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Environmental and Seasonal Adaptations of the Adrenocortical and Gonadal Responses to Capture Stress in Two Populations of the Male Garter Snake, *Thamnophis sirtalis*

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ABSTRACT Stress and reproduction are generally thought to work in opposition to one another. This is often manifested as reciprocal relationships between glucocorticoid stress hormones and sex steroid hormones. However, seasonal differences in how animals respond to stressors have been described in extreme environments. We tested the hypothesis that garter snakes, *Thamnophis sirtalis*, with limited reproductive opportunities will suppress their hormonal stress response during the breeding season relative to conspecifics with an extended breeding season. The red-sided garter snake, *T.s. parietalis*, of Manitoba, Canada, has a brief breeding season during which males displayed no change in either plasma levels of testosterone or corticosterone, which were both elevated above basal levels, in response to capture stress. During the summer, capture stress resulted in increased plasma corticosterone and decreased testosterone. During the fall, when mating can also occur, males exhibited a significant decrease in testosterone but no increase in corticosterone in response to capture stress. The red-spotted garter snake, *T.s. concinnus*, of western Oregon, has an extended breeding season during which males displayed a stress response of increased plasma corticosterone and decreased testosterone levels. The corticosterone response to capture stress was similar during the spring, summer, and fall. In contrast, the testosterone response was suppressed during the summer and fall when gametogenesis was occurring. These data suggest that male garter snakes, in both populations, seasonally adapt their stress response but for different reasons and by potentially different mechanisms. *J. Exp. Zool. 289:99–108, 2001.*

Hormonal responses to physiological stress usually involve activation of the hypothalamic-pituitary-adrenal (HPA) axis and increases in plasma glucocorticoid concentrations, which can result in concomitant decreases in plasma sex steroids (Greenberg and Wingfield, '87). These effects occur primarily because of negative interactions between the HPA axis and the hypothalamic-pituitary-gonadal (HPG) axis at multiple levels with the end result being generalized suppression of reproductive function (Rivier and Rivest, '91) The stress response can be initiated in response to social cues (e.g., Sapolsky, '87; Knapp and Moore, '95, '96; Schuett et al, '96), biotic and abiotic environmental perturbations (e.g., Wingfield et al., '82; Wingfield, '88), as well as in response to the stress of capture and handling (e.g., Moore et al., '91; Zerani et al., '91).

However, animals inhabiting extreme habitats with limited breeding opportunities, will often suppress their stress response during the breeding season to maximize their limited reproductive chances (Silverin and Wingfield, '98; Wingfield et al., '98). While this could result in an increased probability of mortality, it minimizes the chances the animal will miss a reproductive opportunity (Wingfield et al., '95). Studies of birds have found that although some species do exhibit a stress response during the breeding season (Dawson and Howe, '83, Astheimer et al., '95), others do not or have a diminished one (Wingfield et al., '94; Silverin and Wingfield, '98). This modulation of the stress response occurs both in the extreme environments of the arctic (Wingfield et al., '95) and the desert (Wingfield et al., '92) and is proposed to be related to the length of the reproductive sea-

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son (Wingfield, '94; Wingfield et al., '98). Although some studies have investigated hormonal responses to capture stress in reptiles (reviewed by Lance, '90; Guillette et al. '95; Tyrell and Cree, '98) only one series of studies has examined seasonal and population variation of the stress response (Dunlap and Wingfield, '95a,b). Differences in the hormonal stress response were found between populations of the fence lizard, *Sceloporus occidentalis*, at the center versus the limit of their geographic range and between the dry versus wet part of the year. Individuals at their range limit and during the dry season displayed the greatest increase in corticosterone in response to the stress of capture. However, there was no consistent pattern of variation in basal levels of corticosterone (Dunlap and Wingfield, '95a). In a seasonal investigation of baseline stress hormone levels in seven populations of the side-blotched lizards, *Uta stansburiana*, levels of corticosterone were positively associated with activity patterns (Wilson and Wingfield, '94). Although these types of studies document seasonal and environmental adaptations of the corticosterone response possibly related to reproductive cycles, they fail to investigate related changes in plasma sex steroid concentrations in response to capture stress.

