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Basal, Diurnal, and Stress-Induced Levels of Glucose and Glucocorticoids in Captive Bats

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ABSTRACT Plasma levels of glucocorticoids and glucose were measured in three species of fruit bats (Chiroptera) sampled from captive populations. Three species of Old World bats *(Pteropus vampyrus, P. Hypomelanus,* and *Rousettus aegyptiacus)* had plasma levels of glucose that were within the normal mammalian range (80–100 mg/dl), with no difference between males and females. All animals had detectable levels of one or both of the major glucocorticoids (cortisol and corticosterone) found in mammals. Steroid levels were highest in *P. hypomelanus* (cortisol: 1,269 ± 207 ng/ml; corticosterone; 590 ± 154 ng/ml) and lowest in *R. aegyptiacus* (corticosterone: 36 ± 4 ng/ml; cortisol not determined). Diurnal changes in these steroids and the effects of handling and restraint stress were further investigated in *P. hypomelanus.* Experimental animals were captured in their roost quarters, bled once by venupuncture within 3 min, placed singly into a small holding chamber for 50–60 min, and bled again. This procedure was performed at four different times over the course of 24 h with different groups of animals. Glucose was at a minimum just before and a maximum just after the period of food presentation. Cortisol levels remained relatively constant throughout the day-roosting period and significantly declined to their lowest level in the period following food presentation. As expected, the effects of handling and isolation caused a significant increase in both plasma cortisol and glucose levels. When individual *P. hypomelanus* were subjected to 3 h restraint stress in small plastic wire-mesh restraining devices, cortisol levels rose approximately 800% by 2 h, with the first significant increase at 20 min. Thus, effects of sampling time (time of day) on plasma levels of cortisol and glucose should be considered when designing field and laboratory studies in which hormones and other blood borne parameters are being measured. Handling and bleeding times that exceeded 3 min were associated with elevated plasma levels of cortisol and glucose above resting (unstressed) levels, suggesting that field and laboratory protocols should be designed to reduce or eliminate this problem. Finally, the exceptionally high levels of plasma corticoids in *P. hypomelanus,* and to a lesser extent in *P. vampyrus,* place these bats among the highest known circulating adrenal steroid levels of all mammals.

Global strategies for conservation require multifaceted approaches for ensuring species survival. One such approach involves the captive breeding of threatened and endangered species (Mickleburgh et al., '92). When implementing such programs, consideration should be given to such factors as capture and transport conditions, cage design, group size, social grouping, psychological enhancement, as well as the nutritional and physiological well-being of the animals. For many species, the effects of stress (e.g., physical restraint, high population density, hypothermia, osmotic and metabolic stress) are known to activate the pituitary-adrenal axis, causing an increase in adrenocorticotropic hormone (ACTH) secretion, which in turn stimulates steroidogenesis from the adrenal cortex. The adrenal steroids then contribute to the animal's overall defense mechanisms and protect the animal from further injury (Munck et al., '84). Although glucocorticoid production is under circadian control in mammals, as is adrenocortical sensitivity to ACTH (Kant et al., '86), age and social status of animals may also contribute to variability in circulating steroid hormone levels (Armitage, '91).

Most free-ranging mammals are not likely to experience chronic stress unless they are subject to severe environmental perturbation, continuous high population density, severe drought or food shortage, or stress induced by thermal or chemical pollutants. Often wild animals that are used in captive-breeding or laboratory studies are housed under conditions for which there is little, if any, knowledge regarding requirements for maintaining healthy, reproductively successful populations. In laboratory situations that require periodic bleeding for hormone or other assays, protocols are

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designed to minimize stress associated with capture, handling, and blood sampling. Protocols for field studies (capture methods, capture times, handling, and temporary cage restraint) are often difficult to control or predict; thus, special care should be taken to design such studies to minimize the variation which may affect other variables.

