

Effects of Corticosterone on Social Behavior of Male Lizards

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Adrenal corticoid release is a major component of the stress response which can affect many body functions including behavior. The purpose of our studies was to examine the effects of corticosterone (B) on both the agonistic and courtship components of social behavior in male side-blotched lizards (*Uta stansburiana*). Of particular interest was the effect of B on plasma testosterone (T), a hormone known to influence aggression, and the importance of this action on the behavioral effects of B. Experiments included either castrated males, hormone (either B, T, or B + T)-implanted intact males, or sham males. Behavioral observations were recorded when these males were challenged with "immigrant" males; measurement of plasma steroids confirmed the efficacy of implants in elevating B and T. Castration, B implantation, and combined B and T implantation significantly reduced aggressive behavior to varying degrees, while T implants in intact animals had no effect. B implants significantly decreased plasma T levels (from 1.87 to 0.33 ng/ml), but this decrease was not essential for the inhibitory effect of B on aggression since B + T implantation also reduced aggression, even though plasma T was elevated above normal (67.6 ng/ml). In contrast, B implantation did not affect male courtship and copulatory behavior when males were presented with estrogenized females. These results suggest that the effect of B on social behavior is not through just a single route, that of decreasing plasma T, and that B can affect various intra- and intersexual behaviors differently. © 1993 Academic Press, Inc.

Stress can have dramatic effects on many body functions including reproduction, and the adrenal axis is thought to play a major role in modulating these effects. Adrenal hormones have been shown to influence reproduction in fishes (Van den Hurk, Gielen, and Terlou, 1984), amphibians (Moore and Zoeller, 1985), reptiles (Tokarz, 1987), birds (Deviche, 1983), and mammals (Matteri, Watson, and Moberg, 1984), including humans (Cunningham, Caperton, and Goldzieher, 1975).

Reptiles exposed to stress show an increase in plasma levels of corticosterone (B), the primary adrenal hormone (Gist and Kaplan, 1976; Lance and Lauren, 1984; Dauphin-Villemant and Xavier, 1987), and a decrease in levels of reproductive hormones including testosterone and the gonadotropins (Licht, Breitenbach, and Congdon, 1985; Lance and Elsey, 1986). Reproductive behavior and stress show a reciprocal interaction, with each influencing the other. Intact lizards that lose agonistic

encounters have increased B levels (Greenburg, Chen, and Crews, 1984), while subcutaneous B pellets reduce aggressive behavior in the lizard *Anolis sagrei* (Tokarz, 1987).

In territorial reptiles, reproductive behavior of males can be divided between agonistic behavior with other males and courtship behavior with females. Agonistic behavior is essential for establishing a quality territory which can greatly affect the number of females available to a male (Tinkle, 1967; Fox, 1983), while courtship behavior precedes successful gamete transmission to available females. The side-blotched lizard (*Uta stansburiana*) is an ideal model for studying both components of reproductive behavior: males almost totally exclude other males from their territory (Tinkle, 1967), females maintain smaller territories that are partially or completely overlapping with the territories of males, and the side-blotched lizard is vigorous in the laboratory and incorporates stereotypical displays which can be easily quantified (Ferguson, 1970; Ferguson and Bohlen, 1978). Here we investigate further the role of adrenal steroids as possible mediators of the effect of stress on intra- and intersexual reproductive behaviors. Of particular importance is the extent to which the effects of B are mediated through changes in plasma T levels. To address this issue, we performed experiments involving B treatment alone and in combination with T treatment. Complimentary experiments using T implantation alone and castration to elevate and reduce T, respectively, were also carried out to provide behavioral extremes against which we could reference the experiments using B. We also quantified the effect of B on courtship behavior with females.