We tested the hypothesis that populations of garter snakes with limited breeding opportunities will suppress their hormonal stress response during the breeding season. This was done by comparing the stress response, in terms of corticosterone and testosterone, between populations with brief and extended breeding seasons as well as between seasons within each population. Thus, this study investigated both environmental and seasonal adaptations of the adrenocortical and gonadal responses to capture stress in two free-living populations of the garter snake, *Thamnophis sirtalis*. This species is the widest ranging reptile in North America and thus occupies a wide range of habitats (Gregory, '77; Larsen and Gregory, '93; Gregory and Larsen, '96). Males of this species appear to exhibit a rather conserved annual testosterone cycle with peak plasma levels during the late summer associated with spermatogenesis and declining through the winter and spring breeding season (Fox, '52, Crews et al., '84; Weil, '85; Krohmer et al., '87). The red-sided garter snake, *T.s. parietalis*, of Manitoba, Canada is active for 4 months of the year and mates during a brief 3–4-week period in the spring. Previous studies of this population have shown that males are behaviorally resistant, at least in terms of sexual behavior, to capture stress (Moore et al., 2000a). Earlier evidence suggested that they were hormonally resistant to capture stress (Krohmer et al., '87) and more recent studies have demonstrated a hormonal response of increased plasma corticosterone and decreased testosterone in response to capture stress (Moore et al., 2000a). In contrast, the red-spotted garter snake, *T.s. concinnus*, of western Oregon is active for 10 months of the year and breeds during an extended 10–12-week period in the spring (Moore et al., 2000b). Because of their limited reproductive opportunities, we predicted that male *T.s. parietalis* would suppress their stress response during the spring mating period while maintaining it during other times of the year. Furthermore, *T.s. concinnus*, with their longer breeding season, would maintain a similar stress response throughout the year. We predicted that differences in initial levels of corticosterone would exist and would be associated with differences in body condition (mass per unit length) during different times of the year. These predictions were tested by subjecting males from both populations to capture stress and serial blood sampling during three distinct periods in the reproductive cycle: the spring breeding season, the summer feeding season, and the fall immediately preceding winter dormancy.

MATERIALS AND METHODS

Study sites and sampling periods

Free-living male red-sided garter snakes, *T.s. parietalis*, were captured and subjected to serial blood sampling during four times of the year. The first series of samples (early spring) was obtained at the beginning of the mating period immediately following winter dormancy on April 27, 1998. The second series (late spring) was obtained on May 19, 1998, towards the end of the mating period. The third series (summer) was obtained from 2–4 August, 1998 at the feeding grounds when there is no evidence of mating. To extend our comparison between breeding and non-breeding seasons, we used previously collected samples from the fall period when the animals had returned to the dens to prepare for winter dormancy and mating had been documented (Mendonca and Crews, '89). These samples (fall) were obtained between 10–22 September, 1995. Both spring and fall samples were from animals captured at the Narcisse Wildlife Management Area in the Interlake region of Manitoba, Canada. Summer samples were from animals that had migrated from the dens to the feeding grounds, and were captured on the

banks of Fish Lake, approximately 15 km west of Gimli, Manitoba.

Free-living male red-spotted garter snakes, *T.s. concinnus*, were captured from beneath cover boards at E.E. Wilson Wildlife Area, 15 km north of Corvallis, Oregon. Spring samples were obtained during the middle of the breeding period between April 2 and 12, 1999. To make comparisons between years, a second set of spring samples was obtained on April 5–6, 1995. The summer series of samples was obtained between July 6 and 15, 1999 when gonadal activity is minimal (Moore et al., 2000b). The final period of sampling occurred between September 8–15, 1999 when gonadal activity and testosterone levels peaked (Moore et al., 2000b).

Blood sampling

Each individual was bled from the caudal vein using heparinized 1-cc syringes and 25-g needles. A 100-µl whole blood sample was collected immediately upon capture and again at 1 hr and 4 hrs later. During the summer sampling period, *T.s. parietalis* were also bled 24 hr after capture. Animals were isolated in cloth bags (20 cm × 20 cm) between bleeds. Ten individuals were sampled at each period and site, except during the spring of 1995 when six male *T.s. concinnus* were sampled. Initial blood samples were obtained as quickly as possible from the time each animal was captured and always within 3 min. Blood samples were stored on ice until return from the field when they were centrifuged and the plasma separated. In Manitoba, samples were stored at –4°C until return to Oregon State University where they were stored at –60°C until assayed. All samples obtained in Oregon were stored at –60°C until assayed.

Body condition

Body size measurements of snout-vent length (SVL) and body mass were obtained for each individual. Body condition was defined as each individual's residual from the regression of body mass on SVL for each population, across seasons. Seasonal differences in body condition were compared. Plasma levels of testosterone and corticosterone were compared and correlated with body condition as well.