Recent interest in maintaining captive-breeding colonies of endangered and threatened species has raised concern about the conditions under which the animals are housed. In such colonies, it is important that housing conditions (water, food, shelter), including the density and social conditions of the animals, be closely monitored so that healthy, successfully breeding colonies can be maintained. It has been postulated that social stress in mammals due to high population densities can lead to reproductive failure secondary to increased adrenocortical activity (Christian and Davis, '64; Christian et al., '60). While there is extensive evidence that mammals respond to stress by increasing adrenocorticoids, the hypothesis that an adrenocortical response acts as a population-regulation mechanism remains unproven (Seal et al., '83). If captive animals are subject to chronic stress, this may affect not only their reproductive success but also their longevity.

The present study was designed to establish the sensitivity of the adrenal cortex to the stresses of handling, blood sampling, and restraint in captive colonies of Old-World fruit bats. The following questions were asked: 1) How do plasma levels of glucocorticoids and glucose vary over 24 h; 2) How do handling and restraint stress affect plasma levels of cortisol and glucose; and 3) How do plasma cortisol levels in bats compare with those reported for other mammals?

MATERIALS AND METHODS

Study species

Pteropus hypomelanus, Pteropus vampyrus, and *Rousettus aegyptiacus* are members of the megachiropteran family Pteropodidae, which ranges from the Indo-Australian Archipelago eastward to Papua New Guinea and westward to Thailand and the Mergui Archipelago. *P. hypomelanus* and *P. vampyrus* are common inhabitants of small islands, where they are most abundant in low-lying coastal areas. *R. aegyptiacus* ranges from Israel southward throughout most of Africa and eastward to India. It is a common inhabitant of small caves and manmade structures throughout its range. Members of this family of bats roost individually or in small family groups within larger colonies or camps. Such colonies may number from tens to several thousand individuals. *P. hypomelanus* is a highly social species with a polygynous mating system (Mickleburgh et al., '92).

Each species or social group is housed in separate flight cages at captive-breeding facilities of the Lubee Foundation, Inc., Gainesville, Florida. The colonies of *P. vampyrus* and *P. hypomelanus* were established in 1990 from wild-caught animals taken in Borneo and shipped to Gainesville, Florida. The colony of *R. aegyptiacus* was established in 1989 from captive-bred animals obtained from the Philadelphia Zoo. Captive colonies are permanently housed in double-wire, hexagonal flight cages, each approximately 9 m in diameter and 2 m high. Approximately 10–20 adult bats of each species are housed together in separate flight cages. A centrally located, hexagonally shaped (3 m diameter) building located within each of the flight cages provides shelter for the bats and places where food and water are provided beginning at approximately 1700 h each day. Stainless steel feeding and drinking cups are removed and cleaned each day between 1000 h and 1600 h. Water and food, including freshly cut fruits (apples, bananas, grapes, cantaloupe, peaches, pears), dates or raisins, cooked carrots and sweet potatoes, chopped spinach and lettuce, and concentrated fruit juice, are supplemented with monkey chow and Vionate (multivitamin). Except for periods of inclement weather, bats are allowed to move freely between the enclosed roost building and the flight cage through hinged doors located on the walls of the building. Temperatures within the roost buildings are maintained between 20 and 25°C and humidity ranges from 40–80%. Members of the *P. vampyrus* and *P. hypomelanus* colonies can be distinguished individually by numbered monel alloy or stainless steel bands placed on one thumb and by a uniquely coded transponder (Devon, Inc.) injected beneath the skin in the mid-scapular region. Members of the *R. aegyptiacus* colonies were individually marked either with colored, plastic split-ring forearm bands or with bead-chain necklaces.

Initial measurements

Male and female bats of each species were hand captured and then sequentially weighed, measured, and bled for determination of hematocrit, glucose, and glucocorticoid levels. The interval from capture to completed blood withdrawal was approximately 15 min. Blood was drawn by venipuncture from a small wing vein using a 22 gauge needle and collected in microhematocrit tubes. From five to six aliquots of blood (40–50 μl each) were collected in heparinized microhematocrit tubes from the larger megabats, but only two to three aliquots were obtained from the smaller megabat, *R. aegyptiacus*. Microhematocrit tubes were sealed with Critoseal, centrifuged for 3 min, and the hematocrit read directly from a standard microhematocrit scale. The serum fraction was separated from the packed cell column and immediately frozen until the serum was analyzed for glucocorticoids and glucose. These procedures were performed during the month of August.

