

Seasonal Specificity of Hormonal, Behavioral, and Coloration Responses to Within- and Between-Sex Encounters in Male Lizards (*Sceloporus undulatus*)

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This study reports the gender and seasonal specificity of hormonal, behavioral, and coloration responses displayed by “resident” male lizards (*Sceloporus undulatus*) exposed to male or female “intruders” during staged encounters in outdoor enclosures. Resident males were engaged in staged encounters with males or females for 1 h per day on 9 consecutive days during the breeding and postbreeding seasons. Male-specific responses occurred during the breeding but not the postbreeding season. These included (1) a transient increase in plasma testosterone (T) that was evident on Day 4 and had subsided by Day 10, (2) behavioral displays of aggression (full shows and chases), and (3) a lightening of dorsal integumental color. Female-specific behavioral responses (nod sets) were displayed in both seasons. Season-specific responses consisted only of a transient increase in plasma corticosterone (B) during the breeding season that was evident on Day 4 and had subsided by Day 10. Pushups were displayed in response to both genders during both seasons, although the frequency of pushups was significantly higher in response to females than to males during the postbreeding season. The coloration of residents did not change in response to male intruders during the postbreeding season or to females during either season. These results define the gender and seasonal specificity of hormonal, behavioral, and coloration responses of resident male *S. undulatus* in social interactions with conspecifics. Thus, our results clarify the biological significance of these responses in terms of potentially aggressive versus courtship interactions and breeding versus postbreeding contexts. © 1999 Academic Press

Social encounters within (e.g., aggression) and between (e.g., courtship) sexual genders are nearly ubiquitous in animal mating systems (West-Eberhard,

1983, 1989). Such interactions can determine which among competing males will gain access to a female as well as a female’s acceptance of a male. The outcomes of these encounters are usually facilitated by communicative signals (Endler, 1992), which can be behavioral, involving ritualized actions associated with aggression or courtship, and visual, involving the orientation and pigmentation of body surfaces. One difficulty in determining the social function of a signal is to differentiate between its importance in inter-versus intrasexual encounters (Hews, 1990; Andersson, 1994).

Social interactions often elicit endocrine (and neuroendocrine) responses in temporal association with behavioral and visual displays, and these responses can themselves serve as regulators of the very social displays that caused them. Thus, a comparison of endocrine responses in social encounters can help to clarify the biological significance of inter and intrasexual signals. A large body of literature has focused on gonadal and adrenal steroids (Harding, 1981; Wingfield, Hegner, Dufty, and Ball, 1990; Moore and Lindzey, 1992). In the present study on lizards, we focus on testosterone (T), the primary testicular androgen, and corticosterone (B), the adrenal “stress” hormone (glucocorticoid) in these animals.

Previous studies on hormonal responses to social interactions in squamate reptiles (lizards and snakes) have produced mixed and inconclusive results, due in part to methodological and species differences among investigations. While most studies indicate that squamates do not undergo rapid (i.e., within minutes or hours) androgenic responses to social interactions (Moore, 1987; Thompson and Moore, 1992; Knapp and

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Moore, 1995; Schuett, Harlow, Rose, Van Kirk, and Murdoch, 1996; Klukowski and Nelson, 1998; but see Greenberg and Crews, 1990), as is common in birds (see Wingfield *et al.*, 1990), there is no consensus on the direction and very existence of delayed (i.e., within days) androgenic responses to short- or long-term interactions (Greenberg, Chen, and Crews, 1984; Greenberg and Crews, 1990; Seitz and John-Alder, 1994; Knapp and Moore, 1995, 1996).

With regard to socially induced adrenal responses in squamates (usually measured as plasma B), the current understanding is equally clouded. Investigators have reported both rapid and delayed adrenal responses in short- and long-term encounters, and the responses are not uniformly associated with social status (Brackin, 1978; Greenberg *et al.*, 1984; Greenberg and Crews, 1990; Seitz and John-Alder, 1994; Knapp and Moore, 1995, 1996; Schuett *et al.*, 1996; Klukowski and Nelson, 1998).

In the present study, we document hormonal, behavioral, and coloration responses to social interactions in a male lizard, *Sceloporus undulatus*. In this species, behavioral displays are augmented by displays of gular and ventrolateral color badges, which facilitate communication between males and females (Cooper and Burns, 1987), and by changes in dorsal pigmentation, which appear to convey information about social status (Carpenter, 1962; Seitz and John-Alder, 1994). Thus, *S. undulatus* is well suited for studies on the specificity and regulation of communicative signals.

Our primary goal was to identify the suite of responses in males uniquely associated with challenges by male intruders during the breeding season. We report fully controlled hormonal, behavioral, and coloration responses of male lizards in staged encounters with male and female "intruders" during the breeding and postbreeding seasons. While it is known that hormonal responses in agonistic interactions can differ between breeding and postbreeding individuals (Wingfield, 1994; Wingfield and Hahn, 1994) and that the presence of a female can influence a male's response (Harding, 1981), previous experiments have generally not been fully controlled due largely to logistical constraints. This study tests the hypothesis that plasma T in squamate reptiles is insensitive to social stimuli [Social Insensitivity Hypothesis: as coined by Thompson and Moore (1992) in reference to predictions of Wingfield *et al.* (1990) regarding the Challenge Hypothesis]. Based on previous work (Seitz and John-Alder, 1994), we predicted that plasma T

would increase in response to social challenges from males.

MATERIALS AND METHODS

Study Animal

Sceloporus undulatus, the eastern fence lizard, occurs over much of the southeastern two-thirds of the United States (Conant, 1975) and is locally abundant in the pinelands of New Jersey (approximately 40°N, 74°30'W), where we collected our animals. *Sceloporus* are active in New Jersey from March to October. Breeding occurs in April and May, when agonistic and courtship interactions are most readily observed. Social interactions are less frequent in July and August, although males occasionally court and bask with females throughout the active season (unpublished field observations). In common with most lizards, this species has an associated reproductive pattern (Moore and Lindzey, 1992), in which highest annual testicular activity and high plasma T levels occur during the breeding season (Altland, 1941; McKinney and Marion, 1985; Rand, 1990). *Sceloporus* are polygamous lizards (Haenel, Seitz, and John-Alder, unpublished), and their population structure places a high premium on the outcome of social encounters (Seitz, Haenel, and John-Alder, 1997).

