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REPRODUCTIVE AND POST-REPRODUCTIVE HORMONE LEVELS IN THE LIZARD *SCELOPORUS VIRGATUS*

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RESUMEN

Los niveles plasmáticos de seis hormonas (estradiol, progesterona, testosterona, dihidrotestosterona, androstenediona y corticosterona) en machos y hembras de *Sceloporus virgatus* (Phrynosomatidae) fueron obtenidos durante y después de la temporada alta de apareo. Se encontró variación en los niveles hormonales relacionados con la temporada de la actividad reproductiva. Las hembras tuvieron un nivel de corticosterona más alto en agosto (después de la oviposición) que en abril (inmediatamente después de la eclosión), mientras que en los machos el nivel fue más bajo en agosto. La variación basal de la corticosterona podría reflejar diferencias sexuales en la época de máximo estrés fisiológico. Los machos presentaron altos niveles de las hormonas androgénicas en los meses de abril y mayo, coincidiendo con la temporada alta de apareo. Muchas lagartijas de la familia Phrynosomatidae muestran coloración ventral durante los despliegues sociales. En algunas especies de lagartijas se han reportado influencias androgénicas sobre esta coloración ventral. Tanto los machos como las hembras de *S. virgatus* presentan una gran reducción en la cantidad e intensidad de la mancha azul en la parte ventral en comparación con otras especies del mismo género. Sin embargo, la variación en el tamaño y brillo de la mancha azul, en la parte ventral del cuello, no está relacionada con la variación de los niveles hormonales. Los niveles máximos de testosterona en los machos de *S. virgatus* son similares a los encontrados en otras especies de *Sceloporus* con manchas azules más grandes y brillantes.
Palabras Clave: Hormonas, *Sceloporus virgatus*, coloración, lagartijas

ABSTRACT

Plasma levels of six hormones (estradiol, progesterone, testosterone, dihydrotestosterone, androstenedione, and corticosterone) were obtained for males and females of *Sceloporus virgatus* (Phrynosomatidae) during and after the seasonal peak of mating activity. Seasonal variation in hormone levels was found. Females had higher corticosterone levels in August (well after oviposition) than in April (soon after emergence), but male corticosterone levels were lowest in August. Seasonal variation in basal corticosterone levels may reflect between-sex differences in the time of peak physiological stress. Male androgen levels peaked in April and May, coinciding with the peak of mating activity. Ventral coloration is exhibited during the social displays of many phrynosomatid lizards. Androgenic influences on ventral coloration have been documented in some lizards. Males and females of *S. virgatus* have a greatly reduced amount and intensity of blue ventral coloration relative to most other species in the genus. Variation in the size and color intensity of the blue ventral throat patch in males

was not associated with variation in male hormone levels. Male peak testosterone levels in *S. virgatus* were comparable to those reported for other *Sceloporus* species with larger and brighter blue patches.
Key Words: Hormones, *Sceloporus virgatus*, coloration, lizard.

INTRODUCTION

Although the field endocrinology of some lizard species has been well studied (*Sceloporus jarrovi*: Moore, 1986; *Sceloporus occidentalis*: Dunlap and Schall, 1995; *Urosaurus ornatus*, Moore *et al.* 1991), there exist few comparative data on breeding-season hormone levels for related species. This paper documents hormone levels in a sample of free-living males and females of *Sceloporus virgatus* during and after the breeding season. Plasma levels of estradiol (E2), progesterone (P4), testosterone, dihydrotestosterone, androstenedione, and corticosterone were sampled in April and May (during the breeding season), in June (early in the post-mating season), and in August (well after the breeding season). Corticosterone is of particular interest, as it is a possible indicator of physiological stress in vertebrates (Greenberg *et al.* 1984; Moore *et al.* 1991). For example, food-deprived *Sceloporus occidentalis* have elevated levels of corticosterone (Dunlap, 1995b). As possible indices of body condition, I also examined seasonal trends in hematocrit and plumpness. Hematocrit, the percent red cell volume in blood, is lower in food-deprived *S. occidentalis* than in control lizards (Dunlap, 1995b). Trends identified in the current analysis suggest areas for future research on the field endocrinology of this species.

