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Relation of Glucocorticosteroids and Testosterone to the Annual Cycle of Free-Living Degus in Semiarid Central Chile

G. J. Kenagy,*[,1] Ned J. Place,*[,2] and Claudio Veloso†[,3]

*Department of Zoology and Burke Museum, University of Washington, Seattle, Washington 98195; and †Departamento de Ecología, Pontificia Universidad Católica de Chile, Casilla 114D, Santiago, Chile

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We investigated seasonal patterns of plasma glucocorticosteroids (GCs) in both sexes and testosterone (T) in males in relation to the annual cycle in central Chile of a natural population of the degu (*Octodon degus*), a caviomorph rodent. We wanted to find out which GCs are present in degus, whether their seasonal variation suggests suppressive or synergistic interrelationships with T, and whether seasonal variation in GC levels indicates a relationship with energy mobilization and demands of reproduction. Degus mated in late autumn, and female body mass increased in pregnancy and remained high during lactation and throughout spring. Over the subsequent period of summer drought both sexes declined to a minimal body mass before the next mating season. Cortisol appears to be the principal GC in degus. In fact cortisol levels were so high that the extremely low levels of corticosterone measured were probably largely due to the cross-reactivity of our corticosterone antiserum with cortisol. Titers of cortisol in females exceeded 1000 ng/ml at lactation in the spring of 2 years; cortisol declined greatly following lactation and during the summer and reached its lowest mean level of about 500 ng/ml at mating. Males were more difficult to capture than females and thus our sampling was limited, but male cortisol levels were similar to those of females during the times of year when we measured them. Male T levels remained within a low range all year, but at mating, when mean T was highest (0.16 ng/ml) and when most males had detectable T, degus showed their lowest cortisol levels. The minimal cortisol level of males during mating represents a possible suppressive effect of T, as described in other mammals. At the time of their spring emergence, 60% of juvenile males had detectable T levels comparable to those of adults, suggesting important organizational effects of T at that time in their maturation. Peak cortisol titers in both sexes were associated with lactation in females, when energy mobilization, production, and body mass were at their greatest.

Key Words: glucocorticosteroids; cortisol; corticosterone; testosterone; body mass; annual cycle; field endocrinology; degu; *Octodon degus.*

Promotion of survival by maintenance of physiological homeostasis has been shaped by natural selection to operate under the natural conditions in which animals live, yet the foundations of physiology and its branches such as endocrinology have been largely developed with studies under isolated laboratory conditions. Recent attention has been given to understanding how regulatory physiological processes function in free-living animals. Knowledge of the relation of hormone levels in nature to the changes of state that occur

[1] E-mail: kenagy@u.washington.edu.
[2] E-mail: nplace@u.washington.edu.
[3] E-mail: cveloso@genes.bio.puc.cl.

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in animals during their natural annual cycle, including breeding, is needed to develop a more complete view of how hormones function and how they have evolved.

The glucocorticosteroid (GC) hormones, which include cortisol and corticosterone, are involved in the regulation of energy balance in rodents (King *et al.*, 1988), in which they produce a variety of anabolic effects (Berdanier, 1989). Corticosterone acts directly in the hypothalamus to promote feeding behavior (Green *et al.*, 1992). Depending on the timing of the annual cycle of a species, GCs can either inhibit or facilitate reproductive physiology (Brann and Mahesh, 1991). Acute (transient) and chronic stress, including socially mediated behavioral stress, are associated with the activation of GC hormone secretion, and these responses may have inhibitory influences on reproductive physiology and endocrinology and on the status of individuals within social groups (Selye, 1976; Sapolsky, 1987).

We have undertaken a study to address several basic questions involving natural patterns of GC hormones during the annual cycle of a South American rodent, the degu (*Octodon degus*). Degus belong to the caviomorph, or New World hystricognath, lineage of rodents (Woods, 1993; Nedbal *et al.*, 1996), which includes South American species such as guinea pigs, chinchillas, and the capybara. Which GCs, cortisol or corticosterone, are present in the plasma of the degu and in what relative amounts? Studies of guinea pig (*Cavia porcellus*) endocrinology have shown cortisol to be the major glucocorticoid (Dalle and Delost, 1974). With what phases of the annual cycle, reproductive state, and body condition are the lowest and highest levels of these hormones associated? How do these patterns differ between the sexes and age classes? What can we infer about seasonality of energy balance of degus from the seasonal variation in hormone profiles? Although low levels of T were reported in captive male degus (Bustos-Obregón and Ramirez, 1997), we expected that males in the field might show higher T levels due to the social context of aggressive male-male interactions associated with competition for females (Wingfield *et al.*, 1990).