In a preliminary experiment (Seitz and John-Alder, 1994), we found hormonal and coloration responses to continuous staged encounters between captive pairs of male *Sceloporus* during the breeding season. Within a few days of pair formation, plasma T was significantly higher in dominant males than in subordinates, and the coloration of dorsal surfaces had diverged such that dominant males were consistently lighter than subordinates. In the present study, we followed a protocol of intermittent rather than continuous staged territorial intrusion to simulate social interactions in the field. We included female intruders and a postbreeding experiment to enable us to define the seasonal and gender specificity of the responses of resident males. Our differentiation between "breeding" and "postbreeding" males is based on the breeding biology of field-active *S. undulatus*. "Breeding" males were captured before and "nonbreeding" males after females laid their eggs.

Experimental Design

We followed identical experimental designs and procedures in separate experiments done during the

breeding and postbreeding seasons of *Sceloporus undulatus*. Protocols were approved by the Institutional Review Board for the Use and Care of Animals of Rutgers University prior to the study. In all cases, we report responses of male lizards that had been established as “residents” in outdoor enclosures prior to the beginning of experiments. The first experiment was performed in April 1995 (breeding season), and the second during August 1995 (postbreeding). Free-living lizards were captured (under permit from the N.J. Department of Environmental Protection) in the New Jersey pinelands immediately before each experiment. Lizards were bagged and housed in individual terraria in the laboratory for ≤ 5 days until all of the experimental lizards had been caught. Each lizard was given a unique toe clip for permanent identification, and was measured for mass and snout-vent length.

Ten days before the beginning of experimentation, a “resident” male was placed into each of 32 outdoor enclosures located in an open field at the Hutcheson Memorial Forest (Rutgers University, East Millstone, NJ). The enclosures were circular galvanized steel tanks (approximately 1.75 m in diameter, 40 cm in depth) covered with a wire frame to prevent entry by predators. Each enclosure was filled to a depth of 15 cm with sand and contained one concrete block and one wooden plank for perching and concealment. Water and food (crickets, *Acheta domestica*) were provided ad libitum daily throughout the preexperimental and experimental periods.

Resident males were arbitrarily assigned to one of three treatment groups: unchallenged controls (group C, $n = 10$), males challenged by female “intruders” (group F, $n = 11$), and males challenged by male intruders (group M, $n = 11$). Each resident in group M was matched with a smaller intruder. The size and residency advantages of our asymmetrical male-male interactions ensure that residents “win” contests and establish social dominance in at least 91% of contests (Seitz, 1997). Residents in group F were matched with females of similar body size. (Female *Sceloporus undulatus* are larger than males after controlling for age.) Pairings between residents and intruders remained constant throughout the experimental period.

To simulate repeated encounters between neighboring males or females in the wild, residents were intermittently exposed to intruders for 1 h per day on each of 9 consecutive days. Daily introductions were staggered in two time slots (1100–1200 or 1230–1330) within a 3-h period. This schedule minimized potential diel effects while providing sufficient time for behavioral observations. Between encounters, intrud-

ers were housed individually in terraria in the laboratory and were transported inside cloth bags from the laboratory to the outdoor enclosures.

Under natural conditions, males occasionally court unreceptive females even into the postbreeding season of late summer. In the present experiment, we used unreceptive females in both the breeding and the postbreeding experiments.

Hormone Sampling

Resident males were held in the outdoor enclosures for 1 week before a preintroductory blood sample was taken for measurements of plasma testosterone (T) and corticosterone (B) levels 3 days before experimentation. Subsequently, blood was sampled 4 and 10 days after the onset of daily encounters, approximately 24 h after the previous day’s encounters and before the encounter scheduled for that day.

Blood was collected into a heparinized microhematocrit capillary tube from the postorbital sinus within 2 min of capture. Samples were held on ice for ≤ 2 h and were then centrifuged for separation of plasma from red blood cells. Plasma samples were stored at -20°C until hormones were assayed.

Behavioral Observations

Each resident male was observed for a total of 2 h consisting of four separate 30-min observation periods while the male or female intruder was present. Controls were observed for the same length of time during the same observation periods. Behavioral samples were randomized across the schedule of social interactions but were not done on Day 4 to avoid the influence of the blood sampling on behavior.

Observers stood quietly and motionlessly approximately 3 m from each enclosure and wore sunglasses to hide their eye movements from the lizards (Burger, Gochfeld, and Murray, 1991). The total number (pushups, nod-sets, fullshows, chases, bites) or duration (fullshow-hold) of behavioral displays were recorded for each resident male.

Our behavioral nomenclature generally follows Carpenter (1962):

Pushups: Head and trunk are raised and lowered by extension and flexion of the front legs. This display can occur singly or in bouts (see Martins, 1994).

Nod-sets: Head is held low and moved rapidly from side to side. This display has also been described as a shudder (Carpenter, 1962) and occurs almost exclu-

sively when males encounter females. Bouts of nod-sets are interspersed with pushups in courtship displays. Since nod-sets are very rapid movements, we counted bouts instead of individual nods.

Fullshows: Movement is the same as for a pushup with the addition of an arched back and lateral compression of the sides. This display is thought to convey more intense aggression than a pushup (Martins, 1993).

Fullshow-hold: Body is in the same position as in a fullshow, but the position is held without being accompanied by pushups.

Chase: One lizard rapidly approaches or charges the other.

Bite: One lizard briefly grips some part of the body of another lizard with the mouth.

Integumental Color

Dorsal and ventrolateral color of resident males was measured with Munsell color chips immediately after seven of the staged encounters, excluding Days 4 and 10 when blood was sampled for hormone assays. At the end of an encounter *h*, the resident male was captured and held next to the Munsell color chips against a neutral background. Color measurements were completed within about 15 s to preclude color changes due to the stress of capture. To verify the objectivity of color evaluations, color was measured independently by two observers at three of the sampling points. Using Munsell terminology, dorsal color ranged from "black" (chip No. 5YR 2.5/1) to "reddish yellow" (chip No. 7.5YR 7/8) (Munsell Soil Color Charts, 1994, GretagMacbeth, New Windsor, NY). The blue colors on the ventrolateral surface ranged from aqua blue to royal blue, as ascertained by examination of males before the start of experiments, and the following five Munsell color chips accounted for this variation: 10 BG 5/6, 2.5 B 4/8, 7.5 B 4/8, 10 B 3/8, 2.5 PB 3/8, 5 PB 4/10.

