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# Corticosterone and insulin interact to regulate plasma glucose but not lipid concentrations in molting starlings

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## Abstract

Captive starlings (*Sturnus vulgaris*) undergoing a prebasic molt were given exogenous insulin (INS) and corticosterone (CORT), to determine how these counterregulatory hormones would affect glucose and triglyceride concentrations during stress. Experiments were conducted at both morning (11:00) and night (23:00) to monitor daily variation in these responses. Concentrations of CORT, glucose, and triglycerides were measured in blood plasma within 3 min of disturbance (basal) and at 40, 70, and 150 min thereafter (stress-induced) to monitor the effect of injecting saline, INS, CORT, or INS + CORT. Saline injection (which included the stress of handling and restraint) increased CORT concentrations, decreased triglycerides, but had no effect on circulating glucose. Daily variation was not evident in CORT or glucose, but concentrations of triglycerides were higher at night than during the day. INS markedly suppressed glucose concentrations, but had no effect on plasma CORT or triglycerides. Glucose levels did not change in response to stress, but exogenous CORT elicited hyperglycemia during the day. Injected CORT also hastened the recovery of glucose concentrations from INS-induced hypoglycemia at night, and had no effect on circulating triglycerides. Basal concentrations of CORT, glucose, and triglycerides exhibited photoperiodic (mimicking seasonal) changes when combined with data from an earlier study in starlings held on long- and short-day photoperiods. During the prebasic molt, all three measurements were lower compared to other photoperiods. Together, these data suggest that glucose and triglycerides concentrations are regulated differently during molt, but INS and CORT maintain their traditional effects.

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## 1. Introduction

Metabolic investment during the prebasic molt makes this period a costly time of year for passerines (Murphy and King, 1992). The full-scale replacement of body and flight feathers involves heavy protein deposition that may require a shift away from using amino acids as energy substrates (Cherel et al., 1988). Studies from wild and captive birds have shown that the basal tone of catabolic hormones such as corticosterone (CORT, the primary glucocorticoid in birds (Holmes and Phillips, 1976)) is reduced during molt vis-à-vis other times of the year (Dawson and Howe, 1983; Romero and Ramage-Healey, 2000; Romero et al., 1998a,b,c). This seasonal rhythmicity provides an opportunity to examine

CORT's metabolic effects during stress when CORT is at both elevated and reduced natural levels throughout the annual cycle.

CORT and insulin (INS) are known to work in opposition in regulating energy stores in birds and mammals alike (Dallman et al., 1993; Houssay et al., 1954; Malchoff et al., 1982; Ramage-Healey and Romero, 2001; Strack et al., 1995). During stress, a rise in plasma CORT is concurrent with increases in glucose concentrations (Brown et al., 1982; Carragher and Rees, 1993; Curi et al., 1990; Ramage-Healey and Romero, 2000; Widmaier and Kunz, 1993) and mobilization of plasma lipids (Bray, 1993; Heald et al., 1965; Hershock and Vogel, 1989; Ramage-Healey and Romero, 2001; Starzec and Berger, 1986).

Although birds reduce CORT output while undergoing molt, it is unclear whether CORT-mobilized energy sources, such as lipids and glucose, are also

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regulated seasonally. Plasma glucose levels during molt are reported to be either reduced or unaffected, depending upon species (Cherel et al., 1988; Remage-Healey and Romero, 2000; Totzke and Bairlein, 1998). Increases in plasma fatty acids (Cherel et al., 1988) and decreases in triglyceride concentrations, a stored form of fatty acids in the plasma (Totzke and Bairlein, 1998) however, suggest that plasma lipids are regulated during molt.

The present study is complimentary to a previous examination of CORT and INS influences on glucose and triglyceride levels during stress in European starlings (*Sturnus vulgaris*) held on both short days (mimicking winter) and long days (mimicking summer, (Remage-Healey and Romero, 2001)). Starlings have distinct daily and photoperiodic rhythms in plasma CORT and glucose concentrations (Remage-Healey and Romero, 2000; Romero and Remage-Healey, 2000) as CORT concentrations are significantly lower during molt. Presently, we address the following questions in starlings undergoing a prebasic molt: (1) What is the result of the antagonism between INS and CORT on stress-induced hyperglycemia and hyperlipidemia in molting starlings? (2) Do these responses vary during the night and day? (3) How do these results from molting birds compare to complimentary data on birds held on short- and long days?