Stress experiments

To determine if steroid and glucose levels obtained above were representative of resting conditions, and to establish the extent of daily variability and responsiveness to stressful stimuli, *P. hypomelanus* was chosen for further analysis. This species was chosen because it had the highest resting steroid levels and, due to its mass, sufficient quantities of blood could be taken without causing additional stress (body fluid loss). Groups of five bats (male and female) were captured from their roosts in January at four different times of the day (0300–0430 h, 1000–1130 h, 1430–1530 h, 2200–2300 h) over the course of the 24-h experiment. Bats were alternately captured from two different roosting groups to avoid causing repeated stress to the same individuals. To minimize handling stress, each bat was captured by hand and bled within 3 min of capture. Blood samples were processed as described above. All bats included in these experiments were in a non-breeding condition so as to avoid introducing additional variation due to pregnancy or lactation. We assumed that all initial samples taken within 3 min of capture represent "unstressed" samples.

After the initial "unstressed" blood samples were taken, bats were housed together in temporary wire cages (1 × 1 × 1 m) that were located separately from the parent colonies. After being housed under these conditions for 1 h, a second blood sample was taken from each bat using the same procedure as described above. We assumed that the stress caused from the initial capture and handling, the confined housing conditions, and the second blood-sampling procedure was comparable to stress that these bats might encounter during other laboratory-based procedures (e.g., periodic weighing, taking linear measurement, routine blood sampling, milking, and feeding trials). After the "stressed" blood sample was taken, each bat was returned to its original flight cage.

In a separate experiment, six female *P. hypomelanus* bats were captured individually in March, bled within 3 min of capture without any prior handling or manipulation, and placed individually into specially constructed restraining devices. The device consisted of a cylindrical plastic wire-mesh enclosure (9 × 25 cm) that was used to stress the bats for three hours. During this time, animals inside their restraining devices were kept in a well-ventilated laboratory and were not subjected to hyperthermic or hypoxic conditions. Six additional blood samples were collected at intervals of 10, 20, 30, 60, 120, and 180 min following initial capture and onset of restraint.

Assay procedures

Glucose was determined by the glucose oxidase method (Trinder Kit; Sigma Chemical Co., St. Louis). Corticosterone and cortisol were determined using commercially available radioimmunoassay kits (ICN Biochemicals, Inc.). Samples from *P. hypomelanus* were checked for parallelism with the cortisol standard curve by assaying serial dilutions of unextracted or methylene-chloride extracted plasma. Absolute values for cortisol were compared before and after extraction.

RESULTS

Reference data for each of the four species are summarized in Table 1. Mean (± SE) hematocrits ranged from 49.7 ± 1.0% to 53.6 ± 1.0%. Body weights ranged from 136 grams to over 1 kg.

Glucocorticoid (cortisol and corticosterone) and glucose measurements for each species are summarized in Table 2. Levels of blood glucose were in the normal mammalian range for *P. vampyrus, P. hypomelanus,* and *R. aegyptiacus* (Table 2) and were similar in both sexes (not shown). In the two species for which sufficient plasma was available for two separate analyses, cortisol levels were approximately 6 *(P. vampyrus)* and 2 times *(P. hypomelanus)* greater than corticosterone levels. Following extraction, the mean cortisol level in *P. hypomelanus* was 1,025 ng/ml, or 80% of the value in unextracted plasma (Table 2). Glucocorticoid levels were similar in male and female *P. vampyrus,* but were 2 times greater in male than in female *P. hypomelanus* (not shown).