MATERIALS AND METHODS

Animals and Husbandry

Adult side-blotched lizards (*U. stansburiana*) were collected during the peak reproductive season (April through July) from the east side of California's coast range; in this study population male territoriality and egg-laying occur through August. Lizards were collected from two sites, Corral Hollow Road in San Joaquin County and Billy Wright Road in Merced County. The lizards were housed in an environmentally controlled room with a 14 light:10 dark photoperiod at $26 \pm 1.5^\circ\text{C}$. Lizards were housed singly in clear plastic rodent cages ($25 \times 48 \times 20$ cm) with screen lids, and aluminum foil on one side of each cage prevented visual contact between lizards. Sand was used as a substrate and a 75-watt Sylvania Spot-Gro floodlight was suspended over the far side of each cage to provide a temperature gradient of $27\text{--}42^\circ\text{C}$ within the cage. Lizards were fed crickets and/or mealworms three times per week in quantities which maintained good body condition, while water was provided by misting cages twice a week. All lizards were allowed at least 1 week to adjust to

their captive environment before being assigned to a study. Once acclimated, male lizards were randomly assigned to either an experimental, control, sham, or "immigrant" group. Mean lizard mass of all groups ranged from 5.7–7.4 g; average mass of groups within an experiment never differed by more than 0.2 g.

Behavioral Tests for Agonistic Behavior

Behavioral testing began approximately 5 days after experimental manipulation to allow time for surgical recovery and hormone level equilibration. Testing of agonistic behavior involved introducing an immigrant male into the cage of a "resident" male which had undergone either an experimental or sham procedure. The number of push-up displays, lateral displays, and attacks was recorded for both the immigrant and resident male (Ferguson, 1970). A "winner" was qualitatively determined as follows: Lizards that showed greater aggression at the end of the session were deemed winners while those showing escape behavior (e.g., scratching at walls or burying in the sand) were considered "losers." If there was no obvious winner, the trial was considered a draw. Sessions lasted 10 min or until one lizard buried. Test males were exposed in random order to a different immigrant male every 2 days until each test male had been exposed to all immigrants. The 2-day hiatus between sessions was designed to minimize any effects a session may have on subsequent sessions. All sessions were conducted in the morning from 0800 to 1000 hr.

Behavioral Tests for Courtship Behavior

Studies of courtship behavior were similar to those of agonistic behavior except that an estrogenized female was introduced into a cage housing either a sham or B-implanted male. Tongue flicks, copulatory attempts, and successful copulations were recorded in addition to displays and attacks.

Experimental Manipulations

Individual experiments were composed of a single manipulated group (either castrate, B-implanted, T-implanted, or B+T-implanted) and a simultaneously run sham group. Animals were prepared for each experiment as detailed below. Because of limitations of space and animal availability, each experiment used separate freshly collected groups of lizards.

Experiment 1: Effect of castration on agonistic behavior. The first study sought to establish the role of endogenous T in agonistic behavior of *U. stansburiana*. Using clean surgical procedure, experimental lizards were anesthetized with isoflurane and a 3- to 5-mm incision was made through the skin and muscles of the left flank. The testis was exteriorized from the body cavity and then gently teased free from surrounding tissue. The incision was closed with a single horizontal mattress suture made with 5-

O Vicryl (Ethicon). This procedure was repeated on the right side. Sham lizards experienced the same procedures, except that the testes were re-placed into the coelomic cavity instead of being removed. Control and immigrant lizards were unmanipulated.

Experiment 2: Effect of exogenous B on agonistic behavior. The objective of the second study was to determine the effect of B on both agonistic behavior and plasma T levels. Experimental lizards were anesthetized with isoflurane and a 3-mm incision was made through the skin and muscles of the left flank using clean surgical procedure. A Silastic tubing implant filled with corticosterone (Sigma) was placed intracoelomically and the incision was closed as above. Sham lizards received saline-filled silastic implants. Implants consisted of a 3-mm piece of 0.078-inch (inside diameter) Silastic brand medical-grade tubing (Dow Corning No. 602-305) plugged with 1-mm wooden caps at each end, thus leaving 1 mm of fillable space. Implants were soaked in sterile saline for 24 hr prior to implantation. To determine the reversibility of the B effects, we removed the implants after the completion of the first set of trials and retested the males 12 days later.

Experiment 3: Effect of combined B and T treatment on agonistic behavior. This test examined if B had an effect on agonistic behavior independent of the effect of B on plasma T levels. Preparation was the same as that for experiment 2, except that experimental lizards were implanted with both B and T implants, while sham lizards were implanted with two saline implants.