Radioimmunoassay

Plasma levels of T and B were measured by radioimmunoassay (RIA) following published procedures (Wingfield and Farner, 1975; Moore, 1986). Briefly, samples of approximately 30 μ l were extracted twice in diethyl ether and dried under a stream of ultrafiltered air. Samples were reconstituted in 10% ethyl acetate:90% isooctane (v/v), and steroids were then separated on diatomaceous earth (Celite, Sigma) minichromatography columns. Subsequently, dried

samples were reconstituted in assay buffer and allowed to equilibrate overnight prior to radioimmunoassays. Recovery of T and B was measured for each sample.

For RIAs, tritiated hormones were obtained from Dupont-NEN (Wilmington, DE), T antiserum from Wien Laboratories (Succasunna, NJ), and B antiserum from Endocrine Sciences (Calabasas, CA). The sensitivities of the assays were 8 pg per tube for both B and T. All samples were analyzed in two assays with interassay variations of 7.5 and 6% for B and T, respectively. Intraassay variations were 8 and 7% for B and T, respectively.

Statistical Analyses

The breeding and nonbreeding experiments were analyzed separately and were then compared for seasonal effects. Initially, snout-vent length was used to analyze the possible size dependence of behaviors, integumental color, and hormone levels. No evidence of size dependence was found for any of the variables, and body size was excluded from all subsequent analyses.

Behavioral scores were initially examined in a principal components analysis (PCA) to identify the behavioral displays that helped to explain variation among treatment groups. Scores were expressed as cumulative values over the four observation periods for each individual. A value of 1 was added to all scores to eliminate zeros. Subsequently, ANOVA was used to investigate potential behavioral differences among treatment groups and between seasons for only those behavioral variables that were retained by PCA. For this analysis, behavioral scores were log-transformed to normalize distributions. Testosterone and corticosterone were analyzed via repeated-measures ANOVA to investigate potential treatment and season effects. Post hoc multiple comparisons for hormones and behaviors were performed with Tukey's Honestly Significant Difference Test (Sokal and Rohlf, 1981). Dorsal and ventrolateral Munsell color scores were transposed into sequential numerical scores to rank colors from lighter to darker hues (Table 1). These numerical scores were analyzed via nonparametric ANOVA (Kruskal-Wallis). Analyses were done using SAS-PC (SAS Institute, Cary, NC). In all cases, statistical significance was accepted at the $P \leq 0.05$ level. For dorsal color, we had no a priori expectation of how residents challenged by males would compare with those challenged by females. However, we hypothesized that residents challenged by males would

TABLE 1
Munsell Color Chips Used for Color Evaluations versus
Nominal Color Scores Used for Statistical Analyses

Nominal color score	Dorsal Munsell chip No.	Ventral Munsell chip No.
1	7.5YR 7/8	10BG 5/6
2	5YR 6/8	2.5B 4/8
3	5YR 5/8	7.5B 4/8
4	5YR 5/6	10B 3/8
5	5YR 3/1	2.5PB 3/8
6	5YR 2.5/1	5PB 4/10

lighten relative to controls, based on our earlier observations that the lighter-colored of paired males was socially dominant (Seitz and John-Alder, 1994). To test this *a priori* hypothesis, we performed a one-tailed *t* test on ranked color scores of resident controls versus those challenged by males. This procedure is equivalent to a Wilcoxon rank sum test (SAS Institute).

RESULTS

Hormones

Testosterone levels varied from 0.8 to 58.6 ng/ml and from 1.1 to 47.0 ng/ml during the breeding and postbreeding experiments, respectively (Fig. 1). Levels of plasma T observed in field-active males at comparable times of the year vary from 0.4 to 77.4 ng/ml (breeding) and from undetectable to 33.1 ng/ml (postbreeding) (Seitz *et al.*, 1997). Thus, experimental levels of plasma T were generally within normal ranges.

Preexperimental plasma T did not differ among treatment groups in either of the experiments (breeding: $F = 1.53$ [2,28], $P = 0.235$; postbreeding: $F = 0.25$ [2,26], $P = 0.779$). However, the responses of resident males to staged encounters differed between seasons and with the gender of the intruder. During the breeding season, plasma T in resident males increased transiently in response to encounters with male (group M) but not female (group F) intruders (Fig. 1a). Plasma T was significantly higher in residents of group M than in either of the other two groups on Day 4 ($F = 25.15$ [2,28], $P < 0.0001$), and this difference subsided by Day 10 ($F = 0.79$ [2,28], $P = 0.487$). During the postbreeding season, however, plasma T did not vary significantly among the three treatment groups at any of the sampling points (Fig. 1b; Day 4: $F = 1.04$, [2,26] $P = 0.369$; Day 10: $F = 0.320$ [2,26], $P = 0.727$). Postbreeding plasma T was significantly higher on Day 4

($F = 22.97$ [1,2], $P < 0.0001$) and Day 10 ($F = 22.97$ [1,2], $P < 0.0003$) than at the preexperimental point, but this pattern did not differ among groups.