Radioimmunoassay

Plasma levels of testosterone and corticosterone were measured by radioimmunoassay following the procedures of Moore et al. (2000b). Briefly, duplicate plasma volumes of 10 µl were used in these assays. For individual recovery determination, each sample was equilibrated overnight with 2,000 cpm of tritiated testosterone and corticosterone (Amersham). Each sample was then extracted twice in 2 ml of diethyl ether and the ether phase removed and dried in a warm water bath, under a stream of nitrogen gas. The extracts were then resuspended in 10% ethyl acetate in isooctane. The samples were chromatographed through individual celite columns to separate the steroid fractions and neutral lipids. The fractions were eluted using stepwise increasing proportions of ethyl acetate in isooctane. The purified eluates were dried and resuspended in 500 µl of buffer (phosphate buffered saline with 0.1% gelatin) for the assay.

For the assay, individual sample recoveries were determined from 50 µl of the sample while 200 µl of the sample was allocated to each of two duplicates. Serial dilutions for the standard curves were performed in triplicate. All samples, including serial dilutions and 100% bound, were incubated overnight with 100 µl of antibody (testosterone antibody T-3003 from Wein and corticosterone antibody B21-42 from Endocrine Sciences) and 100 µl of tritiated steroid. Unbound steroid was separated using dextran-coated charcoal and the bound steroid decanted into scintillation vials. The samples were resuspended in 4 ml of toluene-based scintillation fluid, incubated for 12 hr and counted on a Beckman LS1800 scintillation counter. A cubic spline curve was fitted to the standard curve points and final steroid concentrations were calculated from this curve and adjusted based on individual recoveries. Recoveries averaged 60% and 93% for corticosterone and testosterone respectively. Intraassay variation was 14% for corticosterone and 10% for testosterone calculated from an assay of standards (n = 16) in the hands of ITM. Samples were analyzed in two assays with an interassay variation of 15% for both corticosterone and testosterone. Limits of detectability were approximately 5.17 ng/ml for corticosterone and 0.36 ng/ml for testosterone.

Statistics

Changes in plasma hormone levels following capture were analyzed by one-way repeated measures ANOVA. Differences in initial and stress hormone levels between the sampling periods were analyzed by one-way ANOVA. The relationships between plasma levels of testosterone and corticosterone, between snout-vent length and mass, and between hormone levels and body condition

were analyzed by linear regression analysis. Differences in body condition between seasons were analyzed by ANOVA or ANOVA on ranks if data were not normally distributed. For all tests the level of significance was $P < 0.05$. All data were analyzed using Jandel SigmaStat Version 2.0 statistical package.

RESULTS

Thamnophis sirtalis parietalis

Male *T.s. parietalis* exhibited a hormonal response to capture stress during non-breeding times of the year and not during the primary mating season (Fig. 1). During the early spring sampling period, neither plasma corticosterone levels (repeated measures ANOVA, F = 2.30, $P = 0.13$) nor testosterone levels (repeated measures ANOVA, F = 3.25, $P = 0.063$) changed in response to capture stress. Similarly, during the late spring neither plasma corticosterone levels (repeated measures ANOVA, F = 0.27, $P = 0.77$) nor testosterone levels (repeated measures ANOVA, F = 0.52, $P = 0.61$) changed in response to capture stress. During the summer sampling period, plasma corticosterone levels increased significantly in response to capture stress (repeated measures ANOVA, F = 16.71, $P < 0.001$) while plasma testosterone levels declined significantly (repeated measures ANOVA, F = 25.81, $P < 0.001$). There was no difference between 4-hr and 24-hr samples in either steroid (corticosterone: t-test, $t = -0.94$, $P = 0.36$; testosterone: Rank sum test, $t = 82.0$, $P = 0.089$). In contrast, during the fall sampling period, plasma corticosterone levels did not change in response to capture stress (repeated measures ANOVA, F = 1.77, $P = 0.198$) while plasma testosterone levels fell significantly (repeated measures ANOVA, F = 3.70, $P = 0.045$).