Experiment 4: Effect of exogenous T on agonistic behavior. This study complemented experiment 3 by determining the effect of exogenous T alone on agonistic behavior of intact males. Preparation was the same as that for experiment 2, except that experimental implants contained T (Sigma) rather than B.

Experiment 5: Effect of exogenous B on courtship behavior. The last study was to determine whether B affected the courtship component of reproductive behavior. Males were prepared as in experiment 2, but were presented females rather than males. To minimize variability in female receptivity over the course of the behavioral trials, females were injected with 0.50 μg estradiol (Sigma) dissolved in 0.05 ml peanut oil three times per week during the test period.

Hormone Assays

Twenty-four hours after the completion of the behavioral tests, test males were decapitated and trunk blood was collected in heparinized hematocrit tubes. The tubes were centrifuged to obtain plasma which was stored at -70°C until analyzed. Hormone levels were determined using radioimmunoassays (Licht, McCreery, Barnes, and Pang, 1983). For analysis, 10–35 μl of plasma was extracted in ether and then resuspended in

1.0 ml of a phosphate buffer. Each sample was serially diluted 10-fold to provide two samples for each lizard. Samples taken for experiments 1 and 2 were chromatographed on microcolumns of celite to separate testosterone (T) and corticosterone (B) (Wingfield and Farner, 1975). Additional columns with known amounts of [^3H]T and [^3H]B were run with each assay to determine recoveries. Samples for experiment 3 were extracted but not chromatographed; separate aliquots were used for each hormone. Unfortunately, samples for experiment 4 were lost due to column failure.

Statistical Analysis

Mann-Whitney *U* tests were used to analyze both behavioral data and plasma steroid levels between groups. Paired *t* test was used when serial recordings were made. Results were considered significant if $P \leq 0.05$.

RESULTS

Although the four male-male experiments spanned a 4-month period (April-July) over 2 years, the repeatability of behavioral results among sham groups was high, with no differences (by Kruskal-Wallis test) in displays ($P = 0.378$) or attacks ($P = 0.346$) (see Figs. 1-4).

Experiment 1: Castration Depresses Agonistic Behavior

Castration greatly reduced but did not eliminate a male's display and attack frequency ($P = 0.004$ for displays; $P = 0.016$ for attacks) (Fig. 1A). Castrates showed attack behavior in only 36% of the trials, and only 14% of the trials had more than one attack. In contrast, shams attacked the immigrant lizard in 86% of the trials, attacking more than once 83% of the time. Sham males won all of their trials, while castrates won only 47% of their trials, based on combined measures including display, attack, and escape behavior. Castration resulted in markedly reduced plasma T levels ($P = 0.004$), but had no effect on plasma B levels ($P = 0.749$) (Fig. 1B).

Experiment 2: Exogenous B Reduces both Plasma T Levels and Agonistic Behavior

Lizards implanted with B also had significantly reduced display and attack behavior compared to sham levels ($P = 0.025$ for displays; $P = 0.010$ for attacks) (Fig. 2A). B-implanted males showed attack behavior in 44% of their trials, with only 28% of the trials having more than one attack. Corresponding sham values were 89 and 69%, respectively. Sham males won 97% of their trials, while B-implanted won only 61%.

B implantation caused a rise in plasma B levels ($P = 0.021$) and a concomitant decrease in plasma T levels ($P = 0.021$) (Fig. 2B). Removal of B implants followed by a 12-day resting period before retesting returned