Corticosterone levels varied from 0.7 to 63.2 ng/ml and from 0.69 to 34.0 ng/ml during the breeding and postbreeding experiments, respectively (Fig. 2). Levels of plasma B observed in field-active males at comparable times of the year vary from 0.3 to 91.4 ng/ml

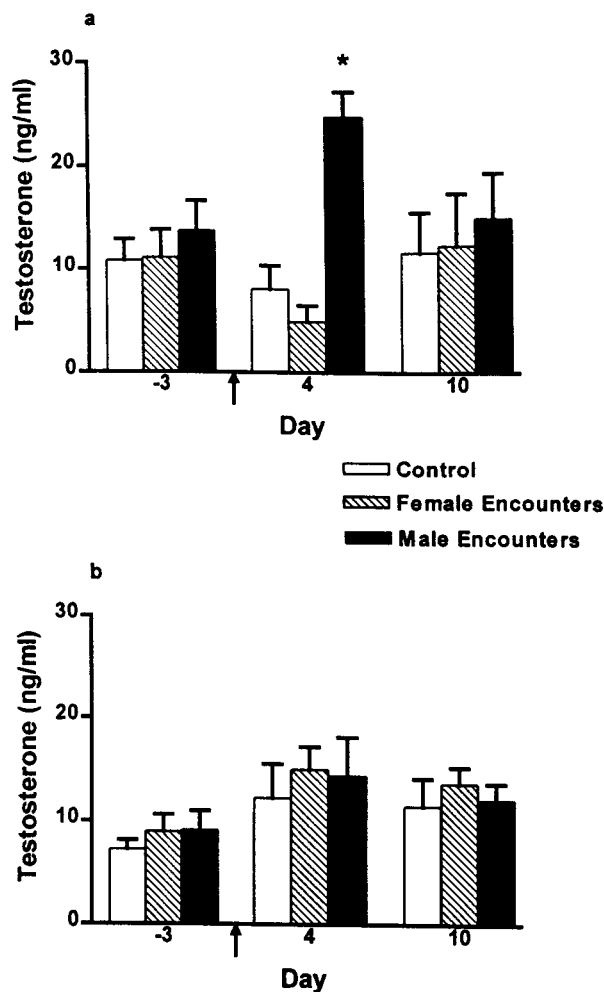


FIG. 1. Plasma testosterone in controls and in resident males exposed to encounters with females or males during the breeding (a) and postbreeding (b) seasons. Values are reported as means \pm SE at 3 days before and on the 4th and 10th days after the onset of daily hour-long encounters, indicated by the bold arrow on the X axis. During the breeding season (a), sample sizes were for group C, $n = 10$, and groups F and M, $n = 11$. Plasma T did not differ among treatment groups prior to interactions ($P = 0.235$) or on Day 10 ($P = 0.487$). On Day 4, plasma T was significantly higher in group M than in either of the other two groups ($P < 0.0001$, marked by asterisk). During the postbreeding season (b), sample sizes were, for group C, $n = 9$, and groups F and M, $n = 10$. Plasma T did not differ significantly among treatment groups at any of the sampling points.

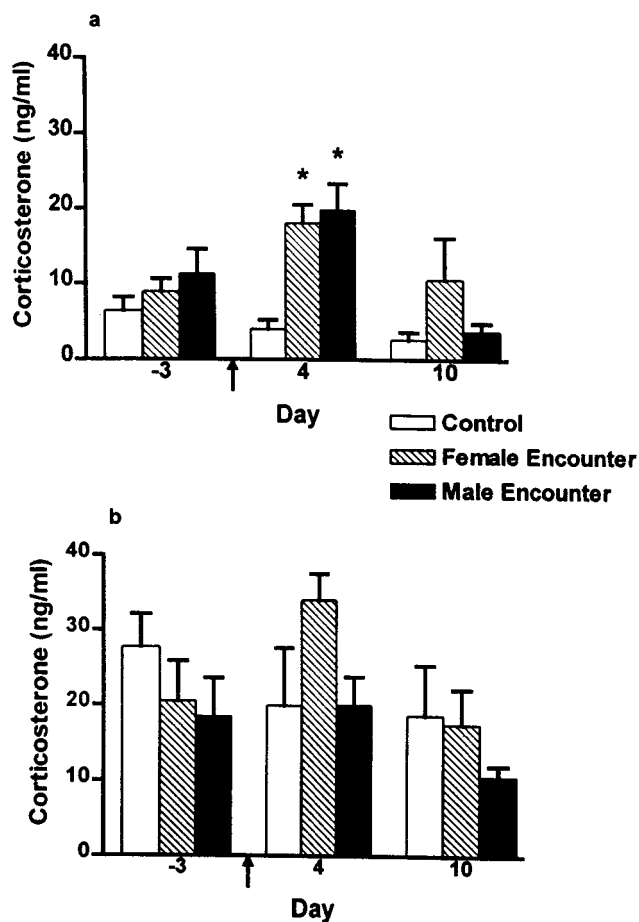


FIG. 2. Plasma corticosterone in controls and in resident males exposed to encounters with females or males during the breeding (a) and postbreeding (b) seasons. Values and sample sizes are as reported in Fig. 1. During the breeding season (a), plasma B did not differ among treatment groups prior to interactions ($P = 0.401$) or on Day 10 ($P = 0.252$). On Day 4, plasma B was significantly higher in groups F and M than in controls ($P < 0.0009$, marked by asterisks). During the postbreeding season (b), plasma B did not differ significantly among treatment groups at any of the sampling points, although the increase in group F failed to attain statistical significance ($P = 0.080$).

(breeding) and from 1.1 to 21.1 ng/ml (postbreeding) (Seitz *et al.*, 1997). Thus, as with plasma T, experimental levels of plasma B were generally within or close to normal ranges.

Preexperimental plasma B did not differ among treatment groups in either of the experiments (breeding: $F = 0.94$ [2,28], $P = 0.401$; postbreeding: $F = 0.91$ [2,26], $P = 0.416$). The B responses of resident males to staged encounters differed between seasons, although unlike the situation with plasma T, the gender of the intruder had no significant effect. During the breeding

season, plasma B in resident males increased transiently in response to encounters with male (group M) and female (group F) intruders (Fig. 2a). Plasma B was significantly higher in residents of groups M and F on Day 4 ($F = 9.04$ [2,28], $P < 0.0009$) than in group C. This difference subsided by Day 10 ($F = 1.45$ [2,28], $P = 0.252$). During the postbreeding season, plasma B showed a tendency to increase transiently in response to female but not male intruders (Fig. 2b), but this increase in group F on Day 4 failed to attain statistical significance ($F = 2.76$ [2,26], $P = 0.080$).