The degu occurs throughout central Chile where it is the only rodent active in the daytime, which has provided good knowledge of its ecology, distribution, and behavior (Meserve *et al.*, 1984; Contreras *et al.*, 1987; Vásquez, 1997). Degus are herbivores and seasonal breeders, typically mating in late autumn, as the precipitation of fall and winter yields fresh green vegetation growth that supports reproduction and postnatal growth (Fulk, 1976; Contreras and Bustos-Obregón, 1977; Rojas *et al.*, 1977; Yáñez and Jaksic, 1978; Morales, 1982). Despite considerable information on its occurrence in rodent communities of the semiarid environment of central Chile, little is known of its physiology and behavior under natural conditions. In particular, we are not aware of any published reports of the endocrinology of the degu under field conditions.

METHODS

Animals. Degus were studied near Santiago, Chile, within the Región Metropolitana de Santiago, using Sherman live-traps. Most of the captures were made on the same 3-ha grid, using 150 traps, at Quebrada de la Plata, a field station of the University of Chile, School of Agronomy (elevation 800 m), and a small number of captures were made, in September–October 1997, near the town of Lampa (elevation 500 m), on a population that was reproductively synchronous with the population at Quebrada de la Plata. Thus the data from the two sites were combined for the present analysis. Both sites are within about 25 km of downtown Santiago.

Sampling. Animals were captured and released following examination and obtaining a small blood sample of about 400 μl during six time intervals, described as follows (with a median date in parentheses) in 1996, 27 September–4 October (1 October), 31 October–7 November (3 November), and 20 November–13 December (1 December); and in 1997, 22–27 March (25 March), 29 May–2 June (1 June), and 15 September–3 October (24 September). Analyses of body mass and hormone titers are based on combining data from each of these intervals, to produce a single mean ± SEM, and data are plotted on the median date. Traps were opened and baited with oats in the morning and animals collected about 2 h later. The traps were taken to a central area for processing where the animals were removed and anesthetized briefly in a large jar (10–20 s exposure) with ethyl ether inhalant prior to taking a blood sample from the infraorbital sinus which we accomplished within about 2 min of

removing the animal from its trap. Despite the rapid handling of individuals when removed from their traps, we noted that capture and detention of the animals, despite their tendency to rest quietly in the traps, were likely to have, as commonly assumed, some stimulatory influence that can lead to a modest rise of hormone titers above truly basal levels. The animals were also weighed, after transfer to a bag, with a Pesola spring balance, and examined for externally apparent reproductive condition. A distended penis and slightly enlarged scrotal area were indicative of the mating season in males. Enlarged teats, from which milk could often be expressed, indicated lactation. A gestation period of 90 days (Morales, 1982) was used to express the phase of the annual cycle of the population from mating through lactation.

Whole blood was stored in a cooler from the time of sampling for several hours, after which it was brought to a laboratory for centrifugation and removal of plasma to a 200-μl plastic container, in which it was frozen at −20°C. The frozen plasma was subsequently transported to the University of Washington on dry ice and stored again at −20°C until analysis.

Hormone radioimmunoassays. Cortisol was measured using a solid-phase radioimmunoassay (RIA) kit with ^{125}I purchased from Incstar (Stillwater, MN). Plasma samples were diluted 2× or 5× with the serum blank provided and aliquoted in 10-μl amounts into duplicate assay tubes. Cross-reaction of the cortisol antibody with corticosterone is <0.4%, as reported by the manufacturer. Preassay validations demonstrated no detectable cortisol in charcoal-stripped degu plasma. A dilution curve of a cortisol standard in charcoal-stripped plasma was parallel to the standard curve. Intraassay and interassay variation were 5.6% and 4.1%, respectively.

Corticosterone was measured as described by Boswell *et al.* (1994) and Wingfield *et al.* (1992). Plasma samples of 20 μl were extracted with 4 ml of dichloromethane, dried under nitrogen, reconstituted in 550 μl of phosphate-buffered saline, and aliquoted into duplicate assay tubes of 200 μl each and one recovery tube of 100 μl. Reconstituted extracts were incubated with a primary antibody to corticosterone (B21-42, Endocrine Sciences, Tarzana, CA) and [1,2,6,7-^{3}H]corticosterone (NEN Research Products, Boston, MA), and dextran-coated charcoal was used to separate bound and free-labeled hormone. Cross-reaction of the corticosterone antibody with cortisol was 5.2%, as reported by the manufacturer. All samples were run in a single assay, within which the variation was 3.6%.