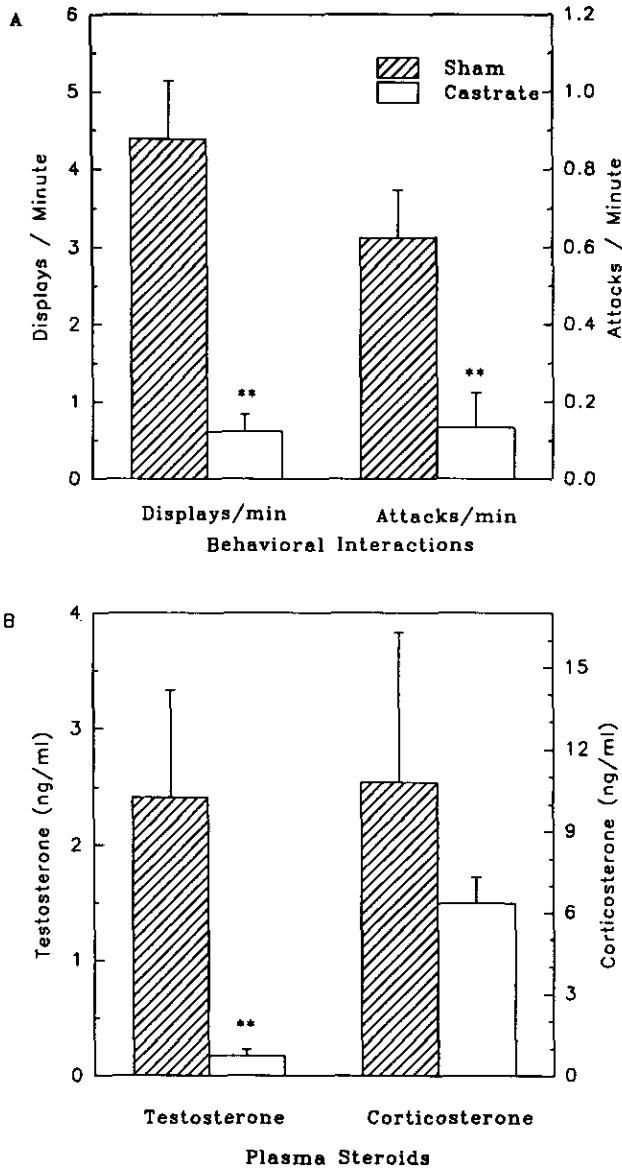


FIG. 1. Effect of castration on (A) frequency of agonistic behaviors and (B) plasma T and B levels. $N = 6$ for both sham and castrated groups (* $P < 0.05$; ** $P < 0.02$).

both plasma B and T levels to sham values ($P = 0.327$ for B; $P = 0.462$ for T). Both display and attack frequency postimplant removal were significantly greater than display frequency during B implantation ($P = 0.031$

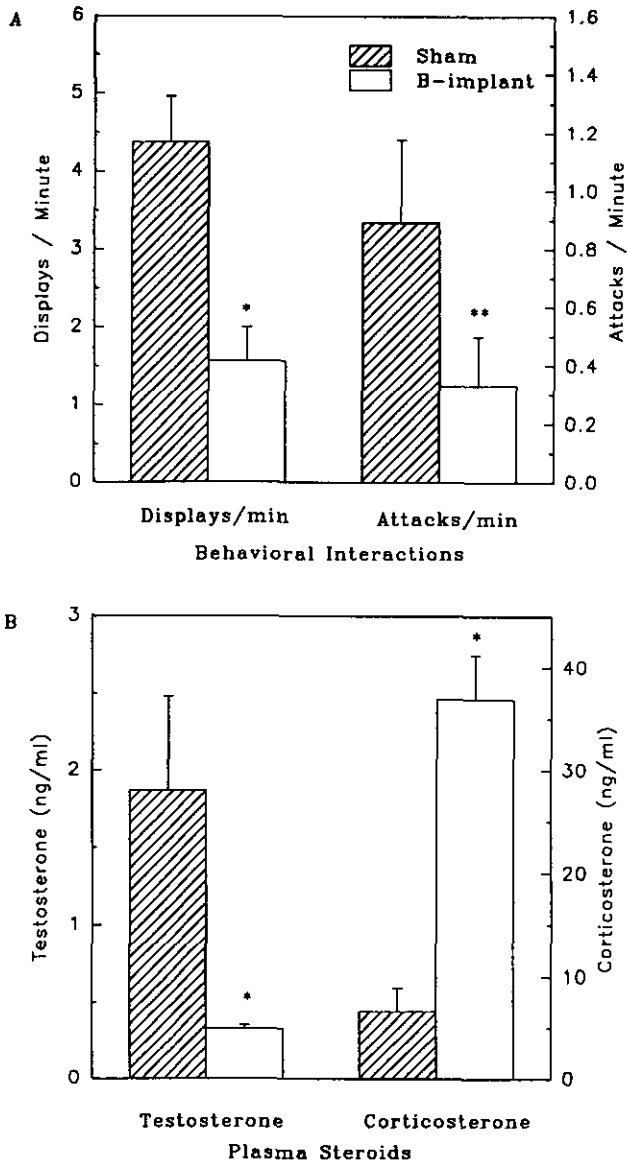


FIG. 2. Effect of intracoeleomic B implantation on (A) frequency of agonistic behaviors and (B) plasma T and B levels. $N = 6$ for both sham and castrated groups (* $P < 0.05$, ** $P < 0.02$).