A detailed analysis of *P. hypomelanus* revealed daily patterns of plasma glucose and glucocorticoids. Glucose levels varied significantly during the 24-h period in the non-stressed bats (one-way ANOVA, $P < 0.05$), with the lowest levels recorded before the time of food presentation and maximum levels recorded in the period following food presentation (Fig. 1). Plasma glucose levels were significantly higher after food presentation than those recorded at other times (Scheffe test, $P < 0.05$). There also was a significant effect of confinement stress on plasma glucose (Fig. 1), with glucose lev-

TABLE 1. Body mass, forearm length, and baseline microhematocrit levels in three species of captive bats[1]

Species	Body mass (g)	Forearm length (mm)	Microhematocrit (%)
Pteropus vampyrus	1,018 ± 44 (9)	220 ± 2 (8)	49.7 ± 1.0 (9)
Pteropus hypomelanus	516 ± 34 (9)	156 ± 2 (10)	51.4 ± 1.1 (10)
Rousettus aegyptiacus	136 ± 7 (10)	94 ± 1 (10)	52.7 ± 1.0 (10)

[1] Mean ± SE (n). Samples were obtained between 1000 h and 1800 h.

TABLE 2. Baseline glucose, corticosterone, and cortisol levels in captive bats[1]

Species	Glucose (mg/dl)	Corticosterone (ng/ml)	Cortisol (ng/ml)	Cortisol after extraction (ng/ml)
Pteropus vampyrus	88 ± 9 (10)	102 ± 38 (8)	596 ± 67 (9)	N.D.[3]
Pteropus hypomelanus	94 ± 11 (9)	590 ± 154 (9)	1,269 ± 207[2] (9)	1,025 ± 178 (9)
Rousettus aegyptiacus	108 ± 13 (10)	36 ± 4 (1)	N.D.[3]	N.D.[3]

[1] Mean ± SE (n). Samples obtained between 1000 h and 1800 h. Discrepancies in n values between Tables 1 and 2 resulted from insufficient plasma available from all animals for complete analyses.

[2] This value was 1,307 ± 178 ng/ml in a replicate assay.

[3] N.D., not determined.

els elevated above the baseline following the period of stress during each sample period (two-way ANOVA, $P < 0.05$ between-group comparison). Cortisol levels were high at all times of the day, but were lowest in the period following food presentation (Fig. 2). Confinement for 1 h followed by a second blood sampling significantly elevated plasma cortisol levels (two-way ANOVA, $P < 0.05$ between-group comparison) (Fig. 2).

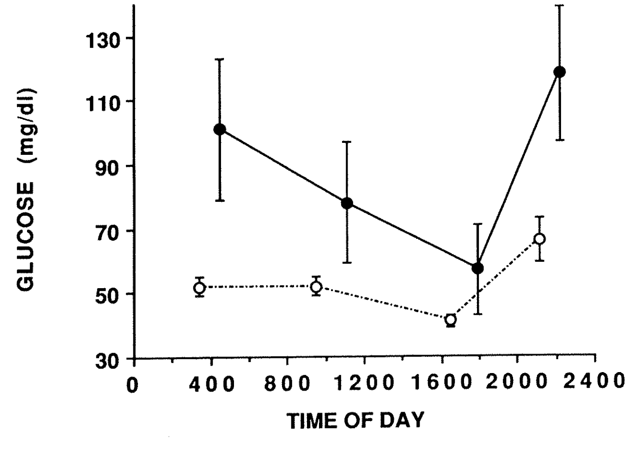

Fig. 1. Changes in glucose levels in *P. hypomelanus* over 24 h, and after 1-h confinement. Different groups of bats were captured at selected times of the day from their roosts, quickly bled from a wing vein, then placed (as a group) in a small holding cage for 1 h. Blood was centrifuged and the plasma frozen for determination of glucose by the glucose oxidase method. Each value is the mean and SE of five animals. Open circles: "baseline" samples. Closed circles: after 1-h confinement in a holding cage (thus, these points are displaced in time from the open circles). Two-way ANOVA revealed a significant treatment effect (baseline vs. post-confinement) but no significant interaction.

The timecourse of cortisol secretion following a protocol for inducing sustained stress is shown in Figure 3. Cortisol began to increase significantly above baseline within 20 min following the placement of bats in restraint devices; cortisol levels remained significantly elevated throughout the 3-h experiment. The mean baseline level for cortisol was 132 ng/ml and this increased to > 1,000 ng/ml over the course of 3 h. There was no significant effect of restraint stress on hematocrit values (not shown).

