

Effects of Steroid Hormone Interaction on Activity and Home-Range Size of Male Lizards

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Steroid hormones play a major role in influencing the physiology and behavior of all animals, including reptiles. Oftentimes, it is an interaction between two or more hormones that is ultimately responsible for the observed response or behavior. We designed a pair of field studies on adjacent communities of side-blotched lizards (*Uta stansburiana*) to provide insight into the interrelationship of testosterone (T) and corticosterone (B) in regulating aggressive behavior. On one site, males were implanted with either T or saline (S), while on the other site males received either two S implants or both a T and a B implant (T + B). T increased both activity (by 31%) and home-range size (by 150%), whereas S-implanted cohorts exhibited a reduction in both of these parameters (by 24 and 50%, respectively). However, when B was given in combination with T, not only were the positive effects of T eliminated, but there was a reduction in activity (31%) and home-range size (72%) similar to that reported in lizards that received B implants alone. S-implanted cohorts in the T + B experiment increased their activity and home-range size by 15 and 43%, respectively. Although these latter changes in the S-implanted males are not statistically significant, they are indicative of a compensatory increase similar to that seen in the T and previously reported B outcrop experiments. Taken together, these results illustrate that regulation of aggressive behavior is complicated, with both hormonal and social interactions playing critical roles in determining an individual's home-range size and, hence, reproductive success. © 1994 Academic Press, Inc.

The importance of testosterone (T) as a primary modulator of aggression has been documented in many animals (Harding, 1981; Ramenofsky, 1984, Wingfield, 1985; Wingfield, Ball, Dufty, Hegner, and Ramenofsky, 1987) including lizards (Fox, 1983, Moore, 1988). While often dramatic, the effect of testosterone on aggression is not a simple one. For example, T is correlated with seasonal aggression in male mountain spiny lizards, *Sceloporus jarrovi* (Moore, 1986), but artificially increasing plasma T levels of nonbreeding season males to levels equivalent to the breeding season is only partially effective at restoring breeding season aggression (Moore

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and Marler, 1987). Additionally, castration has no effect on several measures of aggression in nonbreeding males (Moore, 1987).

More recently, corticosterone (B) has been shown to have a reciprocal relationship with aggression. Intact lizards that lose agonistic encounters with conspecifics in the laboratory have increased plasma B levels (Greenburg, Chen, and Crews, 1984), while exogenous B reduces aggression in similar conspecific encounters (Tokarz, 1987a; DeNardo and Licht, 1993). Additionally, field studies have shown that B-implantation greatly inhibits a lizard's activity and ability to maintain a home range (DeNardo and Sinervo, 1994). This latter effect only exists if non-implanted males are also present, suggesting that the reduced ability to maintain a home range is the result of a competitive disadvantage rather than illness or inherent reduction in home-range size related to the B implant.

Although both T and B have been shown to influence aggressive behavior, little is known of their interaction. Increasing plasma B levels causes a reduction in plasma T levels in several species (Moore and Zoeller, 1985 in amphibians; Wingfield and Silverin, 1986 in birds, Orr and Mann, 1992 in rats), including lizards (Tokarz, 1987a in *Anolis*; DeNardo and Licht, 1993 in *Uta*). T and B are inversely correlated during chronic stress in lizards (Moore, Thompson, and Marler, 1991). Furthermore, inhibition of B activity with the glucocorticoid receptor antagonist RU486 partially reverses the reduced T levels seen during stress in the rat (Orr and Mann, 1992). The reduction in plasma T usually associated with an increase in B, however, is not the sole mechanism by which B reduces aggression, since co-implantation with T and B also reduces aggressive behavior between male lizards during staged laboratory encounters (DeNardo and Licht, 1993).

The studies described here were designed to further investigate the interaction between aggression, T, and B in free-living adult male lizards under natural conditions. Specifically, field studies were designed to document whether the increased aggression measured in previous T-implant experiment translates into increased home-range size. We also examined how co-implantation of T and B would effect home-range size and activity. We hypothesized that T would increase activity and home-range size, but co-implantation of T with B would eliminate the effect of T-implantation alone.

MATERIALS AND METHODS

Study Site and Lizards

The side-blotched lizard, *Uta stansburiana*, has been extensively used as a model species for biological research. It is especially valuable for studying behavioral endocrinology in the field, since it exhibits classical home-range defense behavior and is extremely hardy, allowing for surgical

manipulations. Interactive field manipulations and observations are possible on *U. stansburiana* because high-density populations can thrive in relatively simple habitats.