for displays; $P = 0.039$ for attacks), although levels obtained were still significantly less than the sham values ($P = 0.009$ for displays; $P = 0.039$ for attacks).

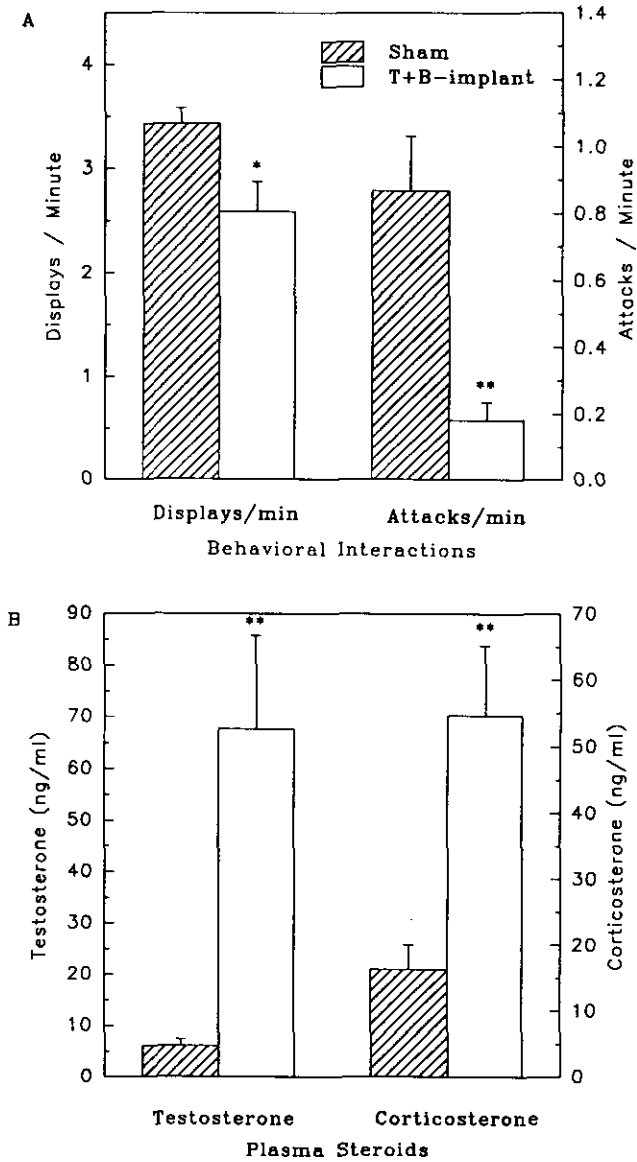


FIG. 3. Effect of intracoelemic B + T implantation on (A) frequency of agonistic behaviors, and (B) plasma T and B levels. $N = 6$ for both sham and B + T behavior measurements and sham hormone measurements. $N = 4$ for B + T hormone measurements (* $P < 0.05$, ** $P < 0.02$).