Testosterone is linked to the expression of many male secondary sexual characters in vertebrates (Ligon *et al.* 1990; Folstad and Karter, 1992; Díaz *et al.* 1994; Galeotti *et al.*, 1997). This leads to the question of whether testosterone contributes to the differential expression of secondary sexual characters among closely related species. One possibility is that variation in the expression of secondary sexual characters may correspond to differences in the absolute level of circulating testosterone among breeding males (Emerson *et al.* 1993).

Lizards in the genus *Sceloporus* vary considerably in the amount and brightness of blue ventral coloration, which is exhibited during social displays (Smith, 1939). The degree of sexual dimorphism in ventral color also varies, even among closely related species. *Sceloporus virgatus* has much less and much paler blue coloration than most congeners (Stebbins, 1985). The degree of sexual dimorphism in the blue ventral color is slight during part of the year, but females develop bright orange coloration during the breeding season (Vinegar, 1972).

Androgenic hormones mediate the expression of blue ventral coloration in *Sceloporus occidentalis* (Kimball and Erpino, 1971) and *Sceloporus undulatus erythrocheilus* (Rand, 1992), as well as in a group closely related to *Sceloporus*

(*Urosaurus ornatus*: Hews and Moore, 1995). In males of *Sceloporus gadoviae*, an ontogenetic increase in blue ventral coloration coincided temporally with testes enlargement (Lemos-Espinal *et al.* 1996). In this paper, possible hormonal correlates of natural levels of blue ventral coloration in males of *S. virgatus* were considered. Circulating levels of testosterone, dihydrotestosterone, and androstenedione were examined relative to variation in the size and brightness of the blue ventral throat patch. Peak plasma levels of testosterone in males of *S. virgatus* were also compared to those of related *Sceloporus* species with greater, more typical levels of blue ventral coloration.

MATERIALS AND METHODS

Sceloporus virgatus is distributed principally in the Sierra Madre Occidental of Mexico at elevations from about 1490 to 3080 m (Stebbins, 1985). I sampled free-living *S. virgatus* at the northern edge of its range, in the Chiricahua Mountains of southeastern Arizona (near Portal) at approximately 1650 m. Between April and August in 1991 and 1992, I obtained plasma from 25 males and 19 females, of which 21 males and 18 females were large enough that they were probably reproductively mature (Vinegar, 1975; Ballinger and Kettels, 1983; Smith *et al.* 1995). Only these individuals (at least 50 mm snout-vent length, SVL) were included in the hormone analyses. I also obtained information on seasonal variation in extent and intensity of blue ventral coloration for an additional 38 males that were captured at the beginning (April) and just after (June) the breeding season in 1992 or 1993.

No animals were killed for examination of reproductive tracts, but females were examined externally and palpated. The April females were captured before the beginning of courtship activity that season (pers. obs.) and had probably not yet been inseminated that year. Three of the April females had faint orange patches. Both females captured in June appeared gravid. They had a plump appearance, and eggs could be felt upon palpation. Females of *S. virgatus* lay a single clutch of eggs in early to mid July (Vinegar, 1975; Rose, 1981), following heavy summer rains. Thus, the August samples represent individuals that already have completed oviposition.

The basic seasonal pattern of male reproductive activity is known from previous studies on *S. virgatus* in the Chiricahuas. Emergence from hibernation is in March and early April, followed by high levels of territorial activity in April (Rose, 1981; Ballinger and Kettels, 1983). Courtship occurs primarily in May. Thus, the breeding season for *S. virgatus* in the Chiricahuas is during April and May. In June females generally perform stereotypical rejection displays in response to male courtship.

In July and August, male territorial and courtship behavior seldom or never occurs (pers. obs.).

Capture and blood sampling were completed within a few minutes of first seeing the animal. After a blood sample (20-100 μl) was taken through the postorbital sinus (MacLean *et al.* 1973; Moore, 1986), I measured the snout-vent length (SVL) and body weight. These measurements were taken because many physiological factors vary with body size (Díaz *et al.* 1994; Dunlap, 1995a) and because seasonal variation in size-adjusted mass has been documented in *Sceloporus* lizards (Méndez de la Cruz and Gutiérrez-Mayén, 1991). I also measured the length and width of the right side blue ventral throat patch (if present) and assessed the intensity of the blue ventral coloration by comparison with a set of color standards (Smithe, 1985). The lizard was then released in a sheltered place near the location it was first seen.