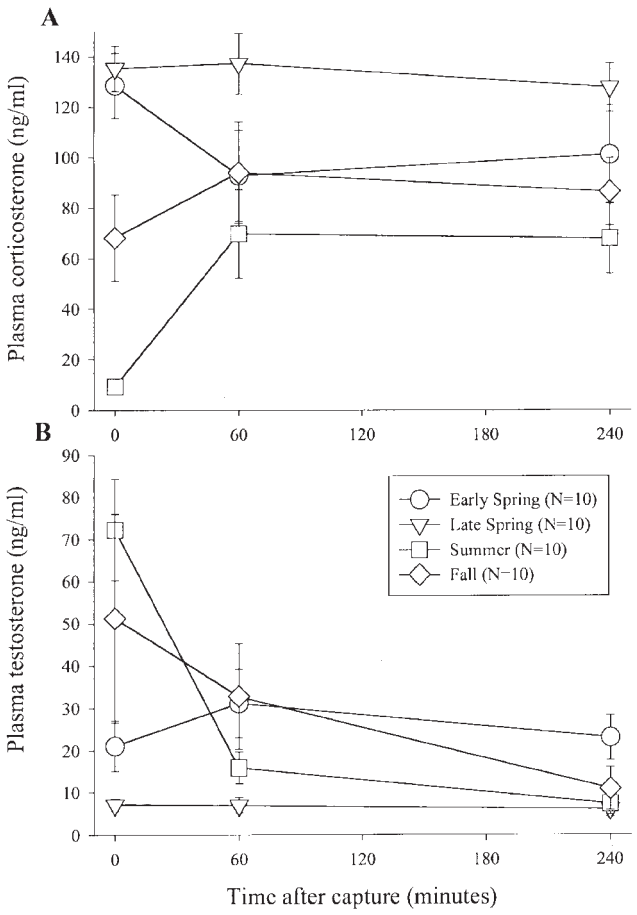

Fig. 1. Plasma corticosterone (**A**) and testosterone (**B**) responses to capture stress and serial blood sampling during four different periods in male red-sided garter snakes, *Thamnophis sirtalis parietalis*, from Manitoba, Canada.

Initial corticosterone levels were significantly different between the sampling periods (ANOVA, F = 25.32, $P < 0.001$) with the lowest levels in the summer, higher levels during the fall and highest levels during the early and late spring (Tukey test, $P < 0.05$). Initial plasma levels of testosterone were significantly different between the sampling periods (ANOVA, F = 4.34, $P = 0.01$) with the summer levels being higher than during the late spring periods (Tukey test: $P < 0.05$). Maximal levels of corticosterone were significantly different between the sampling periods (ANOVA, F = 3.00, $P < 0.043$) with higher levels during the late spring than during the summer (Tukey test: $P < 0.05$). Stressed levels of testosterone were significantly different between the seasons (ANOVA, F = 3.72, $P = 0.02$) with the early spring being higher than both the summer and late spring periods (Tukey test: $P < 0.05$).

There was a significant positive relationship, across all seasons, between snout-vent length and mass in our study population (linear regression, $R^2 = 0.763$, $P < 0.001$). An individual's body condition was defined as its residual from this regression. Body condition varied significantly by season (Fig. 2; ANOVA, F = 10.892, $P = 0.001$). In addition, there was a significant negative relationship between baseline corticosterone levels and body condition (Fig. 3; linear regression, $R^2 = 0.428$, $P < 0.001$). There was no relationship between testosterone levels and body condition (linear regression, $R^2 = 0.022$, $P = 0.365$).

Thamnophis sirtalis concinnus

Male *T.s. concinnus* exhibited a hormonal response to capture stress during all times of the

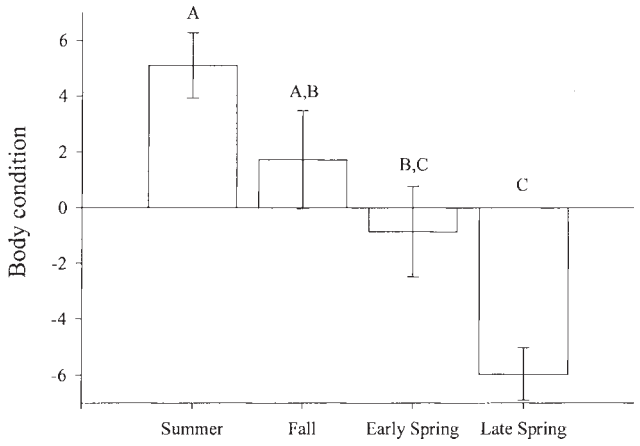

Fig. 2. Body condition during the four sampling periods for male red-sided garter snakes, *Thamnophis sirtalis parietalis*. Significant differences between the groups are signified by different letters above the columns.