Our study site is located on the east side of California's coast range on Billy Wright Road near Los Baños Grandes, Merced County, California. The site consists of numerous variably sized rock outcrops located on cattle rangeland. *U. stansburiana*, the only lizard species permanently inhabiting the site, preferentially resides on the rock outcrops, although some adults can be found sparingly in the grass fields. The spacing of outcrops on the site minimizes lizard movement between outcrops, thereby creating relatively isolated lizard "neighborhoods" which are delineated by natural boundaries. The two studies detailed here were conducted simultaneously during the early breeding season (March–April, 1993) on two adjacent, but isolated, outcrops. The early breeding season represents the time of peak copulatory and aggressive behavior for males on this site. Initially, the T vs. S outcrop had 26 males and 34 females while the T + B vs. S outcrop had 33 males and 37 females.

Determination of Home-Range Size and Activity

All lizards on a study outcrop were captured either by hand or noose, processed, and released at the site of capture which was identified with a surveying flag. Processing included determining sex of the lizard via external appearance (enlarged post-anal scales present in males), measuring body mass (using a 10-g Pesola spring scale), measuring snout-vent length, toe clipping for permanent identification, and painting a unique symbol on the lower back of the lizard with correction fluid for identification at a distance. The correction fluid mark wears off in an average of 2 weeks, at which time the lizards are recaptured and marks reapplied. These marks have no effect on home-range maintenance and survival (unpublished observations).

Home-ranges were determined for all lizards by making repeated passes of the study outcrops. The order in which the two outcrops were visited and the route by which an outcrop was surveyed varied, but each pass involved coverage of both outcrops in their entirety. Passes were made throughout the active part of the day, and involved only visual observations (i.e. rocks and other debris were not moved to locate lizards). Passes were made at least 1.5 hr apart. Each sighting was logged in relation to the site of the lizard's original capture via a compass bearing (to the nearest degree) and distance measurement (to the nearest 0.1 meters using a hip chain). Minimal convex polygons (Tinkle, 1967) were created from the sightings data using a custom computer program (MacTurf, available for Apple MacIntosh from B.S. upon request). Relative activity of the lizards was determined by comparing the total number of sightings for each lizard. While this is a simplistic measure of activity, the topography

and openness of the study site make recognition of active lizards quite easy. Therefore, the number of sightings are a reliable indicator of a lizard's true activity. This measurement does not provide any insight into how time is being allocated to specific activities (e.g. food acquisition, home-range defense, reproduction, thermoregulation).

Experimental Manipulation

Once initial home ranges were determined (13 passes), male lizards were recaptured for implantation. On one outcrop, males were randomly implanted with a Silastic implant containing either physiological saline (S) ($n = 12$) or T ($n = 12$), while males on the other outcrop received either two S implants ($n = 14$) or both a T and a B implant (T + B) ($n = 13$). For the T vs. S outcrop, two males disappeared from the outcrop prior to the implantation date. On the T + B vs. S outcrop, one male disappeared prior to implantation and five males avoided capture during collection for implantation. Only one of the three lizards that disappeared from the outcrops (likely mortality) had a measurable home range during the pre-implantation sightings. All of the five males that avoided capture during collection for implantation were relatively inactive animals during the pre-implantation sighting period (maximum of three sightings and 0.7 m² home range).

Implants consisted of a 3-mm length of 0.078 inch (inside diameter) Silastic medical grade tubing (Dow Corning 602-305) sealed at each end with 1 mm of silicone sealant. These implants thus provided 1 mm length of fillable tubing. Implants were either filled with hormone or left empty. Twenty-four hours prior to implantation, implants were soaked in sterile physiological saline to allow the saline to enter the implants.

Similar implants have been used previously in *U. stansburiana* (DeNardo and Licht, 1993) to create hormone levels equivalent to the high physiological range. These implants are known to keep hormone levels in both captive and free-ranging lizards elevated in excess of 3 months (DeNardo and Licht, 1993), far beyond the length of these studies (approximately 1 month). Therefore, it is relatively safe to assume that our implants provided elevated hormone levels within physiological limits for the entire length of our study. These lizards were not blood sampled for determination of hormone levels since they were part of a larger long-term study to be reported. Additionally, the large blood sample (relative to body mass) that is necessary for proper hormone level assessment may influence survivorship or home-range defense behavior of the individuals in question.