Blood samples were placed on ice in the field. Upon return to the laboratory, the capillary tubes were centrifuged to separate the plasma and red blood cell layers. The total length of blood in the capillary tubes, as well as the length of the red blood cell layer, were measured so hematocrit could be calculated. The plasma was stored at -20°C or -80°C until radioimmunoassay.

The radioimmunoassays were performed using standard techniques (Emerson *et al.* 1993) by the Endocrine Services Laboratory of the Oregon Primate Research Center. The following hormones were measured following ether extraction and purification on Sephadex LH-20 chromatography columns: estradiol (E2), progesterone (P4), testosterone, dihydrotestosterone, androstenedione, and corticosterone. Plasma volumes ranged from 10 to 75 μl per sample. All samples of more than 10 μl were assayed in two or three aliquots (of 5 μl, 20 μl, or 50 μl). Extraction and purification losses were estimated by including samples of ^{3}H steroids in similar volumes of monkey serum. These samples were processed in parallel with the lizard plasma. Recoveries ranged from 69 to 95%. All lizard samples were run in a single assay for each steroid. The intra-assay coefficients of variation ranged from 5 to 11%. Estradiol, progesterone, and androstenedione values for the one sample of only 10 μl volume were at or beyond the limits of the standard curve, so these values were not included in the data analyses.

Data from male and female lizards were analyzed separately. For the sample of males captured more than once within a season, I used a paired t-test and a two-sided sign test to examine whether the patch size or color intensity changed between April and June. Hormone levels were not normally distributed in either males or females, even after $\log_{10}$ transformation, so nonparametric methods were used in analyses involving hormone levels. The area of the blue throat patch was estimated as the area of an ellipse. Spearman's rank correlation (r_s) was used to examine the relationship between blue coloration (both patch area and color

intensity) and the levels of each of the androgens' (testosterone, dihydrotestosterone, androstenedione). Kruskal-Wallis analysis of variance and the Mann-Whitney U test were used to examine changes in hormone levels over time. Analysis of variance (ANOVA) was used to examine seasonal variation in hematocrit, SVL, and the residual of mass on SVL. Pairwise comparisons of time periods were made with Fisher's least significant difference test (LSD). There is no nonparametric equivalent of analysis of covariance (ANCOVA), so I used an alternative method to examine the possibility that apparent seasonal variation in a hormone level could really be explained by seasonal variation in SVL. In cases where significant seasonal variation in a hormone levels was detected, I checked whether this result could be explained by a combination of seasonal variation in SVL along with a significant within-month association (r_s) between SVL and the hormone level.

RESULTS

There was significant seasonal variation in male hematocrit (Fig. 1; April-May, June, and August; $F_{2,18} = 6.71$, $P = 0.007$). Mean hematocrit was significantly lower in August than in April-May ($P = 0.002$, Fisher's LSD) or June ($P = 0.049$, Fisher's LSD). April-May and June males did not differ significantly in hematocrit. Male hematocrit was not significantly correlated with male SVL (Pearson's $r = 0.14$, $n = 21$, $P = 0.554$). Overall, there was no significant variation in male SVL over time ($F_{2,18} = 2.76$, $P = 0.090$), though males captured in June were larger than those captured in August ($P = 0.037$, Fisher's LSD). April-May males, which were of intermediate mean SVL, did not differ significantly in size from those of either June or August. There was significant seasonal variation in male plumpness, measured as the linear regression residual of mass on SVL (Fig. 2; $F_{2,18} = 5.30$, $P = 0.015$). Males were significantly lighter relative to SVL in June than in April-May ($P = 0.006$, Fisher's LSD) or August ($P = 0.026$, Fisher's LSD). April-May and August males did not differ in mean plumpness.

Male levels of estradiol, dihydrotestosterone, and corticosterone in April-May, June, and August varied significantly among the three time periods (Kruskal-Wallis analysis of variance, Table 1). There was also a nearly significant trend for seasonal variation in androstenedione levels ($P = 0.020$, $alpha_{adj} = 0.017$) and a similar trend for testosterone ($P = 0.067$). Estradiol levels were highest in April-May, when mean progesterone levels were also high. Peak levels of all androgens (testosterone, dihydrotestosterone, androstenedione) were observed in April-May (Table 1). Corticosterone levels were lower in August than in April-May or June.

