the two rhythms

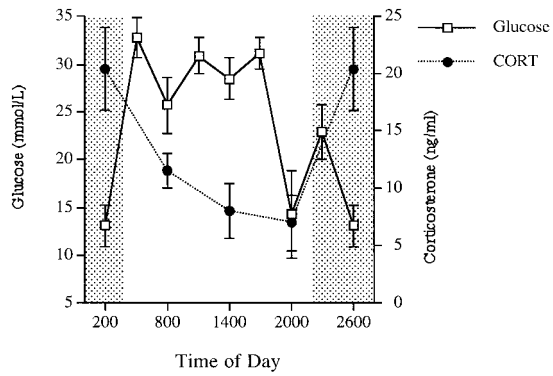


FIG. 6. Circadiel rhythms of glucose compared to CORT in captive starlings held on long days. Glucose data repeated from Fig. 3 and CORT data from (Romero and Remage-Healey, 2000).

may indicate that either there is a lag between a CORT peak and the resulting physiological action or that the two rhythms display a reciprocal relationship in starlings.

Circadiel Rhythms in Stress-Induced Glucose

Although starlings exhibited a daily rhythm in basal glucose levels, stress-induced levels failed to show such a pattern. Stress-induced CORT showed a circadiel rhythm (Romero and Remage-Healey, 2000), so the lack of a glucose rhythm suggests another system may be involved in regulating stress-induced levels of glucose. A likely candidate is the autonomic nervous system, since, in addition to glucocorticoid release, stressful stimuli immediately cause the activation of sympathetic ganglia which can also affect glucose release (Havel and Taborsky, 1989). It is unclear at this point which system is the dominant regulator of endogenous glucose release during the stress response in birds.

Studies conducted in both mammals and birds have shown that a more robust stress response in CORT occurs during the trough of the daily CORT cycle (Engeland *et al.,* 1977; Kant *et al.,* 1986; Bradbury *et al.,* 1991; Bruener *et al.,* 1999). This indicates a heightened sensitivity to stress when CORT levels are at their lowest during the day. This trend is paralleled here in the glucose stress response in starlings. Stress primarily elevated glucose during the inactive scotophase, a

time when glucose levels have reached nadir. It is unclear, however, why glucose levels would be resistant to stress effects during the day. Perhaps this lack of stress-induced glucose elevation is due to the variability associated with food-intake during the active photophase. A bird that has just eaten a meal and is trying to store glucose for an upcoming fast may not be able to turn on a strong glucose stress response until this storing activity has subsided. Another possibility is that birds exhibit a heightened sensitivity to the effects of CORT during the inactive scotophase. Since these starlings are presumably eating throughout the day (food was available *ad libitum*), insulin may never fully clear the plasma of glucose until the inactive period. This would result in tonically elevated insulin levels during the day. Since insulin and CORT are known to work in opposition (Dallman *et al.*, 1993), insulin may be preventing CORT from stimulating hepatic gluconeogenesis. Whether this mechanism can explain the lack of a glucose response to stress in our data remains to be tested, but interestingly, few studies of glucose responses to stress have been performed during an animals active period.

Alternatively, the effects of stress may be blunted during the day. Many studies have shown that stress-induced elevations of CORT are highest during the inactive phase (Breuner *et al.*, 1999; Widmaier and Kunz, 1993; Dallman *et al.*, 1987), although this usually occurs at nadir of the CORT circadiel rhythm. The data presented here, however, are opposite what would be predicted from these earlier studies. Glucose generally increases at those times when CORT levels are highest. It thus appears that the interplay between CORT and glucose during stress may be more complex than hitherto appreciated.

ACKNOWLEDGMENTS

This work was carried out with partial support of a science education grant from the Howard Hughes Medical Institute to Tufts University. The authors thank Dr. Michael Reed for assistance with sampling and advice regarding the life history of starlings, Dr. Michelle Gaudette for assistance with assay spectrophotometry, and Dr. Ross Feldberg for comments on data presentation.

REFERENCES

Bozinovic, F., and Iturri, S. J. (1990). Seasonal changes in glucose and tyrosine uptake of *Abrothrix andinus* (critcetidae) inhabiting the Andes range. *Comp. Biochem. Physiol.* **99A**(3), 437–439.