Testosterone (T) was measured using a solid-phase RIA ^{125}I kit purchased from Diagnostic Products Corporation (Los Angeles, CA). Plasma samples were aliquoted in amounts of 50 μl into duplicate assay tubes, except when insufficient volumes necessitated use of a single assay tube (4 of 48 samples). Cross-reaction of the T antibody with 5 α-dihydrotestosterone was 3.4%, and the lower limit of detectability was 0.04 ng / ml, as reported by the manufacturer. In preassay validations testosterone was not detected in charcoal-stripped degu plasma, and two samples of stripped plasma were spiked to concentrations of 2.5 and 0.25 ng / ml of T, which resulted in measured values of 3.21 and 0.21 ng / ml, respectively, which are similar to expectation. A dilution curve of a T standard was parallel to the standard curve. After running all samples in a single assay and finding that about half had nondetectable T, we reanalyzed all nondetectable samples that still contained sufficient volume for another assay. Fifty microliters of plasma from these four samples was reassayed after addition of 50 μl of T (4.0 ng / ml); the mean testosterone concentration measured (1.5 ng / ml) was about 75% of the actual concentration (2.0 ng / ml). The intraassay coefficient of variation was 4.8%. Values obtained below the level of detectability (0.04 ng / ml) were assigned this nominal value for statistical treatment.

Statistics. Results were analyzed with commercial statistical programs (Statview, Abacus Concepts Inc., Berkeley, CA) using analysis of variance. Few individuals were sampled repeatedly (only three males and seven females, twice each), and thus we analyzed the data according to this test, which assumes all samples are independent. The Fisher PLSD was used as a post hoc test. Some comparisons of paired sets of data were made with the Student *t*-test, for parametric analysis, or with the Mann-Whitney *U*-test, for nonparametric analysis. Sample sizes are given in the figures and table.

RESULTS

Body mass of females showed a cycle of significant variation ($F(5, 53) = 3.144$, $P = 0.0147$) over the year

(Fig. 1), with the lowest values in late summer and autumn (March through June) of the southern hemisphere. The mating season began shortly before the winter solstice (June), when seasonal rains promoted growth of fresh green plant food. Body mass increased during the 3-month period of gestation, and young were born and lactation began in September. After this, adult body mass remained high and continued to increase during the springtime (October through December), which is the end of the usual period of plant food production associated with degu reproduction. At the two times in 1997 when we obtained substantial samples of adult males (onset of mating and early lactation) the females were significantly heavier than the males ($F(1,1,1,50) = 23.54$, $P < 0.0001$; Fig. 1). We note that general trapping and particularly recapture success for adult males were conspicuously poor, by comparison to the success of capturing females, which accounts for the smaller amount of data we obtained on males. The low masses of juveniles in October/November (Fig. 1) represent individuals that had emerged from their natal burrows several weeks earlier and already had shown postweaning growth. The period of lactation in September (preceded by mating

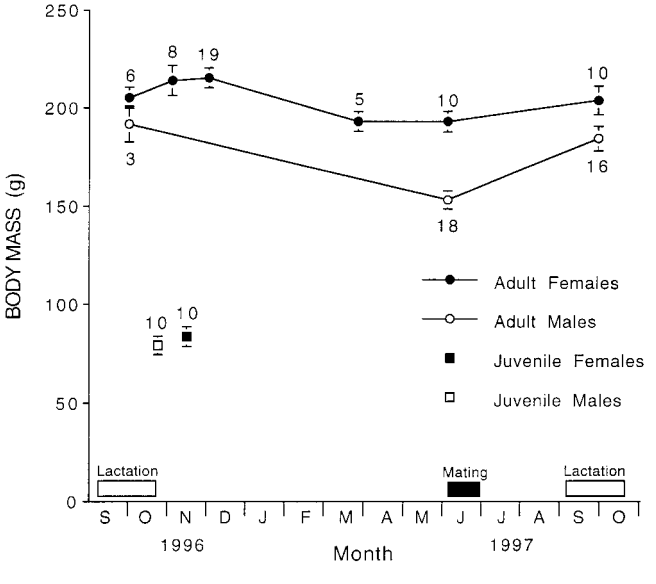

FIG. 1. Seasonal patterns of body mass in degus, according to sex and age class. Values are mean ± SEM, and sample sizes are indicated in the figure. The approximate periods of lactation and mating are indicated by horizontal bars, based on observations of individuals in the field.