## 2. Materials and methods

### 2.1. Birds

European starlings were captured from the wild during the winter of 1998 in Eastern Massachusetts. The group was a mixture of young and older birds, as some may have been first- or second-year birds (Pyle, 1997). Birds were maintained on a winter light regimen (11L:13D) in indoor flight aviaries to acclimate to captive conditions and 10 birds were transferred to individual cages upon initiation of the study. As described in detail previously (Remage-Healey and Romero, 2001), changes in photoperiod mimicking natural seasons induced physiological and morphological changes in the birds; starting with short days (11L:13D), birds were then shifted to long days (19L:5D) for 6 weeks, after which they began a prebasic molt (replacement of flight and body feathers). Birds were maintained on 19L:5D throughout the molt and the experiment began 2 weeks after molt onset. Birds in this study were identical to the birds used in the companion study (Remage-Healey and Romero, 2001). All rooms were climate-controlled and maintained at 25 °C throughout the study. Food and water were provided ad libitum. All experiments were performed according to AALAC guidelines and approved by the Institu-

tional Animal Care and Use Committee at Tufts University.

### 2.2. Stress/sampling procedures

Initial blood samples for assessing basal concentrations were taken from the alar wing vein within 3 min of entering the experimental chamber (see Wingfield et al., 1994). These samples were only taken from birds receiving saline injection (controls) and assumed equivalent to basal concentrations for all other injections, since all injections took place immediately following basal sampling (see below). Birds were then injected and exposed to handling and restraint stress as described previously (Romero and Remage-Healey, 2000). Briefly, birds were held in opaque cloth bags (restraint) for the first sampling interval and then returned to their cages with subsequent blood samples taken at 40, 70, and 150 min post-injection. After the final sample birds were examined for molt progression and returned to individual cages. Experiments were conducted at 11:00 and repeated at 23:00 since these hours approximate peaks and troughs of the circadian cycles of both CORT and glucose (Remage-Healey and Romero, 2000; Romero and Remage-Healey, 2000). Blue light was used during lights-off sampling since it is less likely to reset endogenous rhythms through photostimulation (Oishi and Lauber, 1973).

### 2.3. Injections

A full description of the injections used for this study was presented previously (Remage-Healey and Romero, 2001). Briefly, saline, INS, CORT, or a combination of INS + CORT was injected within 5 min of entering the experimental chamber. Two doses of INS were used (1.0 and 4.0 IU/kg in 0.85% saline), as well as one dose of CORT (200 µg suspended in peanut oil), and 0.85% saline served as a control. These doses were combined into six treatments: (1) saline; (2) 1.0 IU INS; (3) 4.0 IU INS; (4) saline + 200 µg CORT; (5) 1.0 IU INS + 200 µg CORT; (6) 4.0 IU INS + 200 µg CORT. These INS doses have been shown to produce a strong (4.0 IU) and intermediate (1.0 IU) hypoglycemia up to 2.5 h following injection, and the CORT dose (200 µg) maintains high physiological plasma CORT concentrations for at least 1.5 h (to counter the lasting effects of INS; Remage-Healey and Romero, 2001). All birds received the six treatments at both times of day and individual treatment order was randomized.

### 2.4. Sample processing and assays

At each sampling time approximately 60 µl blood was collected into hematocrit tubes and sealed at one end with clay. Tubes were centrifuged at 400g for 5 min and

plasma was removed and frozen until analysis. CORT was extracted using dichloromethane and concentrations determined with radioimmunoassay as described previously (Wingfield et al., 1992). Plasma glucose was measured using a hexokinase reagent (SIGMA) combined with UV spectrophotometry as described previously (Remage-Healey and Romero, 2000). Triglyceride levels were determined with lipoprotein lipase/ESPA reagent (SIGMA) combined with colorimetric spectrophotometry as described previously (Remage-Healey and Romero, 2001). Interassay variability for CORT, glucose, and triglyceride assays was 8.3%, 9.9%, and 4.7%, respectively, and intraassay variability for CORT was 6.9%.

### 2.5. Statistics

Results were analyzed using multiple repeated measures ANOVA for the effects of injection, time-of-day, and season on basal and stress-induced (40, 70, and 150 min) levels of CORT, glucose, and triglycerides.