Behavior

In the initial PCA of behavioral variables, the first two principal components (PC1 and PC2) explained most of the variation in the behavioral data. Furthermore, these two factors could be interpreted to represent two sets of variables which were closely aligned with the gender specificity of responses (see below): pushups and nod sets (PC1) versus fullshows and chases (PC2). Fullshow-holds and bites were not correlated with any of the PCA axes and thus were excluded from all further analyses.

During the breeding season, PC1 and PC2 explained 41 and 25%, respectively, of the variation in the data. Pushups and nod-sets were significantly correlated with PC1 (both $P < 0.001$), while fullshows and chases were significantly correlated with PC2 (both $P < 0.001$). During the postbreeding season, pushups and nod-sets were again significantly correlated with PC1 (both $P < 0.001$), which explained 40% of the variation in behavior, but no other behavioral display occurred frequently enough to be included in the analyses. Males in the unchallenged control group (group C) exhibited no behavioral displays and have therefore been excluded from this presentation.

During the breeding season, resident males exhibited male-specific, female-specific, and nonspecific behavioral displays in response to staged encounters (Fig. 3a). In group M, 9 of 11 males performed pushups while 8 of 11 males performed fullshows and chases. In group F, 8 of 11 males performed pushups and nod-sets. Residents performed pushups, the most common display, at similar frequencies in encounters with males and females ($F = 2.22$ [2,29], $P = 0.344$). Residents in group F performed significantly more nod sets than those in group M ($F = 7.35$ [2,29], $P < 0.001$), while residents in group M performed significantly more fullshows and chases than those in group F ($F = 15.66$ [2,29], $P < 0.001$; $F = 7.54$ [2,29], $P < 0.002$, respectively).

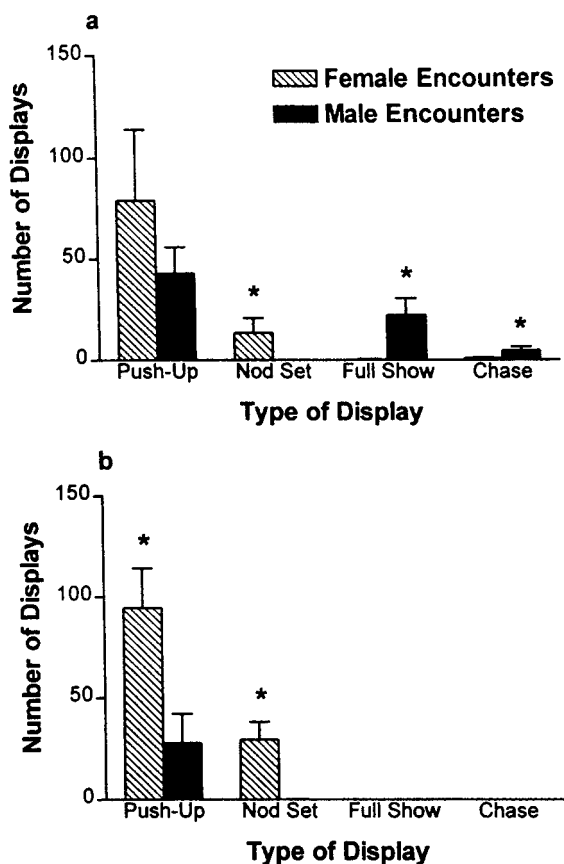


FIG. 3. Behavioral displays exhibited by resident males in response to territorial intrusion from males (group M) and females (group F). None of these displays were ever performed by controls (group C). Values are means \pm SE calculated from the total number of displays performed during the cumulative 2 h of behavioral observation. Significant differences between groups M and F are indicated by asterisks. Pushups and nod-sets were the two most frequently performed displays. During the breeding season (a), residents performed pushups at a similar frequency in response to females and males ($P = 0.344$), while nod-sets were only performed in response to females ($P < 0.001$). Fullshows and chases were displayed almost exclusively in encounters with males ($P < 0.0001$, and $P < 0.002$; respectively). During the postbreeding season (b), pushups and nod-sets were the only displays performed. Residents displayed more pushups and nod-sets ($P < 0.0001$ for both) in encounters with females than with males.

During the postbreeding season (Fig. 3b), pushups and nod-sets were displayed more frequently by residents in group F than in group M ($F = 19.77$ [2,26], $P < 0.0001$; $F = 50.59$ [2,26], $P < 0.0001$; respectively). In group M, 6 of 10 postbreeding males performed pushups while 8 of 10 males in group F performed pushups and nod-sets. Neither of the two male-specific behaviors, fullshows and chases, were ever displayed by any of the residents in group M during the postbreeding season.

Color

Dorsal color ranged from “dark brown” (Munsell chip No. 5YR 2.5/1) to “reddish yellow” (chip No. 7.5YR 7/8), and the range of colors overlapped extensively among groups and between seasons (Fig. 4). Despite this overlap, however, we observed one gender-specific response of dorsal color in our experiments. During the breeding season, dorsal color scores were significantly lower in group M than in either of the other two groups (Fig. 4a; one-tailed $t = 1.871$ [19]; $P = 0.039$), indicating that the average dorsal color in group M was lighter than in the others. During the postbreeding season, dorsal color did not differ significantly among treatment groups (Fig. 4b; one-tailed $t = 0.488$ [17], $P = 0.632$).