year (Fig. 4). During the 1995 spring sampling period, plasma corticosterone levels increased significantly in response to capture stress (repeated measures ANOVA, F = 19.50, $P < 0.001$) while testosterone levels decreased significantly (repeated measures ANOVA, F = 7.33, $P = 0.011$). During the 1999 spring sampling period, plasma corticosterone levels were elevated in response to capture stress (repeated measures ANOVA, F = 4.51, $P = 0.026$) while plasma levels of testosterone decreased significantly (repeated measures ANOVA, F = 18.27, $P < 0.001$). During the summer sampling period, plasma corticosterone levels increased significantly in response to capture stress (repeated measures ANOVA, F = 9.92, $P = 0.001$). During this same period, plasma testosterone levels changed significantly (repeated measures ANOVA, F = 6.77, $P = 0.006$), however the difference was the result of an increase between the 1- and 4-hr samples (Tukey test, $P < 0.05$). During the fall sampling period corticosterone increased significantly in response to capture stress (repeated measures ANOVA, F = 10.92, $P < 0.001$). During this same period, plasma testosterone levels changed significantly in response to capture stress (repeated measures ANOVA, F = 3.66, $P = 0.046$) with the difference occurring within 1 hr (Tukey test, $P < 0.05$) but not maintained at 4 hr.

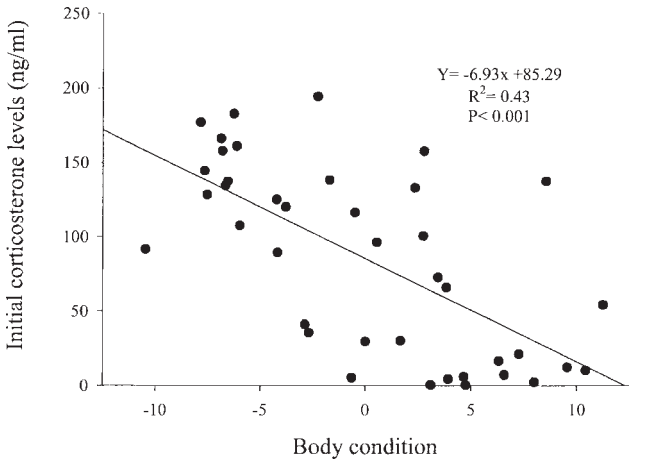

Fig. 3. Regression of initial corticosterone levels on body condition for the male red-sided garter snake, *Thamnophis sirtalis parietalis*.

Initial corticosterone levels were significantly higher during the spring 1999 period relative to the spring 1995, summer, and fall periods (ANOVA on ranks, H = 21.85, $P < 0.001$, Dunn's test: $P < 0.05$). Initial plasma levels of testosterone were significantly higher during the summer than during the fall (ANOVA on ranks, H = 14.03, $P = 0.003$, Dunn's test, $P < 0.05$). Maximal levels of corticosterone were significantly higher during the spring 1999 than during the summer periods (ANOVA on ranks, H = 13.89, $P = 0.003$, Dunn's test: $P < 0.05$). Stressed levels of testosterone were significantly lower during the spring 1999 than during the fall period (ANOVA on ranks, H = 8.99, $P = 0.03$, Dunn's test: $P < 0.05$).

There was a significant positive relationship between snout-vent length and mass in male *T.s. concinnus* (linear regression, $R^2 = 0.954$, $P < 0.001$) and body condition was defined as described for *T.s. parietalis*. There were no differences in body condition between the four different sampling periods (ANOVA, F = 0.83, $P = 0.49$). In addition, there was no relationship between initial hormone levels and body condition (corticosterone: linear regression, $R^2 = 0.0020$, $P = 0.80$; testosterone: linear regression, $R^2 = 0.000021$, $P = 0.98$).