Four random plasma samples from *P. hypomelanus* were checked for parallelism with the cortisol standard curve. All samples diluted in parallel with the

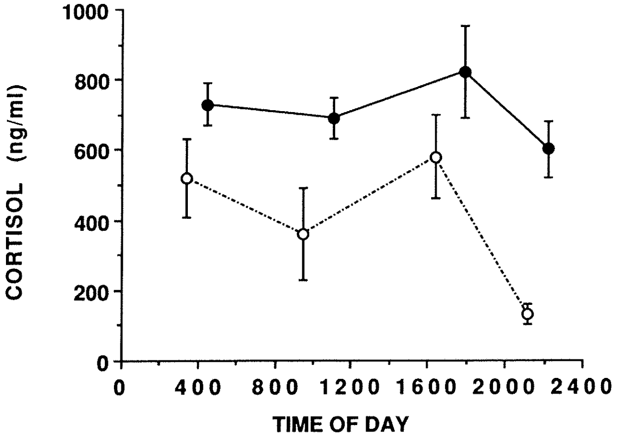

Fig. 2. Changes in plasma cortisol levels over 24 h and before and after confinement for 1 h in *P. hypomelanus*. See legend to Fig. 1 for details; these samples are from the same bats in Fig. 1. The difference in circulating cortisol levels between baseline (open circles) and post-confinement (closed circles) was significant by two-way ANOVA, with no significant interaction.

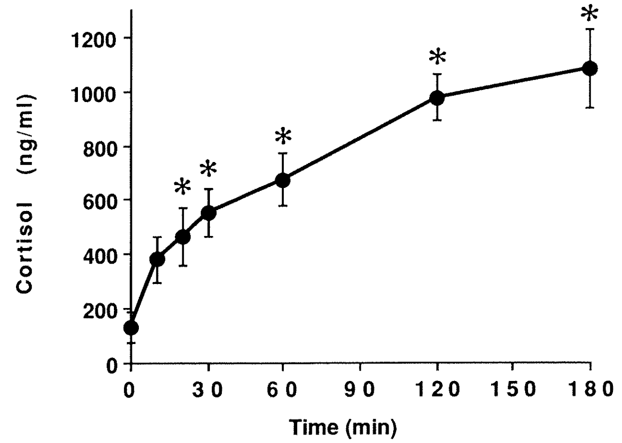

Fig. 3. Timecourse of cortisol response to stress in *P. hypomelanus*. After collection of a baseline blood sample, individual bats were placed singly into small restraining devices and bled via a wing vein at 10, 20, 30, 60, 120, and 180 min beginning at 0900 h. Blood was assayed for cortisol by RIA. Each value is the mean and SE of six animals. The asterisks indicate values significantly different from 0-time baseline by one-way ANOVA followed by Duncan's new multiple range test at the $P < 0.05$ level of significance.

standard curve both before (Fig. 4A) and after extraction (Fig. 4B).