Bradbury, M. J., Cascio, C. S., Scribner, K. A., and Dallman, M. F. (1991). Stress-induced adrenocorticotropin secretion: Diurnal responses and decreases during stress in the evening are not dependent on corticosterone. *Endocrinology,* **128**(2), 680–688.

Breuner, C. W., Wingfield, J. C., and Romero, L. M. (1999). Diel rhythms of basal and stress-induced corticosterone in a wild, seasonal vertebrate, Gambel's white crowned sparrow. *J. Exp. Zool.* **284,** 334–342.

Brown, M. R., Fisher, L. A., Spiess, J., Rivier, C., and Vale, W. (1982). Corticotropin-releasing factor: Actions on the sympathetic nervous system and metabolsim. *Endocrinology* **111**(3), 928–931.

Cabe, P. R. (1993). European starling (*Sturnus vulgaris*). *In* "The Birds of North America" (A. Poole and G. Gill, Eds.), No. 48. The Academy of Natural Sciences, Philadelphia and The American Ornithologists' Union, Washington, DC.

Carragher, J. F., and Rees, C. M. (1994). Primary and secondary stress responses in golden perch, *Macquaria ambigua*. *Comp. Biochem. Physiol.* **107A**(1), 49–56.

Curi, C. M., Ribeiro, E. B., Zaia, C. T., and Dolnikoff, M. S. (1990). Glycemic response to stress stimulation by ether exposure in adrenalectomized rats. *Pharmacol. Biochem. Behav.* **37**(3), 399–403.

Dallman, M. F., Akana, S. F., Cascio, C. S., Darlington, D. N., Jacobson, L., and Levin, N. (1987). Regulation of ACTH secretion: Variations on a theme of B. *Rec. Prog. Horm. Res.* **43,** 113–173.

Dallman, M. F., Strack, A. M., Akana, S. F., Bradbury, M. J., Hanson, E. S., Scribner, K. A., and Smith, M. (1993). Feast and famine: Critical role of glucocorticoids with insulin in daily energy flow. *Front. Neuroendocrinol.* **14**(4), 303–347.

Engeland, W. C., Shinsako, J., Winget, C. M., Vernikos-Danellis, J., and Dallman, M. F. (1977). Circadian patterns of stress-induced ACTH secretion are modified by corticosterone responses. *Endocrinol.* **100,** 138–147.

Feare, C. J. (1984). "The Starling". Oxford Univ Press, Oxford, UK.

Goldstein, R. E., Wasserman, D. H., McGuinness, O. P., Lacy, D. B., Cherrington, A. D., and Abumrad, N. N. (1993). Effects of chronic elevation in plasma cortisol on hepatic carbohydrate metabolism. *Am. J. Physiol.* **264,** E119–E127.

Gregoire, F., Genart, C., Hauser, N., and Remacle, C. (1991). Glucocorticoids induce a drastic inhibition of proliferation and stimulate differentiation of adult fat cell precursors. *Exp. Cell. Res.* **196,** 270–278.

Havel, P. J., and Taborsky, G. J., Jr. (1989). The contribution of the autonomic nervous system to changes of glucagon and insulin secretion during hypoglycemic stress. *Endocr. Rev.* **10,** 332–350.

Holmes, W. N., and Phillips, J. G. (1976). The adrenal cortex of birds. *In* "General, Comparative, and Clinical Endocrinlogy of the Adrenal Cortex" (I. Chester-Jones and I. W. Henderson, Eds.), Academic Press, London. pp. 293–420.

Horner, H. C., Packan, D. R., and Sapolsky, R. M. (1990). Glucocorticoids inhibit glucose transport in cultured hippocampal neurons and glia. *Neuroendocrinology* **52,** 57–64.

Houssay, B. A., Rodriguez, R. R., and Cadeza, A. F. (1954). Prevention of experimental diabetes. *Endocrinology* **54,** 550–553.

Kant, G. J., Mougey, E. H., and Meyerhoff, J. L. (1986). Diurnal variation in neuroendocrine responses to stress in rats: Plasma ACTH, β-LPH, corticosterone, prolactin, and pituitary cyclic AMP responses. *Neuroendocrinology* **43,** 383–390.