DISCUSSION

We tested the hypothesis that populations of garter snakes living in extreme environments, with limited reproductive opportunities, may suppress their stress response during the breeding season (data summarized in Table 1). In support of this hypothesis, male *T.s. parietalis* from Manitoba, Canada have a brief mating period in the spring and do not exhibit a change in plasma testosterone or corticosterone levels in response to capture stress during the mating season but do during other times of the year. In contrast, male

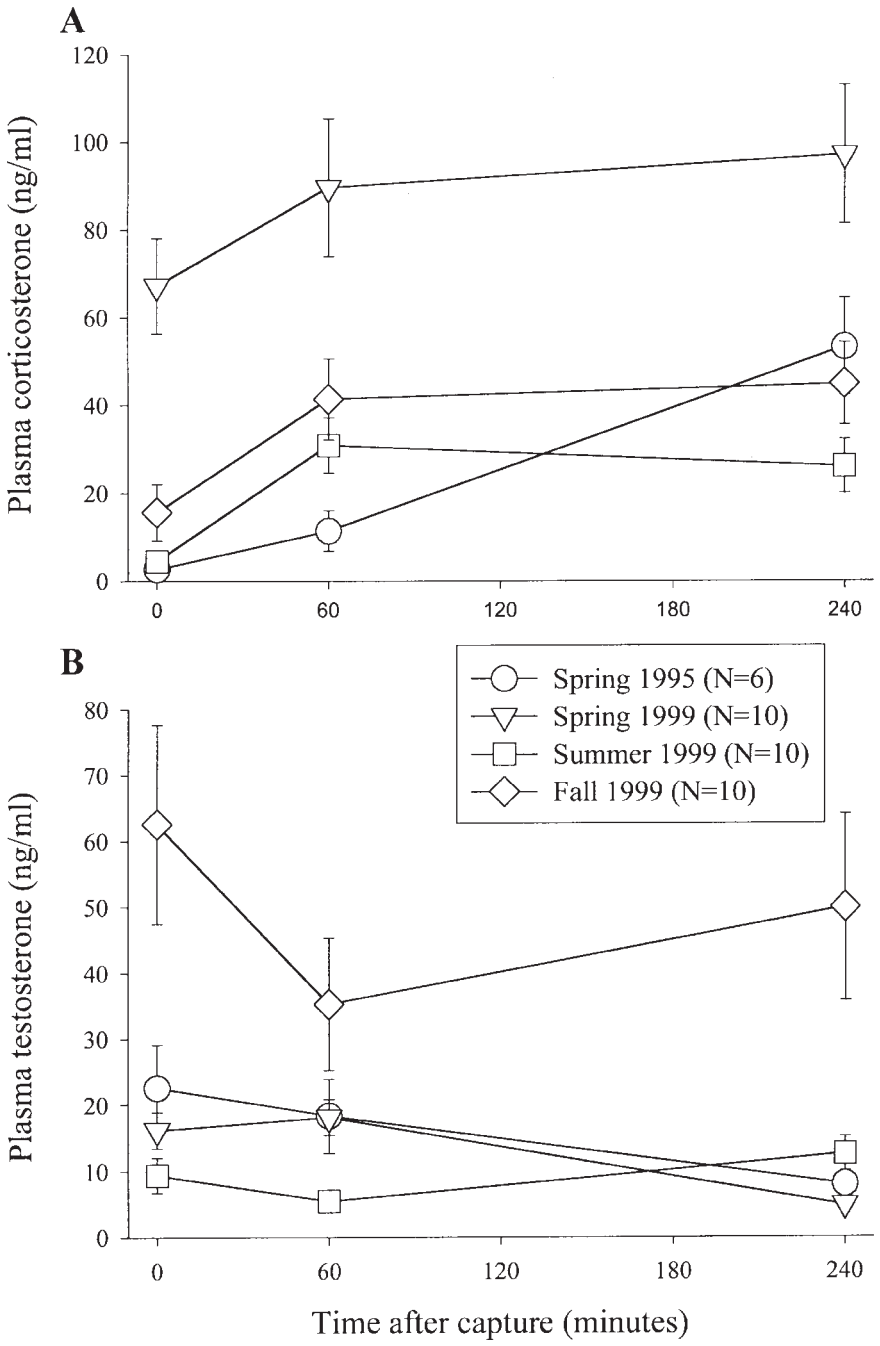

Fig. 4. Plasma corticosterone (**A**) and testosterone (**B**) responses to capture stress and serial blood sampling during four different periods in male red-spotted garter snakes, *Thamnophis sirtalis concinnus*, from Western Oregon.

T.s. concinnus from Oregon have an extended breeding period and display a change in plasma testosterone and corticosterone levels in response to capture stress during the breeding season. However, there are also seasonal differences in the stress response in the Oregon population. Although not addressed in this study, it is possible that the differences in the hormonal stress response result from differences in either production and/or clearance rates of the hormones and/or differences in body temperature and thus metabolism in this poikilotherm. A more detailed analysis shows that seasonal cycles in reproduction and body condition are correlated with seasonal and population differences in the stress response.