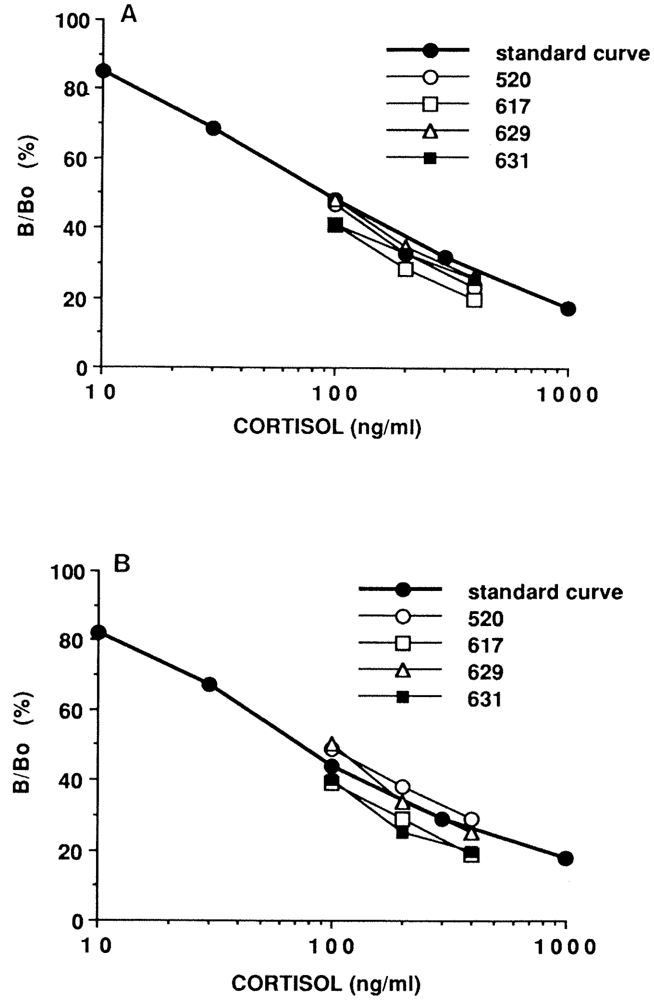

Fig. 4. Parallelism of *P. hypomelanus* cortisol with the cortisol standard curve, using unextracted plasma (**A**) or plasma that was first extracted with methylene chloride (**B**). Serial dilutions of the extract (25, 12.5, or 6.25 μl) or of plasma (10, 5, or 2.5 μl) were added to the assay; total volume was maintained with phosphate buffered saline containing 0.1% gelatin. Each symbol represents a different animal; in both A and B the closed circles represent the standard curve.

DISCUSSION

Efforts to maintain successfully breeding populations of small mammals in captivity have had mixed success, and several factors may account for these results. These include the effects of nutritional factors, social and genetic incompatability, inadequate housing, handling stress, and overly high densities leading to physiological stress. Since captivity alone and the daily maintenance procedures required to care for animals may be stressful, it is not unreasonable to assume that such conditions may result in chronically elevated blood glucocorticoid levels. Stress and glucocorticoids are well known to suppress reproduction in mammals (Munck et al., '84; Rivier et al., '86; Bambino and Hsueh, '81). Thus, efforts to minimize stress associated with handling, transferring, and housing should improve an animal's reproductive potential. In the present study, three species of captive bats were assayed for cortisol, corticosterone, glucose, and hematocrit, and one of these, *P. hypomelanus,* was further examined for basal, diurnal, and stress-induced adrenocortical responses. In the two wild-captured species *(P. vampyrus* and *P. hypomelanus),* total glucocorticoid levels were as high as have been recorded in mammals, whereas in the one captive-bred species *(R. aegyptiacus),* steroid levels were comparable to those observed under basal conditions for most other mammals. The high steroid levels in *P. vampyrus* and *P. hypomelanus* were apparently unrelated to metabolic stress, since glucose levels were in the normal mammalian range.

To determine if "resting" values obtained from *P. vampyrus* and *P. hypomelanus* may have been already elevated due to stresses associated with the other procedures (weighing the animals, etc.), an experiment was conducted in which groups of *P. hypomelanus* were quickly bled within 3 min of capture without any prior handling (baseline) and then placed together in a small holding cage for 1 h. A second blood sample was taken at that time to test for stress responsiveness in these animals. Baseline cortisol levels were again very high, but were $< 50\%$ of those observed when no effort was made to minimize handling and manipulation of the animals prior to sampling. Therefore, prior handling of the bats for only 15 min was clearly associated with elevated steroid levels.