Implants were placed intracoelomically through a flank incision after injecting 0.02 ml of 0.2% lidocaine subcutaneously at the incision site and cooling the lizard in a crushed ice bed. This anesthetic protocol provides appropriate anesthesia and allows for rapid recovery (2–5 min

for total recovery), which is essential to minimize the time the lizard is away from its home range. Total time of captivity for an implant procedure was up to 1 hr, but usually much less. Lizards were released at the site of capture. All implants were performed within 24 hr. The lizards were given 5 days to recover from surgery and interact with neighbors before re-determination of their home ranges as described above.

Statistics

Mann-Whitney *U* tests were used to analyze data between groups, while paired *T* tests were used when sequential data was taken for the same lizards. Results were considered significant if $P \leq 0.05$.

RESULTS

In addition to the males which disappeared from the site prior to the implantation date and the males that avoided capture, several implanted males failed to survive until the end of the experiment. These included 1 S-implanted and 4 T-implanted males from the T vs. S outcrop, and 4 S-implanted and 2 T + B-implanted males from the T + B vs. S outcrop. This mortality left 19 males (11 S and 8 T) surviving the entire study on the T vs. S outcrop and 21 males (10 S and 11 T + B) males surviving on the T + B vs. S outcrop. Twenty-eight females on each outcrop survived the entire study. This survivorship (73% for the T vs. S outcrop and 64% for the T + B vs. S outcrop) was similar to that observed simultaneously in unimplanted lizards on other outcrops on the site (58%). Only lizards that survived through the entire experiment are considered in statistical calculations.

Variation between male home-range size was great, ranging from 0 to 142.3 m² for the T vs. S outcrop and 0 to 130.4 m² for the T + B vs. S outcrop (Figs. 1A and 2A). Mean pre-implantation home-range size was similar for both outcrops, 39.8 (± 10.9) m² and 38.2 (± 8.7) m² for the T vs. S and the T + B vs. S outcrops, respectively. There was no significant difference between the treatment groups on either outcrop ($P = 0.302$ and $P = 0.205$ for the T vs. S outcrop and T + B vs S outcrop, respectively) (Table 1). Similarly, pre-implant sightings did not vary between treatment groups on either outcrop ($\mu = 7.8$ and $P = 0.509$ for the T vs. S outcrop; $\mu = 6.1$ and $P = 1.00$ for the T + B vs S outcrop) (Table 1).

Initial home-range size ($\mu = 5.6 \pm 1.3$ m²) and activity level ($\mu = 4.8 \pm 0.3$) of females (data combined for both outcrops) were significantly less than those of males ($P < 0.001$ for home-range size; $P = 0.001$ for activity). Notably, whereas females were unmanipulated, their home-range size and activity levels significantly decreased during the re-determination of home ranges ($\mu = 2.2 \pm 0.7$ m², $P = 0.015$ for home-range size; $\mu = 3.8 \pm 0.3$, $P = 0.014$ for activity). This observation is more