The seasonal trends in male hormone levels cannot be explained by covariation with SVL. Estradiol, dihydrotestosterone, and corticosterone levels were not

significantly correlated with SVL within either of the time periods for which the sample size was sufficient for Spearman's correlation analysis (April-May and June). Androstenedione levels were significantly positively correlated with SVL in June ($r_s = 0.89$, $n = 6$, $P = 0.05$), but the highest androstenedione levels were observed in April-May, when mean SVL was smaller than in June (though not significantly so).

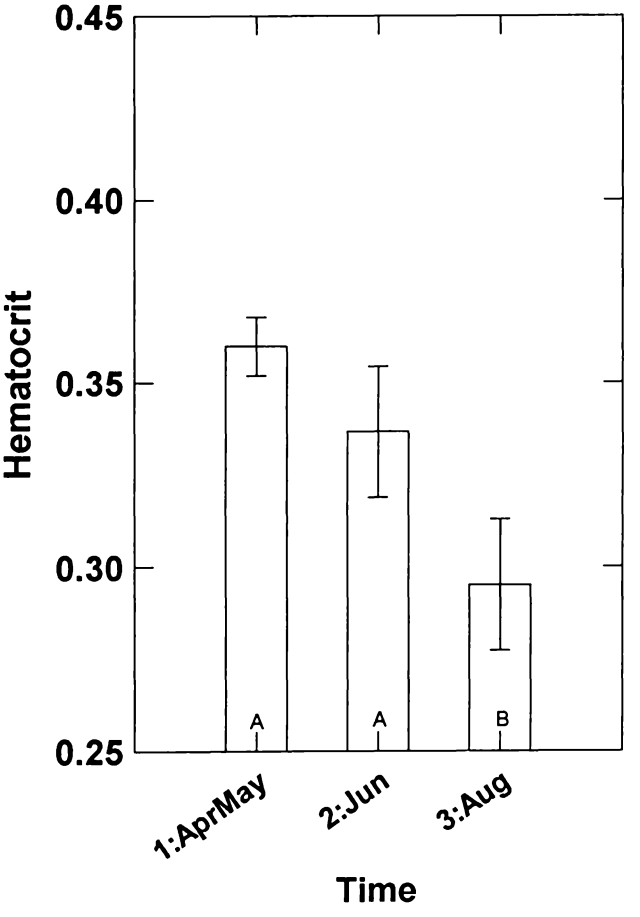

Figure 1

Hematocrit (mean ± SE) of males of *S. virgatus*, during the mating season (April-May), immediately after the mating season (June), and well after the cessation of mating activity (August). Sample sizes are $n = 11$ in April-May, $n = 6$ in June, and $n = 4$ in August. Different letters indicate means that are significantly different (Fisher's LSD, $P < 0.05$).

Among the males captured more than once within a season, patch size (number of blue throat scales) was not significantly different between April and June ($|t| = 1.140$, $df = 37$, $P = 0.262$) and there was no tendency for patch size either to increase or decrease (sign test: $df = 38\text{-}8 = 30$, $P = 0.855$). Similarly, the intensity of the blue coloration did not vary between April and June ($|t| = 0.133$, $df = 37$, $P = 0.895$) and there was no trend for males to become either brighter or duller (sign test: $df = 38\text{-}11 = 27$, $P = 1.000$).