Following the 1-h confinement, cortisol levels rose significantly, again suggesting that the initial sample approximated a true basal sample. The time-course and magnitude of the cortisol response to a standardized stress was next determined by placing individual *P. hypomelanus* in separate restraining devices, in a manner similar to that used commonly in studies on rodents (Bradbury et al., '91). Under these conditions, basal cortisol levels were relatively low, then rose rapidly upon restraint and remained elevated for the duration of the 3-h experiment. Mean cortisol levels following stress reached nearly 1,100 ng/ml, a level far exceeding values reported in other mammals. This is especially significant when it is considered that corticosterone levels, which were not quantitated in this experiment, are also very high in these animals. The stressed values were similar to those reported for the hibernating bat, *Myotis lucifugus* (Gustafson and Belt, '81), and are approached only by those reported for the Australian bush rat (McDonald et al., '88). Only in some New World monkeys are equivalent or higher total glucocorticoid levels found circulating in plasma (Brown et al., '70; Cassorla et al., '82). The continued elevation of plasma cortisol during the 3 h of restraint suggests that this form of stress was sufficiently severe as to override any negative feedback effects of the glucocorticoids on subsequent secretion of adrenocorticotropic hormone, although it is unknown if the HPA axis of the bat possesses a feedback system similar to that described for other mammals (Keller-Wood and Dallman, '84). It is also worth noting that the failure to observe any increase in hematocrit after such a profound stress suggests that the megabats do not have the type of contractile spleen seen in many other mammals.

That we were indeed measuring authentic cortisol and not registering artifactually high readings due to an assay contaminant is supported by four observations: 1) the antibody used possesses little or no cross-reactivity with all the major and minor steroid products of the adrenals and gonads; 2) the mean cortisol values for the nine bats in Table 1 were within 3% in two separate assays; 3) the samples diluted in parallel with the standard curve; and 4) at least 80% of the immunoreactivity remained after extraction. Nevertheless, it is still possible that a previously unrecognized steroid may be present in the blood of these animals and could be interfering with the cortisol radioimmunoassay. As additional samples become available, this issue could be further examined using additional tools such as HPLC separation. In the absence of field measurements, it is impossible to know at this time if these unusually high steroid levels are normally present in free-ranging, unstressed animals, or if they reflect conditions of chronic stress associated with captivity. If the former is true, then bats represent a potentially important model for the study of glucocorticoid action, since such high circulating levels would be considered pathological in most animals and would lead to severe metabolic and immunological disturbances. If the latter is true, then these results suggest that better efforts should be made to design bleeding protocols and housing facilities, or to manage colony densities of captive animals to minimize stress-induced adrenocortical function.

In most species, plasma levels of glucocorticoids follow a circadian pattern with highest levels before the onset of the active period of an animal's daily cycle (Gibson and Krieger, '81; Martensz et al., '87), although occasionally the reverse pattern is observed (Turner, '84). *P. hypomelanus* also showed diurnal variation in cortisol levels, although our results coincide with variation that was apparently linked to feeding. Cortisol levels were lowest at the end of the period when most feeding occurs (1700–2200 h). It is unknown if this pattern of secretion is linked to changes in circulating levels of ACTH, since this hormone has yet to be characterized in Chiroptera.

Plasma glucose levels were relatively low in *P. hypomelanus* at all times of the day, but as expected were highest at the end of the feeding period. These levels of glucose (50–70 mg/dl) are at the low end of normal for most mammals, although we did not note any subjective signs of hypoglycemia in these or the other bats. Nevertheless, glucose was significantly elevated by the stress of a 1-h confinement, and apparently also by the stress of handling (compare Fig. 1 and Table 2). Although not quantitated in this study, it is highly probable that these stressors activated the autonomic nervous system, and this was partly responsible for the increase in blood glucose (Havel and Taborsky, '89).

To our knowledge, this is the first study to describe the metabolic and endocrine changes associated with stress in captive bats. The presence of such high circulating levels of total glucocorticoids potentially represents a new model for the study of HPA function in mammals and raises several interesting questions for further study. For example, are bats resistant to the effects of glucocorticoids in a manner similar to that reported for certain New World monkeys (Chrousos et al., '82)? Also, it would be instructive to quantify the relative proportion of bound and free steroid as it exists in the circulation; perhaps Chiroptera have unusually high circulating levels of steroid-binding globulins, thus maintaining a normal unbound (active) level of cortisol and corticosterone. Finally, the handling, restraining, and transporting of bats clearly are very stressful events that may cause massive secretion of glucocorticoids. In the present study, when blood samples were obtained after prior handling or manipulation of the bats, cortisol levels were as high as those produced by 3 h of restraint. In light of the potentially debilitating effects of chronically elevated adrenal steroids on an animal's physiology, great care should be taken to minimize stress by developing protocols for blood sampling and cage designs for transport and long-term housing conditions. Further studies are needed to investigate the relationship between glucocorticoid levels and progesterone levels in both captive and free-ranging bats. Before field or laboratory studies are undertaken to investigate seasonal changes in reproductive steroids, it would be important to establish the effects of capture stress on glucocorticoid levels and how these may affect plasma levels of reproductive steroids. Lastly, knowledge of circadian or food-induced changes in glucocorticoids and their potential effects on reproductive steroids should be considered in field and laboratory sampling protocols.