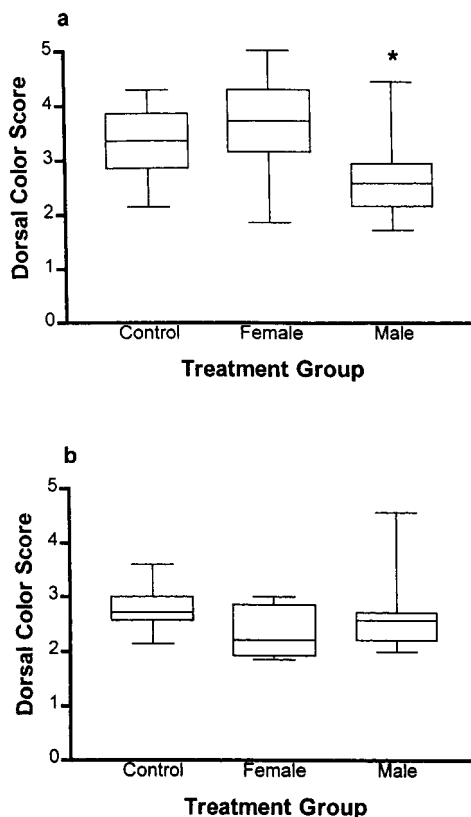


FIG. 4. Dorsal color scores for controls and resident males exposed to encounters with males or females (see Table 1). For each treatment, horizontal bars indicate the 50th percentile, the upper and lower bounds of the box indicate the 75th and 25th percentiles, respectively, and the vertical bars indicate the full range of values. Low versus high color scores represent a progression of color from “reddish yellow” (1) to “black” (6). Dorsal color was significantly lighter in group M than in either of the other two groups during the breeding season (one-tailed $P < 0.035$, marked by asterisk). There were no significant differences among groups during the postbreeding season (one-tailed $P = 0.063$).

TABLE 2
Summary of Season-Specific and Gender-Specific Responses of Resident Males^a

Season and intruder's gender	Plasma testosterone	Plasma corticosterone	Aggression	Courtship	Dorsal lightening
Breeding, male	+	+	+	NA	+
Postbreeding, male	0	0	0	NA	0
Breeding, female	0	+	NA	+	0
Postbreeding, female	0	0	NA	+	0

^a “+” indicates an increase and “0” indicates no change relative to unchallenged controls. Hormonal responses reported here are for Day 4. NA, not applicable.

Ventrolateral color did not vary significantly among the treatment groups during the breeding (CHISQ = 2.29 [2], $P = 0.320$) or the postbreeding (CHISQ = 2.72 [2], $P = 0.257$) experiments.

A qualitative summary of gender- and season-specific hormonal, behavioral, and coloration responses is presented in Table 2.

DISCUSSION

Testosterone: Challenge Response and a Test of the Social Insensitivity Hypothesis

Our results show clearly that plasma T in captive resident male *S. undulatus* increases transiently in response to staged challenges from male intruders during the breeding season. This result is consistent with our earlier report (Seitz and John-Alder, 1994), in which we found that plasma T was significantly higher in dominant than in subordinate males during continuous, long-term encounters. Captive male birds also exhibit a status-dependent, transient increase in plasma T (Ramenofsky, 1984; Dufty and Wingfield, 1986; Hegner and Wingfield, 1986). By this criterion, then, *Sceloporus* clearly exhibit a “challenge response” (Wingfield *et al.*, 1990), seen as an increase in plasma T in the face of territorial intrusion, albeit on a more delayed time scale than in many birds. The increase in plasma T reported here occurs specifically in response to male challenges during the breeding season. Thus, we can reject the Social Insensitivity Hypothesis for *Sceloporus undulatus*.

Most previous studies on squamate reptiles, including a recent report on *Sceloporus undulatus*, failed to detect an increase in plasma T in males challenged by intruding males (Moore, 1987; Thompson and Moore, 1992; Knapp and Moore, 1995, 1996; Schuett *et al.*, 1996; Klukowski and Nelson, 1998), with the exception

that Greenberg and Crews (1990) reported an increase in plasma T in dominant male *Anolis carolinensis* within 1 h of social challenge. The discrepancies between ours and previous studies may, in some cases, reflect biological differences among species. Alternatively, this discrepancy may derive from substantial differences in methodologies, including the nature of staged encounters and the timing of postencounter sampling schedules (see Sachser and Prove, 1984). Certainly, in the light of recent evidence that field-active *S. undulatus* fail to exhibit a rapid increase in plasma T following a social challenge (Klukowski and Nelson, 1998), the most parsimonious explanation for our positive result invokes the obvious methodological differences between studies. In this context, the most salient design features in our present study include (1) the use of outdoor enclosures, thus exposing lizards to natural conditions of photoperiod and relative humidity; (2) the isolation of experimental lizards from potentially confounding social stimuli (see Thompson and Moore, 1992); (3) the use of body size and prior residency to create asymmetrical social contexts (Rosenberg and Enquist, 1991; Stamps and Krishnan, 1994); and (4) the use of intermittent daily challenges to simulate the natural social context of *S. undulatus*. Further experiments on the occurrence and distribution of challenge responses among squamates are needed, and these will have to follow a uniform protocol to facilitate comparisons among species and between field and laboratory studies.

In addition to the very occurrence of challenge responses, the time course of the increase in plasma T warrants further study in squamates. We were heavily influenced by two factors in designing our sampling schedule: (1) our previous observation that the disparity in plasma T between dominant and subordinate males in continuous pairs of *Sceloporus* became greater between the second and tenth days after pair forma-

tion (Seitz and John-Alder, 1994), and (2) reports that plasma T does not respond within min or h of social challenge (Moore, 1987; Thompson and Moore, 1992; Knapp and Moore, 1996). In one report, plasma T increased dramatically within 1 h of social interactions in male *Anolis carolinensis* (Greenberg and Crews, 1990). However, the design of that study (i.e., presence of male, female, or both) was not directly comparable to those of other studies. We used a species of lizard too small to tolerate frequent blood sampling, and we developed our sampling protocol in the light of previous reports to optimize the likelihood of observing an increase in plasma T. In the context of elucidating potential physiological/behavioral consequences of the increase in plasma T and of clarifying differences among studies, it will now be important to characterize more precisely the time course of the response in *S. undulatus*.

Corticosterone: Stress and Social Status

The size and residency advantages of our asymmetrical male–male interactions ensured that residents behaved as if on their home territories: they asserted dominance when challenged by males, and they courted when females were presented. We refer to this social context in discussing the effects of territorial intrusion on plasma B. Furthermore, we interpret an increase in plasma B as an index of stress (Axelrod and Reisine, 1984; Moberg, 1985; Guillette, Cree, and Rooney, 1995).

With these considerations in mind, our results are noteworthy for several reasons. First, levels of plasma B increased in response to staged social challenges even though resident males had been established as dominant territory holders. Second, levels of plasma B increased in response to social challenges presented by male and female intruders. Third, levels of plasma B increased even as plasma T increased in one of our groups of lizards.