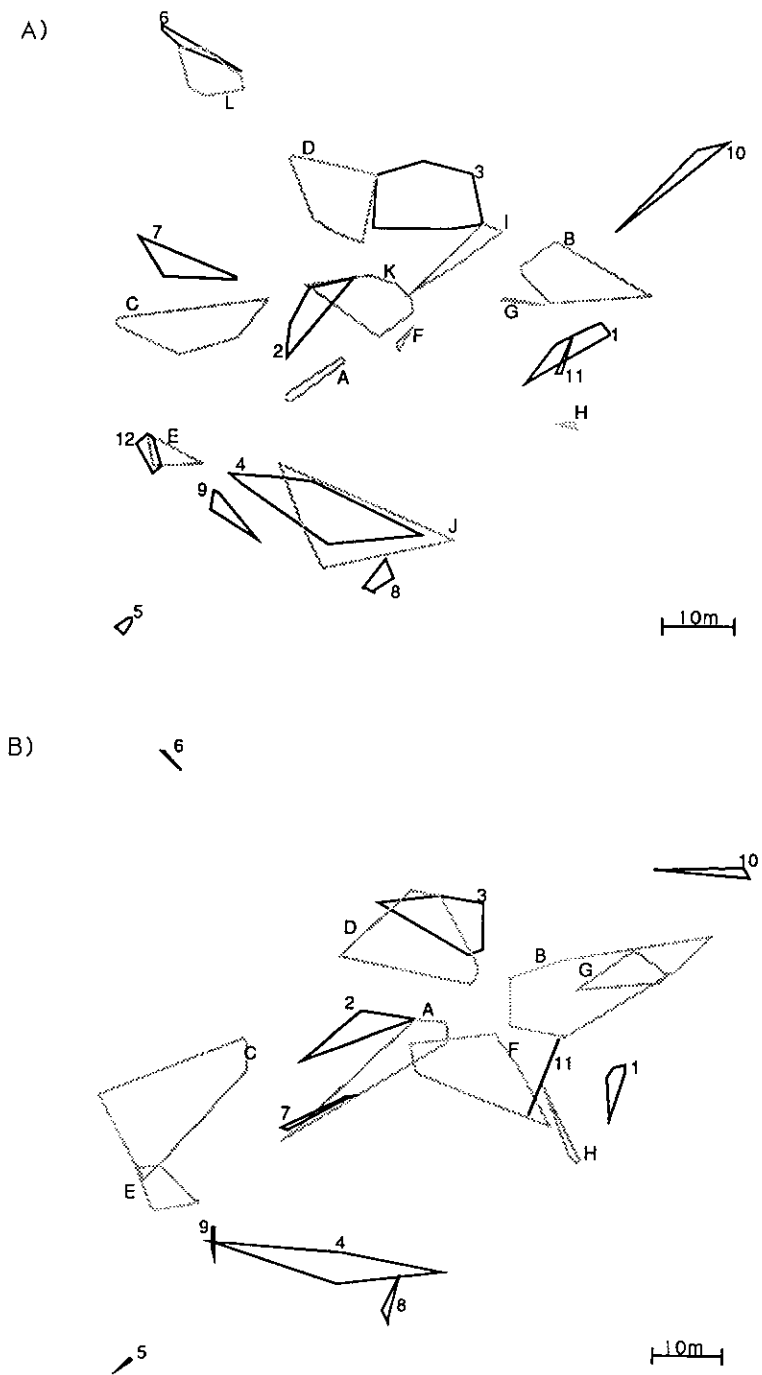


FIG. 1. Map of home ranges of male *U. stansburiana* on the T vs. S outcrop (A) pre-implantation and (B) post-implantation with either T (dashed lines) or S (solid lines). Note the dramatic increase in home-range size of T-implanted males and the concomitant decrease in home-range size in S-implanted males.