TABLE 1. Summary of hormonal (T = testosterone, B = corticosterone) responses to capture stress in two populations of garter snakes during different sampling periods

Sampling period	Change in hormone levels
Seasonal differences in the stress response	
T.s. parietalis	
Early spring	
B	None
T	None
Late spring	
B	None
T	None
Summer	
B	↑ 1 hour
T	↓ 1 hour
Fall	
B	None
T	↓ 4 hours
T.s. consinnus	
Spring 1995	
B	↑ 4 hours
T	↓ 4 hours
Spring 1999	
B	↑ 4 hours
T	↓ 4 hours
Summer	
B	↑ 1 hour
T	None
Fall	
B	↑ 1 hour
T	↓ 1 hour

Arrow represents direction of significant change from initial hormone levels (Tukey test, $P < 0.05$) and time represents the period during which the change occurred.

Seasonal adaptations of the stress response

Male *T.s. parietalis* live at the Northern limit of the species' range and have limited reproductive opportunities (Gregory, '77). Males suppress their stress response during the mating season, presumably to avoid potentially deleterious effects that a stress response could have on reproduction (Greenberg and Wingfield, '87; Rivier and Rivest, '91). This is similar to what has been reported in many species of birds living in the extreme and unpredictable environments both in the arctic and in the desert (Wingfield et al. '92, '95, '98), however a different mechanism appears to be involved in garter snakes. During the spring, plasma corticosterone levels appear maximal and do not rise in response to capture stress. However, testosterone levels are maintained and do not decrease during the early spring period. This appears to be how the stress response is suppressed. Only during the summer did male *T.s. parietalis* display a traditional stress response of a rapid increase in plasma corticosterone and decrease in testosterone levels in response to capture stress. Although mating primarily occurs during the spring, they may mate in the fall (Krohmer et al., '87; Whittier et al., '87; Mendonca and Crews, '89). This could explain the stress response in testosterone, but not corticosterone, seen in the fall. It is possible that the differences in the stress response between the fall and the other sampling periods is the result of annual rather than seasonal differences as the fall samples were obtained during a different year than the spring and summer samples. In either case it is apparent that the stress response is plastic and can be adapted to the prevailing demands placed on the animal.

In addition to seasonal variation in the stress response profile, there is seasonal variation in the initial levels of corticosterone. We hypothesized that elevated initial levels of corticosterone play a pivotal role in mobilizing energy stores during energetically costly periods. During the brief mating season, individual males can lose as much as 1% body mass per day (unpublished data), and this is followed by an extended migrations of up to 15 km to reach the feeding grounds (Gregory, '77). We found a negative relationship between body condition and initial levels of corticosterone, similar to other animals (Wingfield, '94). In another reptile, Wilson and Wingfield ('94) suggest that seasonal variation in baseline levels of corticosterone may not be indicative of the degree of stress that the animals face but are positively associated with annual patterns of activity. Our data support this hypothesis. This may be explained by the known role of corticosterone in energy mobilization (Harvey et al., '74). Finally, elevated levels of corticosterone were different between the late spring and summer. This suggests that there is not an absolute maximum level of the steroid, but that maximum levels are seasonally variable as are initial levels, however probably not to as great an extent.

Data showing the lack of a stress response during the spring mating season, appear to contradict previous data. Moore et al. (2000a) demonstrated that male *T.s. parietalis* have a hormonal response to capture stress of increased plasma corticosterone and decreased testosterone during the first week following spring emergence in 1997. In 1997, initial levels of corticosterone (62 ng/ml) were significantly lower (t-test, $P < 0.001$) than during the early spring period of this study (129 ng/ml), while testosterone levels were similar in the two years. This is not associated with differences in body condition.

Thus, we hypothesize that these animals maintain a testosterone stress response until initial levels of corticosterone reach a critical threshold level, such as during this study, at which point the response is suppressed. This type of plasticity might allow the animals to best adapt to the prevailing conditions in an unpredictable environment. When conditions are optimal and corticosterone levels are low, the animals' response to stressors includes a decrease in plasma testosterone levels. When conditions are harsh and corticosterone levels are elevated, the benefits of high plasma glucocorticoid levels are already in effect and a further increase is unnecessary. In this case testosterone levels remain elevated.