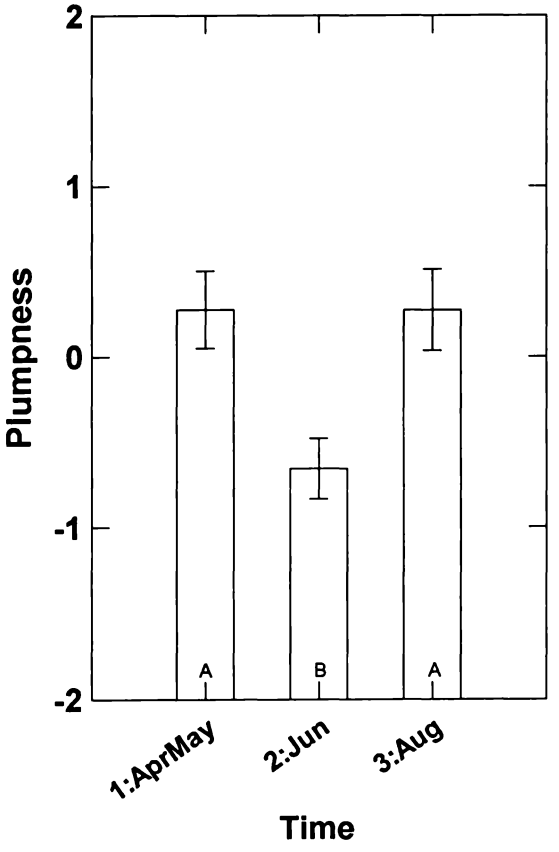

Figure 2

Plumpness (mean ± SE) of males of *S. virgatus*, during the mating season (April-May), immediately after the mating season (June), and well after the cessation of mating activity (August). Plumpness is measured as the linear regression residual of mass on SVL. Sample sizes are n = 11 in April-May, n = 6 in June, and n = 4 in August. Different letters indicate means that are significantly different (Fisher's LSD, $P < 0.05$).

Table 1

Hormone levels in males of *Sceloporus virgatus* from April to August. Hormones are abbreviated by the first letter (E = estradiol in pg/ml, P = progesterone in pg/ml, T = testosterone in ng/ml, D = dihydrotestosterone in ng/ml, A = androstenedione in pg/ml, C = corticosterone in ng/ml. Nondetectable hormone levels are indicated by "ND." Only individuals likely to be reproductively mature (at least 50 mm SVL) are included. Sample sizes are n = 11 in April-May (n = 10 for E and A; n = 9 for P), n = 6 in June, and n = 4 in August. The differences in levels among the three time periods (April-May, June, and August) are tested with Kruskal-Wallis analysis of variance (test statistic KW). Values marked with an asterisk are significant with the sequential Bonferroni correction (Rice, 1989).

Hormone	Reproductive		Post-reproductive					
	April-May		June		August			
	mean	median	mean	median	mean	median		
	(range)		(range)		(range)		KW	P
E	49	43	35	36	21	21	10.3	0.006 *
	(23-122)		(25-44)		(18-24)			
P	127	140	78	65	93	51	0.9	0.629
	(ND-248)		(ND-254)		(ND-272)			
T	75.78	78.52	36.66	34.46	41.38	30.76	5.4	0.067
	(19.57-129.68)		(16.05-66.77)		(24.72-79.29)			
D	2.77	2.36	0.84	0.65	1.55	1.36	9.7	0.008 *
	(1.14-8.06)		(0.33-1.81)		(0.67-2.81)			
A	1029	1124	617	595	293	302	7.8	0.020
	(440-1746)		(246-1061)		(56-513)			
C	15.71	11.76	21.90	19.90	6.88	6.60	10.1	0.006 *
	(6.60-31.96)		(12.87-33.63)		(6.16-8.15)			

The area of the blue throat patch increased significantly with SVL (Pearson's $r = 0.71$, $n = 20$ males, $P < 0.001$). None of the individual hormone levels were significantly correlated with the residual of blue throat area on SVL (Spearman's r_s, $P > 0.05$).

The intensity of blue coloration was negatively correlated with dihydrotestosterone level ($r_s = -0.51$, $n = 16$, two-tailed $0.02 < P < 0.05$), but this trend lost significance when one individual with an extremely high dihydrotestosterone level (8.06 ng/ml) and no blue patch was excluded ($r_s = -0.40$, $n = 15$, two-tailed $P > 0.10$). No other hormone levels were significantly correlated with the intensity of blue coloration.

In contrast to the pattern in males, female hematocrit did not show significant seasonal variation (Fig. 3; April vs. August, $F_{1,14} = 0.54$, $P = 0.473$). Female hematocrit was not significantly correlated with SVL (Pearson's $r = 0.07$, $n = 18$,

P = 0.793). There was also no seasonal variation in average female SVL (April vs. August, $F_{1,14} = 2.28$, P = 0.154). Thus, any seasonal patterns in female hormone levels cannot be attributed to covariation with SVL.

A comparison of female hormone levels in April and August indicated no statistically significant differences between the breeding and non-breeding seasons (Mann-Whitney U-test, Table 2). However, there were several trends of possible biological significance. There was an apparent decrease in female estradiol levels from April to August (P = 0.059). In both April and August, plasma progesterone levels in females varied substantially. Half the females in each month had undetectable progesterone levels. For all three androgens (testosterone, dihydrotestosterone, androstenedione) mean and median values were higher in August than in April, though these differences were not statistically significant. Female levels of corticosterone likewise were higher in August than in April (P = 0.093).