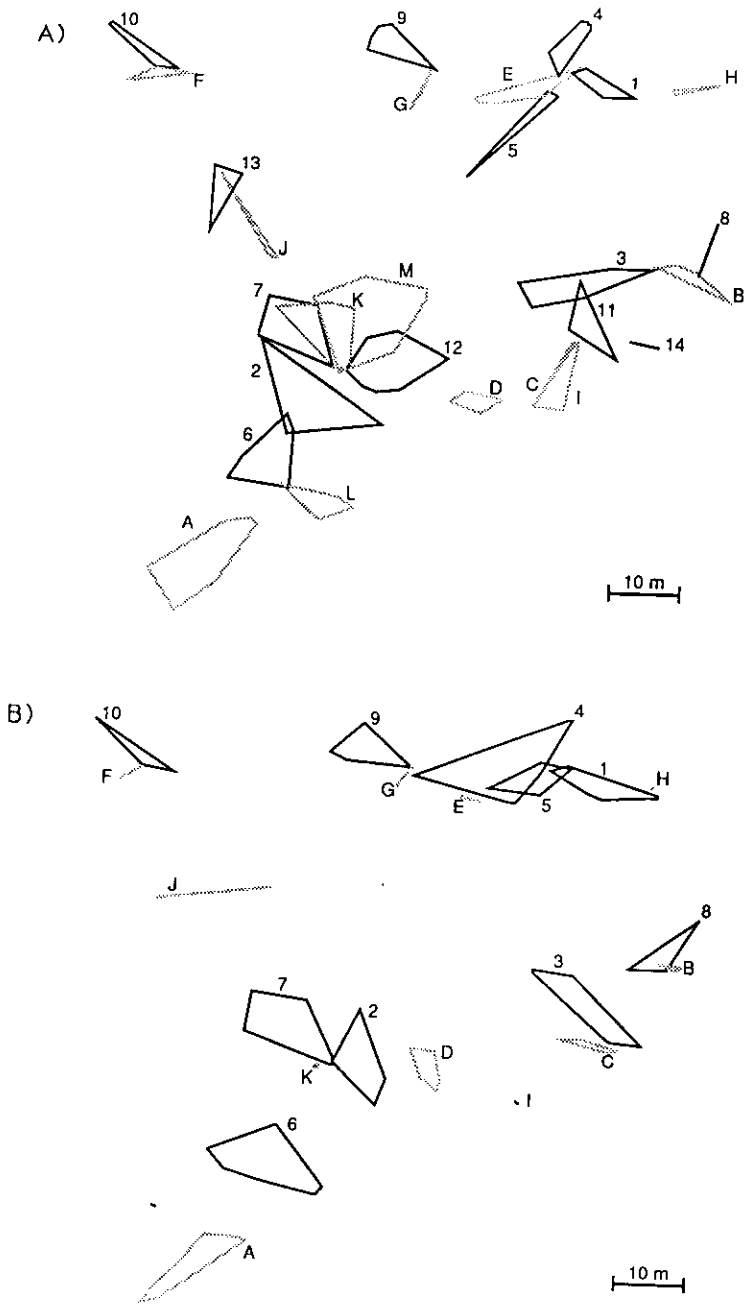


FIG. 2. Map of home ranges of male *U. stansburiana* on the T + B vs. S outcrop (A) pre-implantation and (B) post-implantation with either T + B (dashed lines) or S (solid lines). Note the dramatic decrease in home-range size of T + B implanted males.

TABLE 1
 Mean Number of Sightings and Average Home-Range Size of Male *U. stansburiana* Pre- and Postimplantation

	Preimplant		Postimplant	
	Sightings	Home-range	Sightings	Home-range
T vs. S				
S	8.3 (± 1.2)	39.5 (± 14.8)	6.3* \downarrow (± 0.9)	19.6* \downarrow (± 8.7)
T	7.1 (± 1.1)	40.2 (± 17.3)	9.3* \uparrow (± 0.6)	100.4* \uparrow (± 26.6)
T + B vs. S				
S	6.1 (± 0.6)	47.3 (± 12.9)	7.0' \uparrow (± 0.8)	67.7 (± 13.4)
T + B	6.1 (± 0.8)	30.0 (± 11.7)	4.2' \downarrow (± 0.7)	8.5* \downarrow (± 5.6)

Note. Standard error in parentheses.

*1, *4 Significant increase or decrease compared to preimplant levels (determined using paired *t* tests, $P \leq 0.05$) and compared to other experimental groups (determined using Mann-Whitney *U* test, $P \leq 0.05$).

'1, '4 Significant increase or decrease compared to other experimental groups (determined using Mann-Whitney *U* test, $P \leq 0.05$).

likely attributable to changes in behavior associated with changes in reproductive status (as vitellogenesis was well underway during the latter surveying period) than to changes in male behavior. Unfortunately, reproductive condition of each female was not closely followed, and, therefore, further study is necessary.

As a measure of competitive pressure on a given male's home range, we calculated the area of overlap for each overlapping male (if any), combined these overlaps (if there was more than one overlapping male), and divided this sum by the area of the resident male. This measurement is similar to true home-range overlap, except that it gives added weight to areas where three lizards reside. While such areas are uncommon and usually small, we believe the difference is consequential since the competition for this space is higher than for areas in which only two lizards overlap. We termed this measurement the "overlap pressure."

Mean pre-implant overlap pressure was 12% for the T vs. S outcrop and 7% for the T + B vs. S outcrop. These overlap pressures are relatively low compared to results from previous studies at this study site performed at the same time of year (DeNardo and Sinervo, 1994). However, characteristics of a given outcrop including but not limited to rock density, topography, and orientation to the sun play a role in determining both lizard density and overlap pressure. The pre-implant overlap pressure between treatment groups was not significantly different on either outcrop ($P = 0.216$ for the T vs. S outcrop and $P = 0.460$ for the T + B vs. S outcrop).