## 3. Results

### 3.1. Corticosterone

Endogenous CORT concentrations increased at 40 min but returned to basal by 70 min in response to

stress in birds at 11:00 (Fig. 1a,  $F(3,21) = 4.843$ ,  $p < 0.01$ ), and exogenous CORT further augmented this response and maintained CORT at supraphysiological concentrations for at least 1.5 h (Fig. 1b,  $F(3,21) = 17.077$ ,  $p < 0.0001$ ). Similar changes were seen at 23:00 with both endogenous CORT concentrations (Fig. 2a,  $F(3,18) = 3.793$ ,  $p < 0.03$ ) and after exogenous CORT administration (Fig. 2b,  $F(3,21) = 50.642$ ,  $p < 0.0001$ ).

Molting birds showed no differences between 11:00 and 23:00 in basal CORT concentrations (Table 1,  $F(1,27) = 0.104$ ,  $p = 0.75$ ). Basal CORT concentrations varied with photoperiod, however, when compared with data from a previous study (Remage-Healey and Romero, 2001) with these same birds held on short- and long days (Table 1,  $F(2,46) = 5.762$ ,  $p = 0.006$ ). Both basal and stress-induced concentrations in molting birds were lower than in birds held on short- and long days.

Although it appeared that INS injection resulted in an increased endogenous CORT response to stress compared to control (saline), this trend was not statistically significant (Figs. 1a and 2a,  $p > 0.2$  for all comparisons).

### 3.2. Glucose

Plasma glucose concentrations did not rise in response to stress with control injections at 11:00 (Fig. 1a,  $F(3,21) = 0.672$ ,  $p = 0.58$ ), but administration of exogenous CORT caused a significant hyperglycemic