Table 2

Hormone levels in females of *Sceloporus virgatus* from April to August. Hormones are abbreviated by the first letter (E = estradiol in pg/ml, P = progesterone in pg/ml, T = testosterone in ng/ml, D = dihydrotestosterone in ng/ml, A = androstenedione in pg/ml, C = corticosterone in ng/ml. Nondetectable hormone levels are indicated by "ND." Only individuals likely to be reproductively mature (at least 50 mm SVL) are included. The sample sizes are n = 8 in April, n = 2 in June, and n = 8 in August. The differences in levels between April (reproductive period) and August (post-reproductive period) are tested with the Mann-Whitney U-test.

Hormone	Reproductive		Post-reproductive				
	April		June	August			
	mean (range)	median	(range)	mean (range)	median	U	P
E	172 (61-405)	160	(617-5282)	98 (40-220)	66	50.0	0.059
P	57 (ND-316)	4	(33-4886)	130 (ND-935)	2	33.0	0.911
T	0.53 (0.04-1.09)	0.48	(0.28-31.31)	1.01 (0.10-1.96)	1.02	19.5	0.189
D	0.13 (<0.01-0.59)	0.08	(<0.01-4.41)	0.28 (0.03-0.88)	0.24	17.0	0.115
A	163 (24-324)	163	(121-2732)	232 (83-473)	211	21.0	0.248
C	3.96 (1.53-7.19)	3.35	(3.83-37.74)	7.09 (1.98-13.72)	7.43	16.0	0.093

Statistical comparisons were made only between April and August, but an additional two females were sampled in June. One June female had extremely high levels of all hormones relative to other females (Table 2). This female was the largest individual sampled (70 mm SVL). She was visibly distended with eggs. She also had several light blue scales on the belly. Blue belly coloration is rarely expressed in males or females of *S. virgatus* (pers. obs.). The other June female also had an estradiol level higher than that found in any April or August female, but her other hormone levels were exceeded by those of some females captured in April or August.

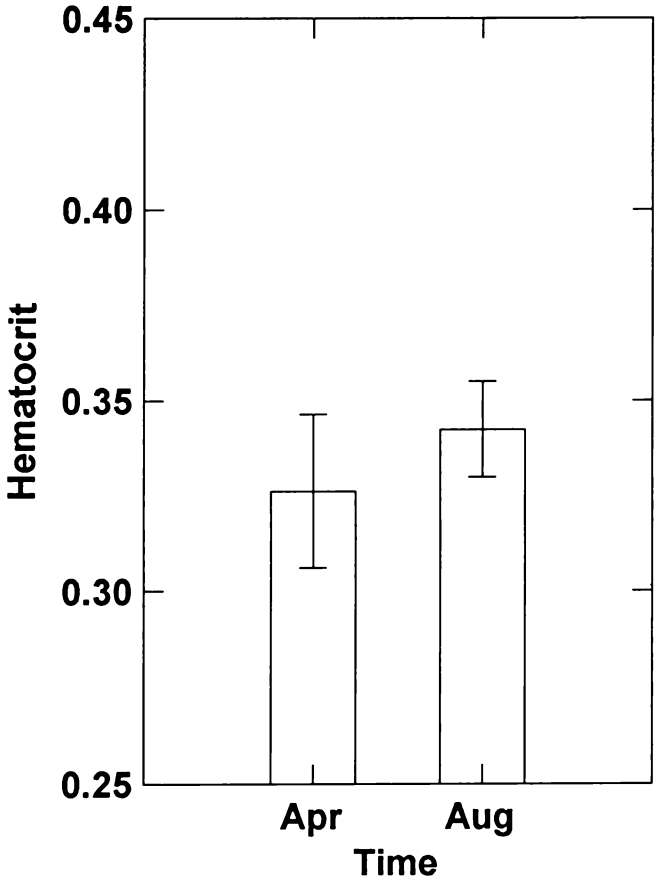

Figure 3

Hematocrit (mean ± SE) of females of *S. virgatus*, during (April) and after (August) the mating season. Sample sizes are n = 8 in each month.