Leung, K., and Munck, A. (1975). Peripheral actions of glucocorticoids. *Ann. Rev. Physiol.* **37,** 245–272.

Malchoff, D. M., Maloff, B. L., Livingston, J. N., and Lockwood, D. H. (1982). Influence of dexamethasone on insulin action: Inhibition of basal and insulin stimulated hexose transport is dependent on length of exposure *in vitro. Endocrinology* **110,** 2081.

Meier, A. H., and Fivizzani, A. J. (1975). Changes in the daily rhythm of plasma corticosterone concentration related to seasonal conditions in the white-throated sparrow. *Proc. Soc. Exp. Biol. Med.* **150,** 356–362.

Munck, A., Gurye, P. M., and Holbrook, N. J. (1984). Physiological functions of glucocorticoids in stress and their relation to pharmacological actions. *Endocr. Rev.* **5**(1), 25–44.

Murphy, M. E., and King, J. R. (1992). Energy and nutrient use during moult by white-crowned sparrows *Zonotrichia luecophrys gambeli. Ornis Scand.* **23,** 304–313.

Norris, D. O. (1997). Secretion and action of glucocorticoids. *In* "Vertebrate Endocrinology", pp. 308–311. Academic Press, Boston.

Pavlidis, M., Greenwood, L., Paalavuo, M., Molsa, H., and Laitinen, J. T. (1999). The effect of photoperiod on diel rhythms in serum melatonin, cortisol, glucose and electrolytes in the common dentex, *Dentex dentex. Gen. Comp. Endocrinol.* **113,** 240–250.

Pyle, P. (1997). "Identification Guide to North American Birds". California Slate Creek Press, Bolinas, CA.

Oishi, T., and Lauber, J. K. (1973). Photoreception in the photosexual response of quail. II. Effects of intensity and wavelength. *Am. J. Physiol.* **224**(4), 880–886.

Romero, L. M., and Remage-Healey, L. (2000). Daily and seasonal variation in response to stress in captive starlings (*Sturnus vulgaris*): Corticosterone. *Gen. Comp. Endocrinol.* **119,** 52–59.

Romero, L. M., Soma, K. K., O'Reilly, K. M., Suydam, R., and Wingfield, J. C. (1997). Territorial behavior, hormonal changes, and body condition in an arctic-breeding song bird, the redpoll (*Carduelis flammea*). *Behaviour* **134,** 727–747.

Romero, L. M., Soma, K. K., and Wingfield, J. C. (1998). Hypothalamic-pituitary-adrenal axis changes allow seasonal modulation of corticosterone in a bird. *Am. J. Physiol.* **274,** R1338–R1344.

Rudman, D., and DiGirolamo, M. (1971). Effect of adrenal cortical steroids on lipid metabolism. *In* "The Human Adrenal Cortex", pp. 241–255. Harper & Row, New York.

Siegel, H. S., Mitchell, B. W., Gould, N. R., Latimer, J. W., and Wilson, R. L. (1976). Circadian rhythms for corticosterone, c.b.c., plasma glucose, heart rate, respiration rate, and body temperature in white rock males. *Proc. Eur. Poult. Conf.* **5,** 1050–1061.

Strack, A. M., Sebastian, R. J., Schwartz, M. W., and Dallman, M. F. (1995). Glucocorticoids and insulin: Reciprocal signals for energy balance. *Am. J. Physiol.* **37,** R142–R149.

Tomas, F. M., Munroe, H. N., and Young, V. R. (1979). Effect of glucocorticoid administration on the rate of muscle breakdown *in vivo* in rats, as measured by urinary excretion of *N*-methylhistidine. *Biochem. J.* **178,** 139–146.

Widmaier, E. P., and Kunz, T. H. (1993). Basal, diurnal and stress-induced levels of glucose and glucocorticoids in captive bats. *J. Exp. Zool.* **265,** 533–540.

Wingfield, J. C., Suydam, R., and Hunt, K. (1994). The adrenocortical responses to stress in snow buntings and Lapland longspurs at Barrow, Alaska. *Comp. Biochem. Physiol.* **3,** 299–306.