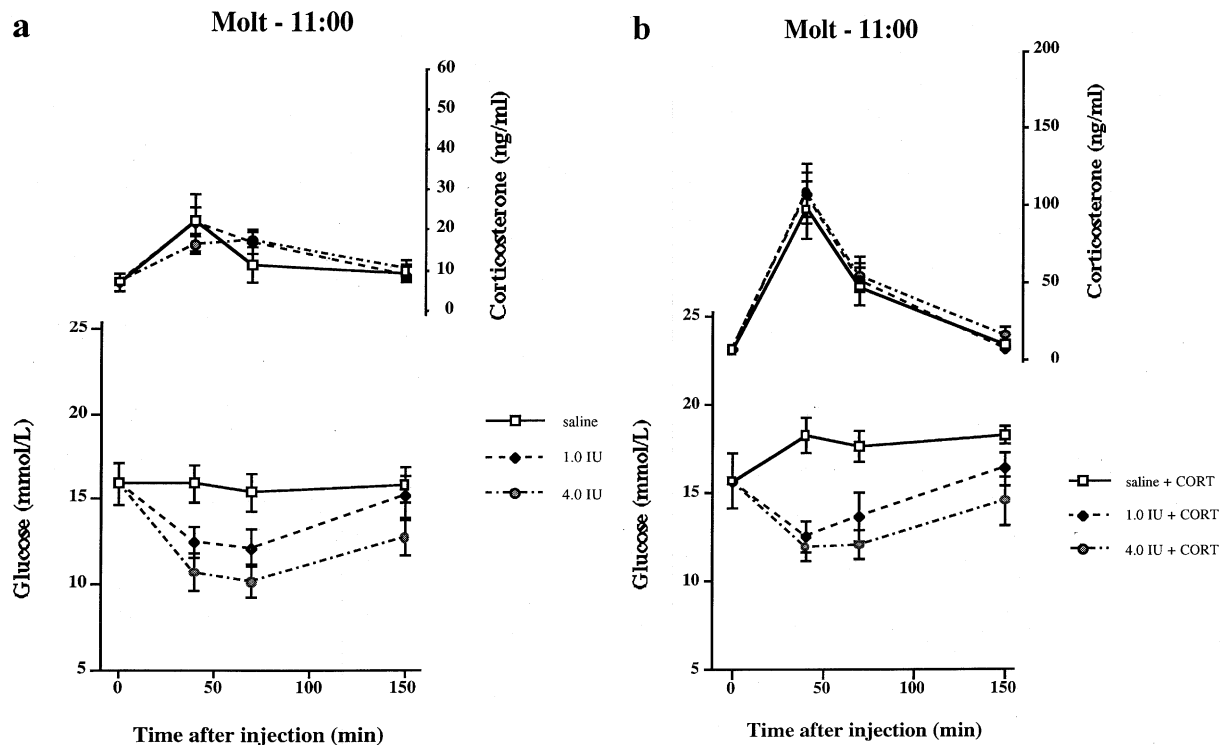


Fig. 1. Glucose and CORT responses to stress after administration of INS (a) or INS + CORT (b) in molting starlings at 11:00. Points represent means  $\pm$  SEM for  $n = 10$ . Note differences in scale for CORT graphs.

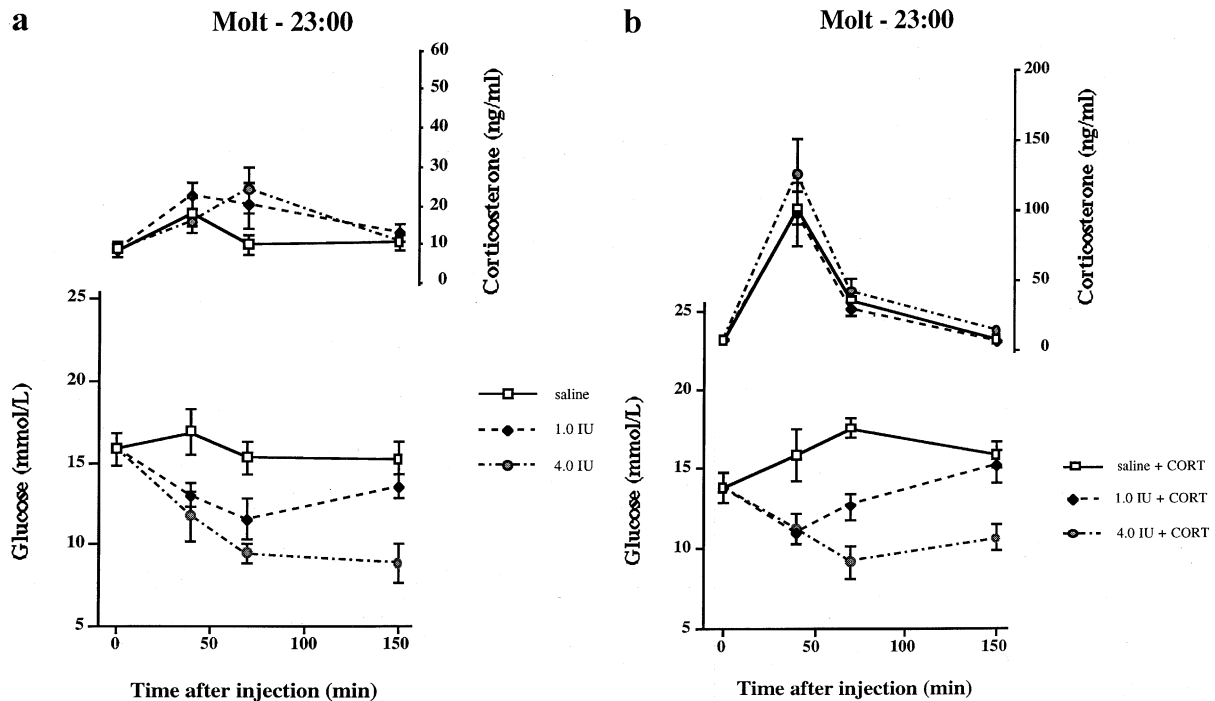


Fig. 2. Glucose and CORT responses to stress after administration of INS (a) or INS + CORT (b) in molting starlings at 23:00. Points represent means  $\pm$  SEM for  $n = 10$ . Note differences in scale for CORT graphs.