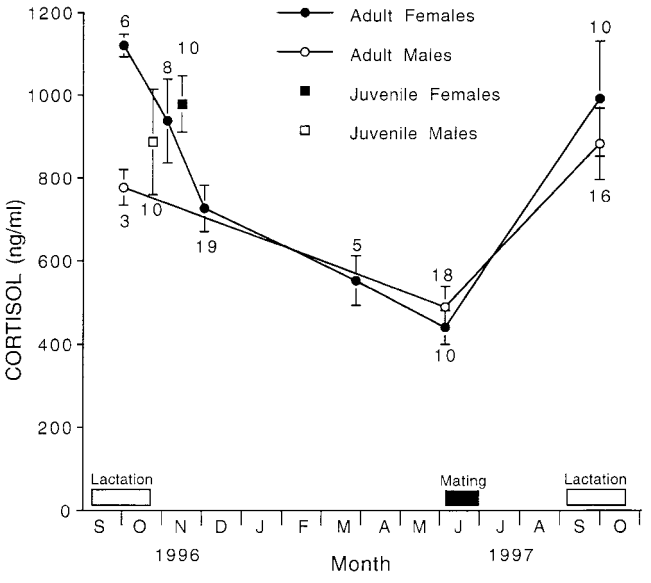

FIG. 2. Seasonal patterns of plasma concentration of cortisol in degus, according to sex and age class. Symbols and plotting as in Fig. 1.

in June) appeared to be similar in timing in both 1996 and 1997.

Cortisol appeared to be the principal and perhaps only glucocorticoid in the plasma of degus. We performed independent radioimmunoassays for both cortisol and corticosterone, and always obtained an indication of substantial levels of cortisol. However, the measured levels of corticosterone were in the range of only 2–5% of the values of cortisol, which does not exceed the level of cross-reactivity of the corticosterone antibody with cortisol. Due to this indication that corticosterone is either insignificant or undetectable, we do not report the data for our assays for corticosterone.

The annual pattern of cortisol in female degus showed a pronounced cycle ($F(5, 52) = 8.04$, $P < 0.0001$) with peak mean levels greater than 1000 ng/ml during the period of lactation, (September–October) of both years (Fig. 2). Cortisol declined greatly following reproduction and into the summer, falling to a mean of less than 500 ng/ml at the onset of mating. Cortisol titers of males were not significantly different from those of females at the two times when we were able to obtain large samples, at mating and lactation in 1997 (Mann-Whitney U test, $P = 0.27$, $P = 0.4$, respectively; Fig. 2). When we measured cortisol of juveniles,

following their weaning and emergence onto the surface, the values were statistically indistinguishable between male and female juveniles (*t* test, $P = 0.54$), and all juveniles were not significantly different from adult females (*t* test, all juveniles vs adult females, $P = 0.97$; Fig. 2).

We examined correlations of body mass with plasma cortisol levels on an individual basis at times when we obtained the largest samples, and we found no significant correlations ($P \gg 0.05$). We did this for females at postlactation ($n = 19$), mating ($n = 10$), and lactation / 1997 ($n = 10$); and for males at mating ($n = 18$) and lactation / 1997 ($n = 16$); these samples are apparent in Figs. 1 and 2.

On one occasion, in December 1996, we tested the apparent effect of handling three females on their cortisol level. These individuals had already been captured and were waiting quietly within their traps for 1–2 h prior to this test. We obtained an initial blood sample within about 2 min of removing each individual from its trap; we took a second blood sample 15 min later. The initial mean ± SD of 596 ± 238 ng / ml rose significantly (*t* test, $P < 0.05$), by nearly 20%, over 15 min to a level of 711 ± 215, suggesting that a 20% increase in plasma cortisol was a response to the degu's being picked up and handled to obtain the blood sample.

Most males (13 / 15) had detectable levels of testosterone at the beginning of the mating season, showing the highest mean value for the year of 0.16 ng / ml (Table 1). A single adult male at this time, with a T titer of 0.04 ng / ml (the lower limit of detectability), was autopsied and showed masses for two testes of 1.3 g, epididymides 0.4 g, seminal vesicles 0.9 g, and greatly enlarged tubules in the cauda epididymis that contained motile spermatozoa. The males all showed distended penes and externally somewhat apparent testes. (Caviomorph rodents typically do not have a fully scrotal placement of the testes (Contreras and Rosenmann, 1982).) The timing of the maximum level of T, at the beginning of mating in June, coincided with the annual minimum of cortisol (Fig. 2). By the time of lactation only two of 15 males had detectable T, and the mean had dropped to about one-third of the mating-season value (0.059 ng / ml). Despite the low mean T and low incidence of detectable T in the population at this time (lactation), we observed mating behavior; and females became pregnant and produced a second bout of reproduction in 1997, with lactation again in December. That did not occur in 1996, when breeding was confined to a single bout, with lactation occurring only in September–October.