Socially dominant, resident males are transiently stressed by territorial intrusion during the breeding season, as indicated by the increase in plasma B. Plasma B did not increase during the postbreeding season, although female intruders may have been somewhat more stressful to residents than intruding males at this time (see Fig. 2). Thus, increases in plasma B were not simply nonspecific responses to the presence of another lizard. Clearly, the resident's perception of territorial intrusion was integrated within the context of the seasonal environment and, during

the postbreeding season, may have differentiated between genders.

Our results on male–male interactions are consistent with the response of *Urosaurus ornatus* (Knapp and Moore, 1995), in which plasma B increased in contest winners on the first and third days after brief encounters. Although our experimental protocols differed, the plasma B of male *S. undulatus* increased in response to male–male interactions in our present study as well as in a recently reported experiment with males from a population in Ohio (Klukowski and Nelson, 1998). However, in other squamates, plasma B increased in losers and subordinates (Greenberg *et al.*, 1984; Schuett *et al.*, 1996), and in still other cases, plasma B failed to undergo short-term responses to staged aggressive interactions in lizards (Moore, 1987; Greenberg and Crews, 1990; Thompson and Moore, 1992). As in the case of plasma T, differences among species and experimental protocols make it impossible to draw general conclusions at the present time. In any case, there is little basis for an a priori expectation that subordinates or contest losers should have higher levels of plasma B than winners (see Schuett *et al.*, 1996; see Castro and Matt, 1997). Studies on other animal models (Hannes *et al.*, 1984; Hannes, 1985; Fox, White, Kao, and Fernald, 1997) indicate that social condition is an important determinant of the direction and magnitude of glucocorticoid responses to social stressors. However, a growing body of literature fails to confirm that social subordinates experience greater stress than dominants in the wild and suggests the emerging view that social dominance rather than subordination presents the greater social stressor (Alberts, Sapolsky, and Altmann, 1992; Wingfield and Lewis, 1993; Creel, Creel, and Monfort, 1996; Creel, Creel, Mills, and Monfort, 1997).

Previous studies of glucocorticoid responses to social stress have focused primarily on agonistic interactions between males, and responses of males to females have received relatively little attention. Despite the prediction that activation of the adrenal stress response would inhibit reproductive functions (Moore and Miller, 1984; Moore and Zoeller, 1985; Moberg, 1985, 1991; Tokarz, 1987), there is ample precedent for glucocorticoid levels to increase in males presented with females, as in the present study. In whiptail lizards (*Cnemidophorus inornatus*), for example, plasma B was substantially higher in males housed with sexually mature females than in those housed alone (Lindzey and Crews, 1988), and in domesticated mammals, cortisol levels increase in association with specific events during mating activity

(Borg, Esbenshade, and Johnson, 1991, 1992). Possibly, solicitation by receptive females would not have elicited an increase in plasma B in resident male *S. undulatus*. However, Lindzey and Crews (1988) found no obvious correlation between plasma B of males and the ovarian states of their female cagemates.

The transient increase in plasma B suggests that the establishment of social relationships presents a temporary social stressor and that this stress dissipates with social stability and familiarity between neighbors. Thus, we would predict that plasma B would increase a second time if a new intruder were presented after Day 10. In primates, glucocorticoid levels increase with social instability (Alberts *et al.*, 1992; Gust, Gordon, and Hambright, 1993) while levels are low in familiar social partners (Levine, 1993; Lyons, Ha, and Levine, 1995). The transient nature of elevated plasma B may be associated with the "dear enemy" phenomenon, in which agonistic behavior is displayed less vigorously to familiar neighbors than to unfamiliar intruders (Krebs, 1982; Ydenberg, Giraldeau, and Falls, 1988). A similar pattern of individual recognition and reduced aggression toward neighbors has been detected in lizards [*Dipsosaurus dorsalis* (Glinski and Krekorian, 1985); *Anolis carolinensis* (Qualls and Jaeger, 1991); *Crotaphytus collaris*, (Fox and Baird, 1992)].

Two general types of experiments suggest the existence of reciprocal interactions between gonadal and adrenal steroid secretion. The first of these are studies in which exposure to stress causes an inhibition of behavioral and physiological aspects of reproduction (Brackin, 1978; Moore and Miller, 1984; Moberg, 1985, 1991; Moore and Zoeller, 1985; Orichinik, Licht, and Crews, 1988). The second type are those in which the administration of exogenous corticosterone (B) leads to an inhibition of reproductive function, including a reduction in plasma T (Moore and Miller, 1984; Moore and Zoeller, 1985; Tokarz, 1987; Orr and Mann, 1992; DeNardo and Licht, 1993). Our results in four distinct circumstances indicate that relationships between plasma levels of T and B fit no single pattern, at least in response to the social stimulus of territorial intrusion. Variable relationships between androgen and glucocorticoid levels have been reported in other animal models (Hannes and Franck, 1983; Hannes *et al.*, 1984; Hannes, 1985; Castro and Matt, 1997). Thus, reciprocal relationships between gonadal and adrenal function elicited via severe stress or exogenous glucocorticoids may not accurately reflect the full range of biological responses and may create a misleading

view of the relationship between stress and reproduction in the wild.

In free-living lizards, investigators have reported a positive association between seasonal patterns of breeding activity and levels of plasma B (Greenberg and Wingfield, 1987; Wilson and Wingfield, 1992, 1994). A similar pattern occurs in free-living *S. undulatus* (Seitz, 1997). The social modulation of plasma B reported in the present study may be at least partially responsible for the elevated levels of plasma B that occur in nature during the breeding season.

Behavior

Pushups were the most common behavior of resident males, displayed in response to males and females during the breeding and postbreeding seasons. Due to this nonspecificity, we interpret pushups as a general salutation to a conspecific (Carpenter, 1962; Rothblum and Jenssen, 1978). We observed no qualitative differences in the pushups displayed to males versus females or between breeding and postbreeding seasons and did not observe control males doing pushups. In addition, we have never observed a solitary, free-living male performing pushups unless in the presence of a male or female (unpublished observations). Pushups tended to be displayed in greater numbers to females than to males, although this quantitative difference between genders attained statistical significance only during the postbreeding season.