Table 1  
Photoperiodic and daily changes in basal CORT, glucose, and triglycerides

Photoperiod	Glucose (mmol/L)		Corticosterone (ng/ml)		Triglycerides (mmol/L)	
	11:00	23:00	11:00	23:00	11:00	23:00
Short day	18.92 $\pm$ 0.85	17.58 $\pm$ 1.80	10.04 $\pm$ 1.12	25.21 $\pm$ 4.60	5.69 $\pm$ 0.54	5.22 $\pm$ 0.79
Long day	18.35 $\pm$ 1.05	15.07 $\pm$ 0.96	10.49 $\pm$ 2.09	16.67 $\pm$ 2.25	3.95 $\pm$ 0.55	3.33 $\pm$ 0.35
Molt	15.90 $\pm$ 1.27	15.86 $\pm$ 1.00	7.21 $\pm$ 1.25	8.72 $\pm$ 1.88	1.98 $\pm$ 0.16	2.57 $\pm$ 0.19

Photoperiodic and daily basal glucose, CORT, and triglyceride concentrations for starlings held on short days, long days, and undergoing molt. Points represent means  $\pm$  SEM for  $n = 10$ . Data for molting birds from present study; for short- and long day from (Remage-Healey and Romero, 2001). The identical 10 birds were used for all photoperiods.

response in comparison to controls that lasted the full 150 min (Fig. 1b,  $F(1, 14) = 9.291$ ,  $p = 0.009$ ). At 23:00 neither stress (Fig. 2a,  $F(3, 18) = 0.538$ ,  $p = 0.66$ ) nor administration of exogenous CORT (Fig. 2b,  $F(1, 14) = 3.60$ ,  $p = 0.078$ ) resulted in hyperglycemia, although the response to exogenous CORT was nearly significant.

In all instances INS administration significantly reduced plasma glucose concentrations at 40 and 70 min in molting birds. INS suppressed glucose dose-dependently at 11:00, with glucose concentrations beginning to recover by 150 min (Fig. 1a, overall insulin effect,  $F(2, 22) = 10.868$ ,  $p < 0.0005$ ; interaction between insulin injection and time course,  $F(2, 44) = 3.49$ ,  $p < 0.04$ ). Similar responses occurred at 23:00, but were not statistically significant (Fig. 2a, overall insulin effect,  $F(2, 38) = 3.017$ ,  $p = 0.061$ ; interaction between insulin injection and time course,  $F(2, 19) = 14.302$ ,

$p < 0.0002$ ). Under different photoperiod regimes, glucose levels did not respond differently to INS injection at either dose or time-of-day (data not shown,  $p > 0.4$  for all interactions between photoperiod and INS).

No changes between day and night in basal glucose concentrations were evident in molting birds (Table 1,  $F(1, 27) = 2.115$ ,  $p = 0.16$ ). However, basal glucose varied with photoperiod at both 11:00 ( $F(2, 23) = 4.58$ ,  $p = 0.02$ ) and 23:00 ( $F(2, 23) = 4.02$ ,  $p = 0.03$ ). Glucose concentrations measured across the entire 2.5 h sampling period also varied according to photoperiod in saline-injected birds at both 11:00 (data not shown,  $F(2, 23) = 6.773$ ,  $p = 0.005$ ) and 23:00 (data not shown,  $F(2, 23) = 3.406$ ,  $p = 0.05$ ). At both times of day the glucose response to saline injection was reduced in molting birds than in birds held on short- or long days. Glucose concentrations in control birds did not differ across photoperiod in response to exogenous CORT

administration at 11:00 (data not shown,  $F(2, 23) = 1.917$ ,  $p = 0.17$ ) but did exhibit a photoperiod-dependent increase in this response at 23:00 (data not shown,  $F(2, 21) = 7.901$ ,  $p = 0.003$ ). Exogenous CORT injection produced a maximal elevation of plasma glucose levels during both short-day and long-day photoperiods, and this glucose response to CORT injection was attenuated, but not nullified in molting birds at 23:00.

The interaction of CORT and INS together on glucose levels was also examined. Exogenous CORT did not aid in glucose recovery from INS injection at 11:00 (Fig. 1b,  $F(6, 56) = 0.207$ ,  $p = 0.97$  for interaction of time and injection) but injected CORT did hasten recovery from INS-induced hypoglycemia at 23:00 (Fig. 2b,  $F(6, 52) = 3.044$ ,  $p = 0.012$  for interaction of time, INS injection, and CORT injection). At both doses of INS (1.0 and 4.0 IU), glucose levels were elevated in birds receiving CORT+INS vs INS alone by 150 min after injection.