Juvenile males, shortly after their emergence onto the surface and while still growing, showed relatively high levels of T, and in fact 6 of 10 juveniles had detectable titers of T (Table 1). The mean ± SD T concentration of the 6 males with detectable levels was in fact 0.187 ± 0.124 ng / ml, which is comparable to the mean of 0.177 ± 0.147 for the 13 adult males with detectable T in June (Table 1). The overall annual range of testosterone titers in degus was low, and variation among individuals was high.

DISCUSSION

Free-living degus show substantial seasonal changes in plasma levels of cortisol that are associated with changes in body mass and reproduction. It is noteworthy, despite the female-male differences in timing of energy demands for reproductive effort, that males have cortisol levels over the course of the year that closely resemble the levels of females. Annually cyclic patterns of glucocorticoids and body mass have also been reported in hibernating sciurid rodents (Armitage, 1991; Boswell *et al.*, 1994). The lowest levels of

TABLE 1
Testosterone Concentrations in Plasma of Male Degus

Age	Date	Reproductive activity	Mean (ng / ml)	SD	Sample size	Number with detectable T
Adult	Sept / Oct 1996	Lactation	0.130	0.156	3	1
Juvenile	Oct / Nov 1996	Post weaning	0.128	0.119	10	6
Adult	May / Jun 1997	Mating	0.159	0.145	15	13
Adult	Sept / Oct 1997	Lactation	0.059	0.052	15	2

cortisol in degus occurred at the time of mating, which also corresponded to an annual minimum of body mass. The highest levels of cortisol in females occurred during lactation, when body mass had increased; the males also showed higher cortisol and body mass at this time. Juveniles showed relatively high cortisol at the time of postnatal growth following weaning and emergence onto the surface, when food availability was good and energy demand high for growth and perhaps dispersal. Although seasonal patterns of variation show clear seasonal cycles and apparent interrelations between cortisol and body mass, we found no correlations at the individual level between cortisol and body mass at any season. Although other investigators have not previously reported such correlations, Boonstra and Boag (1992) have reported a correlation between mass and cortisol level in female meadow voles during lactation. Underlying the patterns of seasonal physiological change of state in adult degus is a distinct sexual dimorphism of body mass, with females about 25% greater than males at the time of mating and about 10% greater at lactation (Fig. 1). The social and mating systems, and their energetic basis, are not well enough known in degus to interpret these sexual differences, but for the polygynous mating system typical of most rodents, the small relative size of male degus, particularly at the time of mating, is unusual. Ralls (1976) has suggested that relatively large female body size could result from selective pressures on the quality of female maternal performance and on ability to compete among females for resources.

It is of comparative interest that cortisol appears to be the principal plasma GC of *O. degus.* Cortisol is also the principal GC in another caviomorph, the guinea pig, *Cavia porcellus* (Dalle and Delost, 1974). Both cortisol and corticosterone are present, though with higher titers of cortisol than corticosterone, in noncaviomorph rodents of several different families, including squirrels, Sciuridae (Boswell *et al.,* 1994; Kastner *et al.,* 1977; Shivatcheva *et al.,* 1988), and gerbils, Muridae / Gerbillinae (Amirat *et al.,* 1980). Laboratory rats and mice, Muridae / Murinae, differ from this trend, in having corticosterone as the principal glucocorticoid (Hawkins *et al.,* 1975; Walker *et al.,* 1992), whereas in hamsters Muridae / Cricetinae both cortisol and corticosterone are present in comparable levels (Ronchi *et al.,* 1998). In addition to differences in the presence or absence of cortisol and corticosterone, the absolute levels of these hormones are of interest in their own right (Claman, 1972). Extremely high absolute levels of GCs in some species have been associated with low binding affinities for the hormones, for example, as in the guinea pig, which has high cortisol and low binding affinity (Keightly and Fuller, 1995). This may be the case for degus, with their extremely high cortisol titers.