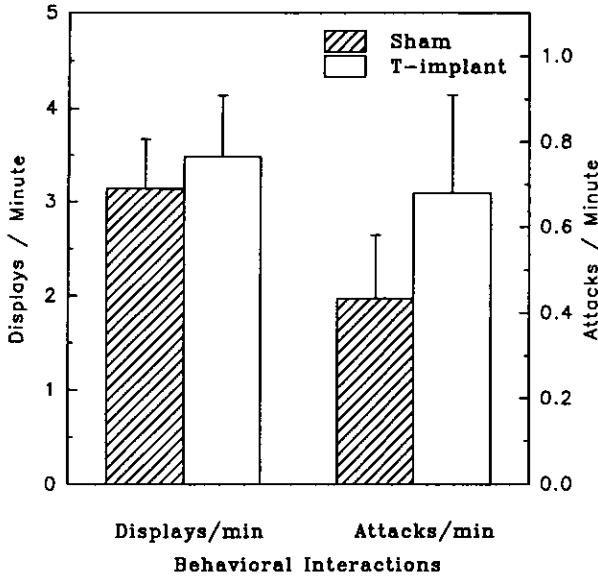


FIG. 4. Effect of intracoelemic T implantation on frequency of agonistic behaviors. $N = 6$ for both sham and T-implanted groups.

Experiment 3: Exogenous T Does Not Inhibit Effects of B

Implantation with both B and T significantly reduced both display and attack behavior ($P = 0.031$ for displays; $P = 0.004$ for attacks) (Fig. 3A). B+T-implanted lizards attacked in 53% of the trials, with 33% having multiple attacks, compared to 92 and 78% for shams, respectively. Shams won all trials while B+T implants won 89% of their trials. B+T implants elevated both plasma B ($P = 0.011$) and T ($P = 0.011$) to levels well above those of shams (Fig. 3B).

Experiment 4: Exogenous T Has No Effect on Agonistic Behavior

Intact lizards implanted with T showed no significant difference from shams in either display or attack behavior ($P = 0.873$ for display, $P = 0.522$ for attacks) (Fig. 4). T-implanted lizards attacked in 83% of the trials, and 69% of the trials had more than one attack (versus 61 and 33%, respectively, for shams). T-implanted lizards won 69% of their trials, while shams won 72% of theirs. Hormone levels were not determined because of assay failure.

Experiment 5: B Has No Effect on Courtship Behavior

When presented with estrogenized females, B-implanted males showed no difference in response compared to sham males. B-implanted males were equally likely as sham males to perform displays ($P = 0.482$), tongue

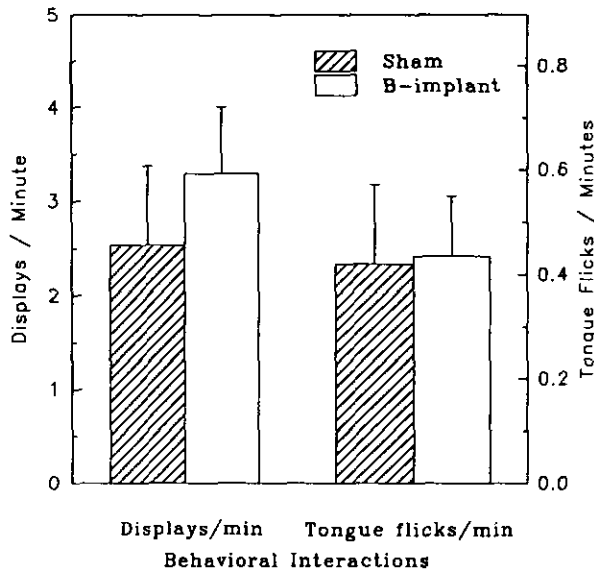


FIG. 5. Effect of intracoelemic B implantation on frequency of display and tongue flick behavior. $N = 7$ for both sham and B-implanted groups.

flick females ($P = 0.949$), attempt copulation ($P = 0.523$), and successfully copulate ($P = 0.338$) (Fig. 5, Table 1). In 96 trials, we recorded only one attack on a female (the male being B-implanted).

At the completion of the courtship trials, the males were tested for male-male aggression. As in experiment 2, the B-implanted males had reduced display and attack behavior. In this experiment, displays were reduced to 55% and attacks to 36% of sham behavior ($P = 0.028$ for display; $P = 0.0009$ for attacks) (data not shown).