### 3.3. Triglycerides

Handling and restraint stress caused a reduction in triglyceride concentrations at both 11:00 (Fig. 3,  $F(3, 42) = 5.336$ ,  $p < 0.003$ ) and 23:00 (Fig. 3,  $F(3, 39) = 6.155$ ,  $p < 0.002$ ). Basal triglycerides also showed a distinct difference between day and night, with concentrations elevated at 23:00 compared to 11:00 (Fig. 3,  $F(1, 27) = 5.443$ ,  $p < 0.03$ ). Basal triglycerides also varied with photoperiod, as concentrations in birds held on short days were higher than those on long days, which in turn were elevated above concentrations from molting birds (Table 1,  $F(2, 46) = 15.893$ ,  $p < 0.0001$ ).

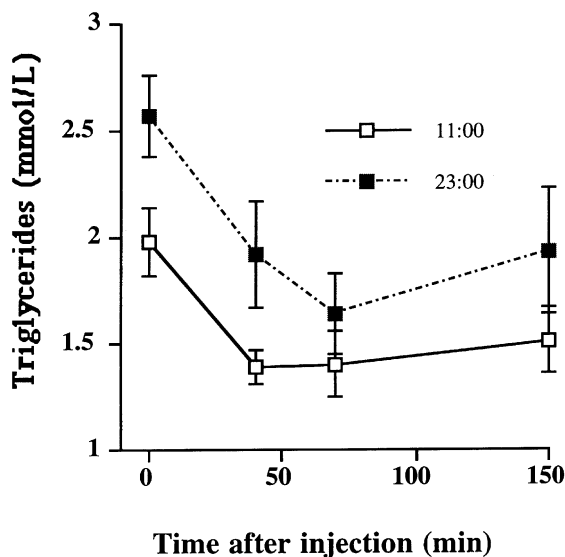


Fig. 3. Triglyceride responses to stress after saline injection at 11:00 and 23:00 in molting starlings. Points represent means  $\pm$  SEM for  $n = 10$ .

Exogenous INS had no direct effect on plasma triglycerides at either 11:00 (data not shown,  $F(2, 22) = 0.339$ ,  $p = 0.72$ ) or 23:00 (data not shown,  $F(2, 19) = 0.553$ ,  $p = 0.58$ ), nor did administration of exogenous CORT produce a change in triglyceride concentrations at 11:00 (data not shown,  $F(1, 14) = 0.082$ ,  $p = 0.78$ ) and 23:00 (data not shown,  $F(1, 13) = 0.472$ ,  $p = 0.50$ ). The triglyceride responses following INS and CORT injections did not differ from the responses shown in Fig. 3.

## 4. Discussion

### 4.1. Corticosterone

Handling and restraint stress caused circulating CORT concentrations to increase at both times of day in molting birds. These results confirm earlier findings in starlings during molt (Romero and Ramage-Healey, 2000) and add evidence for a negative-feedback mechanism in passerines that begins to attenuate stress-induced CORT release by 70 min after exposure to acute stress.

Basal concentrations of CORT at 11:00 did not differ from those at 23:00 in molting starlings. Although a distinct circadian rhythm during molt was demonstrated previously in this species (Romero and Ramage-Healey, 2000), the sampling hours of the present study (11:00 and 23:00) may have missed the peak (02:00) and trough (14:00) of that CORT cycle. These times were chosen, however, to match the diel peak and trough of starlings held on short- and long days, thereby allowing direct comparisons of basal CORT across three photoperiods. Regardless of the time-of-day, basal CORT concentrations were significantly lower in molting birds than in the same starlings held on short- and long days (Ramage-Healey and Romero, 2001).

### 4.2. Glucose

In the previous study with these birds (Ramage-Healey and Romero, 2001), stress-induced hyperglycemia was evident during scotophase (lights-off; nadir in circadian glucose) and absent during photophase (lights-on; peak in circadian glucose) in birds on both short- and long days. This hyperglycemic response to stress was absent during molt. However, this lack of response was only true for endogenous CORT. Injection of exogenous CORT resulted in robust increases in glucose concentrations during photophase. This suggests that CORT-induced hyperglycemia is damped, but not absent, during prebasic molt. Thus, despite the high energetic cost associated with a prebasic molt, the ability to mobilize energy reserves during an emergency situation is retained. However, it is unclear whether this is

physiologically relevant since exogenous CORT exceeded normal levels during molt (although these CORT concentrations are within the physiological range at other times of the year Romero and Remage-Healey, 2000).