The high levels of cortisol in female degus during lactation and the contrasting low levels during mating show that reproductive function in general, together with its endocrine mechanisms and energy demands, does not bear a constant relationship to GC function in females. Thus it seems appropriate to view high GCs as potential suppressors of reproduction only during certain stages of reproductive activity, and in combination with chronic stress, perhaps leading to suppression of ovulation or early gestation. This view is consonant with the interpretation that mammalian GC function has an impact on reproduction that is temporally and situationally variable (Brann and Mahesh, 1991). Levels of GCs have also been shown to peak during lactation in ground squirrels (Boswell *et al.,* 1994) and in rats (Walker *et al.,* 1992). The action of GCs on mammary tissue is known to be a requirement for milk production (Voogt *et al.,* 1969). Levels of energy demand, social stress or stability, and body condition all vary in different phases of the reproductive cycle, and investigations have demonstrated roles of GCs in energy balance and feeding that are independent of reproduction (King *et al.,* 1988; Berdanier, 1989; and Green *et al.,* 1992) and also that appear to be independent of the ''resistance to stress'' concept (Munck *et al.,* 1984). The basic consistency of GC secretion seems to be an elevated level associated with increases in food intake and gain in body mass. Thus it seems reasonable to suggest that cortisol plays a role in the regulation of body mass and energy balance in degus, and that higher levels of the hormone may be associated with anabolic effects, i.e., the energy acquisition associated with lactation (Veloso, 1997).

We obtained initial evidence that a short-term increase in cortisol can occur in response to a transient, acute stressful event, i.e., handling an animal after removal from a trap 1 or 2 h after capture. A pharmacologically induced stress in guinea pigs produced a level of increase in cortisol (Milanes *et al.,* 1990) similar

to that which we observed in degus. The quiet behavior of degus resting in traps and the adrenocortical response to handling do not suggest that trapping per se is a major stressor in degus. More observations are needed to document and understand this GC increase more thoroughly in degus and other rodent species under field conditions. The association of GCs with behavioral stresses (including social stress) in free-living baboons has been described by Sapolsky (1987), but no such data are available for rodents.

The levels of T in male degus over the year remained in a generally very low range. However, during mating, when the mean concentration of T was highest and nearly all males had detectable T (Table 1), degus showed their lowest cortisol levels (Fig. 2). Such a complementary pattern is consistent with the previously described suppressive effect of T on GCs in mammals (Rosner, 1990). This pattern was reversed by the time of lactation in 1997, when cortisol rose greatly and T was undetectable in most males. The low range of T values that we found in the field is similar to those reported for degus in the laboratory (Bustos-Obregón and Ramirez, 1997), using the same commercially available RIA kit that we did. These findings fail to support our hypothesis that T would be significantly higher in the field due to male aggressiveness associated with competition for mates. The plasma T levels of degus are considerably less than those in guinea pigs (Fenske, 1996). Such low levels of T warrant further studies of the mating system of the degu. Interspecific variation in absolute levels of T has been correlated with differences in mating system among other rodents (Klein and Nelson, 1998).

Our analysis was limited to measuring T in unextracted plasma. Future studies might benefit from solvent extraction, e.g., dichloromethane, of steroids from plasma before RIA and measurement of other androgens such as 5-α-dihydrotestosterone and androstenedione. Just as we hypothesized low GC-receptor affinities associated with high cortisol levels in degus, we can likewise hypothesize the presence of an androgen receptor with high binding affinity for the low levels of T.

It is noteworthy that juvenile males, upon postweaning emergence, showed elevated levels of T. This corresponds to the sort of prepubertal ''pulse'' of T that represents an organizational action of this hormone, as known in other mammals (Goldman, 1981).

The mating and initiation of a second bout of reproduction that we observed in September 1997 indicate that at least some males were capable of successful mating despite reduced T production. Female participants in this second bout of breeding apparently entered estrus following parturition and while in early lactation. The concept of reduced plasma T associated with a second breeding bout during a single season has previously been identified in a variety of reproductive systems (Wingfield *et al.*, 1990).

The observation that both male and female degus show a marked natural annual cycle of change in plasma levels of cortisol suggests that the regulation of energy mobilization is mediated to some extent by GCs. The fact that the sex steroid T can show a complementary and possibly suppressive relationship to cortisol further suggests interactions between both these endocrine systems and the basic regulatory physiology associated with reproductive function, energy balance, and the response to stressors. Further field and experimental work is now suggested by these general hypotheses related to cortisol and T and the physiology they control.

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