All other types of behavioral signals were gender and/or season specific. Fullshows and chases were displayed almost exclusively during encounters with males in the breeding season. These behaviors indicate more intense aggression than pushups alone (Carpenter, 1962; Ferguson, 1971; Cooper and Burns, 1987), and their seasonal specificity is consistent with reports on changes in the intensity of agonistic interactions in free-living lizards (Moore, 1988). The seasonal difference in aggressiveness reported here is qualitative, because fullshows and chases were either present or completely absent. In comparison, song sparrows exhibited a quantitatively greater intensity and persistence of aggressive behavior during spring than fall in response to staged territorial intrusions (Wingfield, 1994). Nod-sets, the only female-specific behavior, showed no seasonal specificity, indicating that resident males responded to females with equivalent vigor regardless of breeding condition. In field-active *S. undulatus*, males court and bask with females throughout the activity season, even after female receptivity has ended (Seitz, 1997). As noted previously,

the females used in the present study were all nonreceptive, and an analysis of behavioral responses to receptive females during the breeding season could be particularly insightful.

Coloration

During the breeding season, the dorsal color of resident males became significantly lighter in response to territorial intrusion by males. Previously, we reported that dominants are lighter than subordinates in pairs of male *S. undulatus* housed together continuously for several weeks (Seitz and John-Alder, 1994). The response in the present experiment was specific to males during the breeding season, as it did not occur in response to females or during the postbreeding season.

Dorsal lightening in *S. undulatus* is a reversible response (unpublished observations) and is designated as a physiological color change (Cooper and Greenberg, 1992). Presumably, sustained dorsal lightening requires prolonged neural and/or endocrine input. We have observed in the laboratory that lightening of dorsal skin *in vitro* can be induced by α -adrenergic stimulation and that lightening *in vivo* can be induced with fluoronorepinephrine, a specific α -agonist, and epinephrine (unpublished observations), consistent with reports on other squamates (see Cooper and Greenberg, 1992). Thus, we interpret the dorsal lightening seen in the present study as a general activation of sympathetic output, which is a characteristic response to stress (Axelrod and Reisine, 1984).

Status-dependent changes in color have been reported previously in *S. undulatus* (Carpenter, 1962) and in other species (Zucker, 1989, 1994; Greenberg and Crews, 1990; Cooper and Greenberg, 1992). In *Anolis carolinensis*, dominants in aggressive interactions are lighter in color than subordinates (Greenberg and Crews, 1990), and the development of a dark eyespot reflects activation of the adrenergic component of an acute stress response (Summers and Greenberg, 1994). In that species, α -adrenergic receptors mediate melanosome aggregation, thus lightening of the skin (Goldman and Hadley, 1969), and the same mechanism presumably mediates the lightening of *A. roquet* in response to epinephrine (May and Thillard, 1957 as cited in Cooper and Greenberg, 1992). In *Urosaurus ornatus* (Zucker, 1989, 1994) and in previous reports on *S. undulatus* (Carpenter, 1962), dominant males are characteristically darker than subordinates. Dorsal darkening can be induced by β -adrenergic stimulation and by two stress-related pituitary hor-

mones (ACTH and α -MSH) (Cooper and Greenberg, 1992; unpublished observations). In all cases, then, a change in dorsal color is indicative of one or more components of a typical stress response, including a general activation of sympathetic output (Axelrod and Reisine, 1984). Thus, all of these studies suggest that social dominance is associated with psychobiological stress.

Males did not exhibit significant changes in ventrolateral color in response to territorial intrusion during either season. This is perhaps to be expected, as ventrolateral color in *S. undulatus* is thought to function primarily in gender recognition (Cooper and Burns, 1987) during either season.

In closing, are there functional relationships among the responses seen during the breeding season, or do the relationships reported here represent nothing more than temporal correlations? Obviously, we cannot answer this question definitively, but the responses specific to male intrusion during the breeding season suggest some very plausible functional interactions. With regard to the steroids, a comparison of responses to males versus females during the breeding and postbreeding seasons suggests an association between T and the displays of aggressive behavior. Previous studies have shown that T activates aggressive behavior in lizards (Crews, Traina, Wetzel, and Muller, 1978; Tokarz, 1987, 1995) and other animals (e.g., Wingfield, Ball, Dufty, Hegner, and Ramenofsky, 1987) and that behavioral responsiveness to T depends on when experiments are done relative to the breeding season (Moore, 1988; Wingfield, 1994). The prevailing view is that T exerts a modulatory influence on existing behavioral systems instead of causing or activating behavior directly, thus allowing flexibility in behavioral responses to sensory input (Cottingham and Pfaff, 1986; Churchland and Sejnowski, 1992; Wood, 1997). With regard to integumental color, dorsal lightening may indicate that the activation of the hypothalamo-pituitary-gonadal axis (HPG) is accompanied by a general activation of the sympathetic system as discussed previously, which also could influence behavioral responses. Thus, differences in levels of behavioral reactivity may result from the changing modulatory roles of catecholamines and testosterone (see Summers and Greenberg, 1994).

Finally, we briefly consider the potential significance of our results in free-living lizards. Even though our experiments forced a social dichotomy between males of a territorial species, home range overlap between adjacent sceloporine males is often high such that a social hierarchy may be important to *S. undula-*

tus in the wild (Stamps, 1983). In the population from which our experimental males were sampled, overlap among adjacent male home ranges is very extensive, and neighboring males repeatedly encounter each other (Seitz, 1997; Seitz *et al.*, 1997). The outcome of aggressive interactions between males in the wild is marked by displays of behavioral dominance and a lighter dorsal color in the winner than the loser (Seitz *et al.*, 1997). We cannot be as certain about hormonal responses to social interactions in the wild. Average levels of plasma B in *S. undulatus* increase after emergence from hibernation during the first few weeks of the breeding season, and plasma B in males is correlated with overlapped area between male and female home ranges (Seitz, 1997). However, we have not staged social challenges against free-living males, and it may be hard to isolate responses to specific challenges against the background of ongoing social interactions (Social Modulation Theory, see Thompson and Moore, 1992).

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