DISCUSSION

Peak testosterone levels in males of *S. virgatus* are comparable to those of other *Sceloporus* species (McKinney and Marion, 1985; Moore, 1986; Dunlap and Schall, 1995), suggesting that the extraordinarily small amount of blue coloration in *S. virgatus* is not due simply to lower circulating hormone titers. In the studies of *S. jarrovi* (Moore, 1986) and *S. occidentalis* (Dunlap and Schall, 1995), blood samples were collected in the field immediately after capture, as was done in this study of *S. virgatus*. In the study of *S. undulatus*, seasonal testosterone levels were based on samples obtained up to 24 hours after capture (McKinney and Marion, 1985). Tree lizard (*Urosaurus ornatus*) testosterone levels after one day of captivity were approximately 75% of those measured in free living males bled immediately after capture (Moore *et al.* 1991). Assuming a similar depression in testosterone due to handling, peak values in *S. undulatus* would be within the range found for *S. virgatus*.

Interspecific differences in androgen levels have been investigated for few vertebrate groups. Tropical frog species of several genera varied in average androgen levels, but this variation was not closely associated with the level of expression of secondary sexual characters (Emerson and Hess, 1996). Within the frog genus *Rana*, the distribution of secondary sexual characters is consistent with the possibility that a drop in androgen levels was involved in the loss of these traits in some species (Emerson, 1996).

In males of *S. virgatus*, adult circulating levels of androgens are apparently of no importance in the expression of the size and intensity of blue ventral coloration. In an associated experimental study, there was no apparent influence of exogenously-administered testosterone early in life on the subsequent size or intensity of the blue ventral patches in *S. virgatus* (Abell, in press).

Levels of androgens, estradiol, and progesterone in males of *S. virgatus* were high in April-May, suggesting peak levels around the time of territorial defense and courtship. The close temporal association of gonadal activity, as indicated by sex steroid hormones, and mating activity suggests an associated reproductive pattern, in which mating and gametogenesis are temporally associated (Crews, 1987).

Male body weights relative to SVL were significantly higher in August than in June, suggesting that by August males have usually recovered from the energetic stress of reproductive activity. Male corticosterone levels were lowest in August. Other authors have noted that males of *S. virgatus* have higher activity and movement levels in April and early June than in late June through early September (Rose, 1981) and higher field metabolic rates in May than in August (Merker and Nagy, 1984). In another phrynosomatid lizard, *Uta stansburiana*, male corticosterone levels also peaked in the spring, when reproductive and territorial

activity is maximal (Wilson and Wingfield, 1994). Corticosterone has been suggested as an indicator of stress in lizards (Greenberg *et al.*, 1984; Moore *et al.*, 1991; Dunlap, 1995b). The low male corticosterone levels observed in August may indicate that this time is less stressful than the mating season. However, basal corticosterone levels are not consistently correlated with physiological condition in lizards (review in Dunlap and Wingfield, 1995). In a study of several populations of *Sceloporus occidentalis*, Dunlap and Wingfield (1995) found no consistent seasonal trends in basal corticosterone levels between April and August. High spring corticosterone levels in males of *S. virgatus* may occur due to a need for rapid mobilization of energy to support territorial activity and courting (Wilson and Wingfield, 1994). Mean male hematocrit was lowest in August, but the meaning of seasonal variation in hematocrit is not clear in lizards (Dunlap, 1995a).

In contrast to males, females of *S. virgatus* exhibited nonsignificant trends for higher androgen and corticosterone levels in August than in April, suggesting that seasonal high levels are associated with activity occurring well after oviposition has been completed. During the postbreeding season, females of this species have activity levels higher than those of males (Rose, 1981), as well as higher field metabolic rates and feeding rates than those of males (Merker and Nagy, 1984). It is possible that females in the postbreeding season are stressed by intense competition for food to replenish fat reserves before winter. If this pattern of seasonal variation in female corticosterone levels is verified with a larger sample, it would contrast with the pattern in *Uta stansburiana*, where peak female corticosterone levels generally correspond with the spring peak of reproductive mass (Wilson and Wingfield, 1992, 1994).

The trends identified in this study suggest the opportunity for additional work on seasonal variation in corticosterone levels in the two sexes, relative to indices of body condition such as size-adjusted body mass (Dunlap and Wingfield, 1995) and parasite infestation (Dunlap and Schall, 1995; Salvador *et al.* 1996. Comparative work should include populations in the central part of the species' range as well as this one at the northern extreme.

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