DISCUSSION

Stress induces a complicated neuroendocrine response involving numerous neural pathways and a suite of hormones (see Axelrod and Rei-

TABLE 1
Effect of Intracoelemic B Implantation on Copulatory Attempts and Success

Treatment	Copulations attempted	Copulations successful	% Successful
Sham	24	17	71
B-Implanted	21	13	62

Note. Absolute values represent the total number of attempts or successes in 42 trials (seven males were used for each group and each male was presented with the same six estrogenized females in random order). "% Successful" = the fraction of copulatory attempts that were successful. $\chi^2 = 0.4108$.

sine, 1984; Rivier and Rivest, 1991 for review). The adrenal corticoids play a predominant role in the stress response, with rapid increases in corticosterone having been measured in reptiles during various stressful situations including handling (Lance and Lauren, 1984), bleeding (Gist and Kaplan, 1976), confinement (Dauphin-Villemant and Xavier, 1987; Moore, Thompson, and Marler, 1991), and cohabitation with a dominant individual (Greenberg, Chen, and Crews, 1984).

Although B implantation may not be a true stress mimic, it provides an effective tool to help dissect the constituents of a complex interaction between stress and reproduction. By directly manipulating a hormonal component of stress, we can address its primary effects as a modulator of stress, independent of any confounding effect of the actual condition that is responsible for stimulating the stress response (e.g., excessive heat, desiccation, overcrowding, handling). Our results suggest that B, as an isolated component of the stress response, has complex effects on social behavior, acting not only through decreasing plasma T levels and differentially affecting specific intra- and intersexual behaviors.

As has been shown previously in lizards (Moore, 1987), castration greatly affects agonistic behavior. While agonistic behavior was greatly reduced, it was not eliminated (Fig. 1). Moreover, regardless of the manipulation performed, the experimental males won nearly half if not more trials (the minimum proportion of victories for an experimental group was 47% for castrates). This result may reflect the advantage of being the resident male during a conflict; i.e., there may be a dramatic "home field" advantage. Residency, and possibly other perceptive qualities, may play an important role in behavior independent of plasma hormone levels.

The role of T in agonistic behavior is well documented in many species (Lincoln, Guinness, and Short, 1972 in deer; Wingfield, Ball, Dufty, Hegner, and Ramenofsky, 1987 in birds), including lizards (Fox, 1983; Moore, 1988). Although greatly reduced, T was still detectable in the plasma after castration. Since the surgical technique involved removing the testes still encapsulated in the outer membrane, residual T was most likely an extragonadal, perhaps interrenal, product. The lack of difference in plasma B levels between controls, shams, and castrates suggest that any potential stress due to the castration procedure played little or no role in the reduction of agonistic behavior.

Plasma B levels created by B implantation were similar to the maximal levels recorded in *Uta* immediately postcapture in the wild (Wilson, 1990; Wilson and Wingfield, 1992). It is not known, however, how long B might be elevated in nature. The reduction in T as a consequence of B implantation supports previously reported decreases in T noted after B implantation (Tokarz, 1987) and experimentally induced stress (Moore *et al.*, 1991) in lizards. While B implantation depressed plasma T levels to 18% of sham plasma T levels, this depression was not as severe as that

seen in castrated males, whose plasma T levels were only 7% of sham levels.

B implantation depressed both display and attack behavior, but neither decrease was as dramatic as that seen in castration. Displays were reduced to 37% and attacks to 36% of sham levels compared to castration which reduced displays and attacks to 13 and 18%, respectively. Even though the two experimental treatments were performed in separate experiments, the similarity in sham levels of the two behaviors (see Figs. 1 and 2) justifies such comparison.

While removal of the implants returned plasma B and T to sham levels, agonistic behavior was not fully restored. The incomplete restoration of agonistic behavior in the presence of normal plasma hormone levels could be explained physiologically, behaviorally, or by a combination of both. While the 12-day recovery period between implant removal and retesting may have been sufficient for plasma hormone levels to adjust completely, numerous unmeasured parameters such as hormone receptor number, binding protein concentration, or tissue histology must be considered. Alternately, the incomplete recovery of agonistic behavior may be the result of a learned tolerance to other males similar to the "trained loser" concept of Bernstein (1981). While removal of endogenous T (via castration) had a dramatic inhibitory effect on agonistic behavior, addition of exogenous T to intact animals failed to change behavior significantly. Although hormone levels were not determined for this experiment, it is likely that plasma T was elevated well above normal based on the success of these implants in other experiments (see experiment 3). This result conflicts with work on the mountain spiny lizard (*Sceloporus jarrovi*) in which silastic T implants significantly increased aggression in both castrated males (Moore, 1987) and nonreproductive intact males (Moore and Marler, 1987). This disparity could be related to differences in endogenous plasma T levels; the *Sceloporus* work was conducted on lizards with relatively low endogenous plasma T, while our work was performed on intact males during peak breeding season. We implanted intact males rather than castrates to provide a comparison group for the B+T experiment. If exogenous T increased agonistic behavior, and exogenous B counteracted this increase, then the behavior of B+T-implanted lizards could resemble that of shams. Without knowing the effect of exogenous T alone, such a counteracting effect could be hidden.