Injection of INS at both times of day markedly decreased glucose concentrations in a dose-dependent manner in molting starlings. Recovery from this hypoglycemic state was more rapid in birds sampled during the day than at night, suggesting that mechanisms to restore blood glucose to normal levels are attenuated at night. How these mechanisms change over the course of the day is currently unknown, but may involve the daily cycle in CORT. When CORT was injected concurrently with INS to antagonize hypoglycemia, exogenous CORT hastened the recovery from INS-induced hypoglycemia only at night. This pattern is opposite to that observed in these same birds held on both short- and long days (Remage-Healey and Romero, 2001), where exogenous CORT aided in recovery from hypoglycemia only during photophase. Collectively, these results illustrate the altered state of physiology and energy metabolism in a molting bird. Perhaps, since glucose levels are suppressed throughout the day during molt compared to other photoperiods, molting birds may be better able to mobilize glucose stores in response to high concentrations of CORT.

#### 4.3. Triglycerides

Plasma triglyceride levels were reduced in response to stress in all treatments, independent of time-of-day or hormone injection. Similar results have been reported in mammals (Hershock and Vogel, 1989; Starzec and Berger, 1986) and in birds (Remage-Healey and Romero, 2001). The triglyceride stress response most likely results from a combination of stress-related hormones, since glucocorticoids inhibit synthesis of non-esterified fatty acids (NEFAs) into triglycerides (Bentley, 1998) and epinephrine increases triglyceride lipase activity (Norris, 1985).

Neither INS nor CORT injection produced any alteration in this stereotypic triglyceride stress-induced decrease. INS, which has been shown to increase NEFA levels in white-crowned sparrows (Boswell et al., 1995) and domestic hens (Heald et al., 1965) but also increase triglyceride levels in geese (Nir and Levy, 1973), did not alter triglyceride levels in molting starlings. Triglyceride concentrations in chickens increased in response to administration of ACTH (Latour et al., 1996; Puvadolpirod and Thaxton, 2000) and CORT (Saleh and Ezzat, 1990), but decreased in response to CORT in chicks (Khasani et al., 1981) and stress in rats (Lalitha et al., 1988). In the present study, injected CORT was ineffective at reducing triglycerides below stress-induced concentrations in molting birds. INS and CORT also did not alter triglycerides in birds on short- and long

days (Remage-Healey and Romero, 2001), which suggests that plasma lipid concentrations are tightly regulated in starlings and will not deviate from a precise range, despite the influence of exogenous CORT or INS.

Basal triglycerides were statistically elevated at night over daytime concentrations in molting birds. This result differed from birds on short- and long days, which showed no difference between 11:00 and 23:00 (Remage-Healey and Romero, 2001). Evidence in rats indicates that meal timing may influence daily lipid fluctuations to a greater extent than photoperiod cues (Mlekusch, 1982). Despite their importance as an energy substrate, circadian rhythms in plasma lipids have been relatively unstudied in passerines, so it remains unclear what role this daily variation might play in birds undergoing molt.

Plasma triglycerides also changed with photoperiod, as basal concentrations in birds held on short days were highest, long days were intermediate, and molting birds exhibited the lowest concentrations. Perhaps these elevated triglyceride concentrations during shorter day lengths indicate a substantial apportionment of lipids as substrate for thermogenesis during the winter months. In accordance with these findings plasma NEFAs were elevated in winter in comparison with concentrations in late spring in house finches (O'Connor, 1995). Alternatively, since triglyceride levels are lowest during the prebasic molt, plasma lipid utilization has possibly been increased to provide energy during this costly time of year.

## 5. Conclusion

Plasma glucose, CORT, and triglyceride concentrations are all significantly lower, and therefore perhaps regulated differently, during molt. Molt generally lasts about 90 days in starlings (Pyle, 1997), so these changes will be present for a significant portion of the year. Despite these differences, however, the responses to exogenous INS and CORT change little. Furthermore, both glucose and triglycerides appear relatively insensitive to fluctuating CORT concentrations. Consequently, the natural decrease in CORT seen during molt may be unrelated to energy substrate utilization during this heavily anabolic period.

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