Male *T.s. concinnus* in Western Oregon have a 10-month activity period and an extended spring breeding season. They display a hormonal stress response throughout the year. Males respond to capture stress with increased plasma corticosterone during all sampling periods, except in spring 1999 when initial levels were already elevated. However, the testosterone response was not the same during all seasons. During both spring periods (1995 and 1999) testosterone levels declined in response to capture stress within 4 hr. However, during the summer, testosterone levels were actually higher 4 hr after capture than 1 hr after capture. During the fall, testosterone levels decreased within 1 hr but recovered within 4 hr. Supporting the lack of a persistent effect of stress on testosterone levels, during the summer and fall, is the fact that throughout their annual cycles these two hormones exhibited a significant positive relationship in male *T.s. concinnus* (Moore et al., 2000b). This sex steroid response to capture stress is similar to the increase in plasma estradiol in response to capture that Whittier *et al*. ('87) noted in female *T.s. parietalis*. In addition, male green frogs, *Rana esculenta*, display an increase in plasma estradiol and corticosterone levels and a decrease in androgen levels in response to capture during both the pre-reproductive period and the reproductive period (Zerani et al., '91). During the post-reproductive period, both plasma estradiol and androgen levels decline in response to capture stress in this amphibian. Similarly, male marine toads, *Bufo marinus*, respond to the stress of mating competition with increases in both corticosterone and testosterone (Orchinik et al., '88). Male tree lizards, *Urosaurus ornatus*, respond to capture stress with an increase in plasma corticosterone (Moore et al., '91). However, both in response to capture stress and exogenous corticosterone, the nomadic morph exhibits a greater concomitant decrease in testosterone than the territorial morph (Moore et al., '91; Knapp and Moore, '96, '97). These studies suggest that there are population differences in the relationship between the glucocorticoid and sex steroid response to stress. The traditional reciprocal relationship between the two sets of hormones may not always be true. The current study suggests that these differences are also seasonally variable. Perhaps, at certain times of the year (e.g., during gametogenesis or mating) plasma sex steroid levels must remain elevated to support these functions. During these times, male *T.s. concinnus* maintain plasma testosterone levels in spite of being stressed and display a corticosterone response appropriate to support reproduction and survive the stressor.

There was no seasonal difference in body condition or the relationship between body condition and plasma hormone levels in male *T.s. concinnus* as we documented in male *T.s. parietalis*. In addition, initial and elevated levels of plasma corticosterone were significantly higher during the spring 1999 than during the other three sampling periods. This was probably the result of the spring of 1995 being colder and less favorable than the spring of 1999 (Oregon Climate Service—data for Corvallis-Hyslop, OR).

Environmental adaptations of the stress response

Most studies investigating the hormonal response to stress sample during one distinct part of the year. This is especially true in reptiles (reviewed by Tyrrell and Cree, '98) where conclusions of how these animals respond to stress are often based on single-point studies that may have occurred during a period when the stress response was suppressed (Whittier et al., '87). As evidenced by the current study and those published by Dunlap and Wingfield ('95a,b), there are both seasonal and population differences in the hormonal response to stress. This appears to be an environmental adaptation associated with reproduction.

Male *T.s. concinnus* exhibit a significant hormonal response to capture stress, during the mating season, consisting of an increase in plasma corticosterone and a decrease in plasma testosterone. In contrast, male *T.s. parietalis* suppress their stress response during the mating season. These data suggest that in the relatively mild environment of Western Oregon, *T.s. concinnus* can afford to respond to stressors by activating the HPA axis during the breeding season. This limits mor-

tality and there is a temporally extended period in which to mate. Male *T.s. parietalis* have limited reproductive opportunities that they cannot afford to miss and thus they suppress their HPA axis during the breeding season, which may increase the probability of mortality, but maximizes the limited reproductive opportunity.

SUMMARY

This comparative population study documents environmental as well as seasonal adaptations of the stress response. The hormonal stress response is not fixed within species but rather is adapted to the unique environmental and life history challenges that individuals in the population face. Seasonal adaptations exist in addition to environmental adaptations. This occurs in both extreme and temperate environments. Not only are initial levels of glucocorticoids and sex steroids seasonally variable but the response to capture stress is as well. During any single sampling period, both plasma corticosterone and sex steroid levels can change in response to stress, neither can change, or either one alone can change. Taken together, sampling the stress response in multiple seasons can elucidate seasonal adaptations of the stress response, while interpreting data from a single season can lead to potential generalizations that do not take into effect environmental and annual variation.

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