The resultant decrease in agonistic behavior of males implanted with both T and B reveals that B has an effect on agonistic behavior independent of its effect on plasma T levels. The reduction in attack behavior (to 20% of shams) was similar to the reduction seen in B implantation alone (to 37% of shams). Display behavior was only moderately reduced by B+T implantation (to 75% of shams compared to B implantation alone which reduced display behavior to 36% of shams). These data

suggest that the decrease in plasma T levels measured as a result of an increase in B is a component of B's overall effect on reproductive behavior, but is *not the sole avenue by which these effects are expressed*. The ability of B to inhibit aggression independent of plasma T levels has also been documented in song sparrows, *Melospiza melodia* (Wingfield and Silverin, 1986). Silastic B implantation of male sparrows reduced aggression toward intruders, but only had a slight effect on plasma T levels, leaving T well within normal levels of territorial male sparrows. While the results in song sparrows and in *Uta* do differ in the effect of B on plasma T levels, both studies suggest that B has effects on aggression independent of plasma T levels. Whether this plasma T-independent inhibition is related to T (e.g., T receptor inhibition) or totally independent of T (e.g., directly affecting behavioral centers of the brain) has not been elucidated.

While B effectively inhibits agonistic behavior whether or not T levels are allowed to drop, B has no effect on a male's ability to perform courtship behavior. B-implanted males courted females as intensely as sham males and were just as successful at accomplishing intromission. These results do not provide information on B's effect on reproductive success under natural conditions, since the decreased aggressive behavior of B-implanted males may prevent access to females or unmanipulated females may be less receptive to B-implanted males. Our objective was to measure the effect of B on a male's interest in females and a male's ability to perform courtship behavior. The effect of B on female accessibility and perceptivity would best be addressed in the field which provides the complex social structure required for such work.

The stress response is often considered detrimental, with stress usually leading to negative effects such as decreased production (Cunningham, van Tienhoven, and Gvoryahu, 1988, with chickens) or retarded growth (Hemsworth, Barnett, and Hansen, 1981, with pigs). Alternately, the stress response may be viewed as a survival response. By temporarily "turning off" nonessential physiological components such as those involved in reproduction and growth, an animal can increase its chance of survival during a life-threatening episode.

The differential effect of B on agonistic and courtship behavior may be a result of the relative cost-benefit of such reproductive behaviors. Territorial behavior requires high energy output (Nagy, 1983), yet does not assure female access. During unfavorable times it may be advantageous to eliminate this costly behavior. One example of this potential strategy is tail loss. The loss of a tail is costly to a lizard since it negatively affects both energy reserves (Ballinger and Tinkle, 1979) and locomotory ability (Ballinger, Nietfeldt, and Krupa, 1979). Interestingly, tailless male *Uta* show a reduction in aggression (Fox, Heger, and Delay, 1990) and a decline in social status (Fox and Rostker, 1982). Unfortunately, B's role

in this response is unknown since plasma B levels were not assayed in any of the studies.

Contrary to agonistic behavior, maintaining courtship behavior is less costly, and maintaining such behavior could be reproductively profitable should access to a female arise. Additionally, Greenberg *et al.* (1984) point out that while being effectively nonreproductive, it may be highly advantageous to maintain reproductive capabilities in order to rapidly become reproductive once conditions become more favorable. While these studies have provided insight into the effect of corticosterone on social behavior of lizards, additional work needs to be completed in both the laboratory and in nature to understand fully the interactions between stress and reproduction.

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