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LITERATURE CITED

Armitage, K.B. (1991) Factors affecting corticosteroid concentrations in yellow-bellied marmots. Comp. Biochem. Physiol. A, *98:*47–54.

Bambino, T.H., and A.W.J. Hsueh (1981) Direct inhibitory effect of glucocorticoids upon testicular luteinizing hormone receptor and steroidogenesis in vivo and in vitro. Endocrinology, *108:*2142–2148.

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

Brown, G.M., L.J. Grota, D.P. Penney, and S. Reichlin (1970) Pituitary-adrenal function in the squirrel monkey. Endocrinology, *86:*519–529.

Cassorla, F.G., B.D. Albertson, G.P. Chrousos, J.D. Booth, D. Renquist, M.B. Lipsett, and D.L. Loriaux (1982) The mechanism of hypercortisolemia in the squirrel monkey. Endocrinology, *111:*448–451.

Christian, J.J., and D.E. Davis (1964) Endocrines, behavior, and population. Science, *146:*1550–1560.

Christian, J.J., V. Flyger, and D.E. Davis (1960) Factors in the mass mortality of a herd of Sika deer, *Cervus nippon*. Chesapeake Sci., *1:*79–95.

Chrousos, G.P., D. Renquist, D. Brandon, C. Eil, M. Pugeat, R. Vigersky, G.B. Cutler Jr., D.L. Loriaux, and M.B. Lipsett (1982) Glucocorticoid hormone resistance during primate evolution: Receptor-mediated mechanisms. Proc. Natl. Acad. Sci. U.S.A., *79:*2036–2040.

Gibson, M.J., and D.T. Krieger (1981) Circadian corticosterone rhythm and stress response in rats with adrenal autotransplants. Am. J. Physiol., *240:*E363–E366.

Gustafson, A.W., and W.D. Belt (1981) The adrenal cortex during activity and hibernation in the male little brown bat, *Myotis lucifugus lucifugus:* Annual rhythm of plasma cortisol levels. Gen. Comp. Endocrinol., *44:*269–278.

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

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

Keller-Wood, M.E., and M.F. Dallman (1984) Corticosteroid inhibition of ACTH secretion. Endocr. Rev., *5:*1–24.

Martensz, N.D., S.V. Vellucci, K.M. Fuller, B.J. Everitt, E.B. Keverne, and J. Herbert (1987) Relation between aggressive behaviour and circadian rhythms in cortisol and testosterone in social groups of talapoin monkeys. J. Endocrinology, *115:*107–120.

McDonald, I.R., A.K. Lee, K.A. Than, and R.W. Martin (1988) Concentration of free glucocorticoids in plasma and mortality in the Australian bush rat *(Rattus fuscipes* Waterhouse). J. Mamm., *69:*740–748.

Mickleburgh, S.P., P.A. Racey, and A. Hutson (eds.) (1992) Old World fruit bats: An action plan for the family Pteropodidae. (In press.)

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

Rivier, C., J. Rivier, and W. Vale (1986) Stress-induced inhibition of reproductive functions: Role of endogenous corticotropin-releasing factor. Science, *2321:*607–609.

Seal, U.S., L.J. Verme, J.J. Ozoga, and E.D. Plotka (1983) Metabolic and endocrine responses of white-tailed deer to increasing population density. J. Wildl. Manage., *47:*451–462.

Turner, J.C. (1984) Diurnal periodicity of plasma cortisol and corticosterone in desert bighorn sheep demonstrated by radioimmunoassay. Can. J. Zool., *62:*2659–2665.