Testosterone had a dramatic effect on the sightings and the home-range

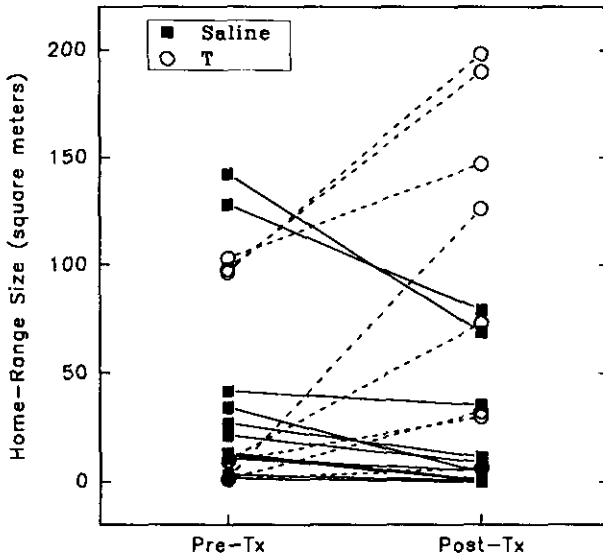


FIG. 3. Effect of S (solid squares and lines) and T (open circles and dashed lines) treatment on home-range size. Note that T-implanted males increased home-range size ($P = 0.005$) and S-implanted males decreased home-range size ($P = 0.015$).

size of most lizards on the T vs. S outcrop (Figs. 1 and 3, Table 1). Males that received T implants significantly increased both their sightings ($P = 0.046$) and their home-range size ($P = 0.005$), while S-implanted males showed a decrease in both measurements ($P = 0.016$ and $P = 0.015$ for sightings and home-range size, respectively). Additionally, T-implanted males significantly increased their overlap pressure ($P = 0.043$) from 5 to 20%. The average number of females within a male's home range significantly decreased for S-implanted lizards (from 2.0 to 1.1, $P = 0.005$) and showed a tendency to increase for T-implanted lizards (from 1.0 to 1.8, $P = 0.080$).

The combined treatment of T and B used on the T + B vs. S outcrop significantly reduced the home-range size of these males ($P = 0.033$) (Figs. 2 and 4, Table 1). S-implanted cohorts showed a suggestive, but nonsignificant, increase in home-range size ($P = 0.174$) on the T + B vs. S outcrop. Similarly, the changes in the number of sightings were directionally consistent, but nonsignificant. However, the difference in sightings between the two treatment groups was significant ($P = 0.024$). This latter comparison combines the changes observed in both groups. Additionally, T + B-implanted lizards showed a significant decrease in the average number of females present in a male's home-range (from 1.1 to 0.1, $P = 0.033$).

DISCUSSION

Inter-male aggression in lizards is considered a critical reproductive behavior, since it is vital to the establishment of home ranges (Greenberg and Crews, 1983; Wingfield and Moore, 1987). Characteristics of a male lizard's home range, including size and location, determine accessibility to females and, therefore, dramatically influence reproductive success (Stamps, 1977; Ruby, 1984; Hews, 1990). The hormonal influence of inter-male aggression in lizards is dominated by testosterone (T). The removal of T via castration greatly inhibits aggressive behavior (Moore, 1987; DeNardo and Licht, 1993), whereas increases in T, either via the natural annual cycle (Moore, 1986) or via exogenous T treatment (Fox, 1983; Moore and Marler, 1987), stimulate aggressive behavior. Furthermore, under semi-natural conditions, juvenile lizards implanted with T were able to attain a higher-quality home range than their sham pair-mates (Fox, 1983).

While natural circulating levels of steroid hormones, even when elevated, are probably more cyclical than in continual release implants, the use of exogenous hormones provide a first approach to understanding the causal relationship for naturally observed correlations between hormones and physiological and behavioral observations. Additionally, exogenous hormone supplementation provides an effective tool for dissecting out components of complex natural interactions.

Our results with T implants are in accordance with the previously reported behavioral changes in that T-implanted lizards on the T vs. S outcrop significantly increased both activity and home-range size (Table 1). Average activity levels increased 31%, whereas average home-range size increased 150%. The effect on home-range size was not related to the size of a male's home-range prior to implantation (Fig. 3).

Not only did T implantation enlarge the home-range size of the males who received the T implant but also there was a significant effect on the home-range size of the S-implanted cohorts on the outcrop (Table 1, Figs. 1 and 3). S-implanted males experienced a 24% reduction in mean activity levels and a 50% reduction in home-range size. Results on the T + B vs. S outcrop also indicated a compensatory change in home-range size of the S-implanted lizards. The mean home-range size of S-implanted males on the T + B vs. S outcrop increased 43%; however, this increase was not statistically significant. The lack of statistical significance is probably a reflection of a combination of small sample size ($n = 10$) and a single male whose home-range decreased nearly 50%. Similar increases in home-range size of S-implanted male lizards as a result of inhibitory manipulations to neighboring males have been previously reported with corticosterone (B) implants (DeNardo and Sinervo, 1994). Together, these results indicate that home-range size is determined by the competitive

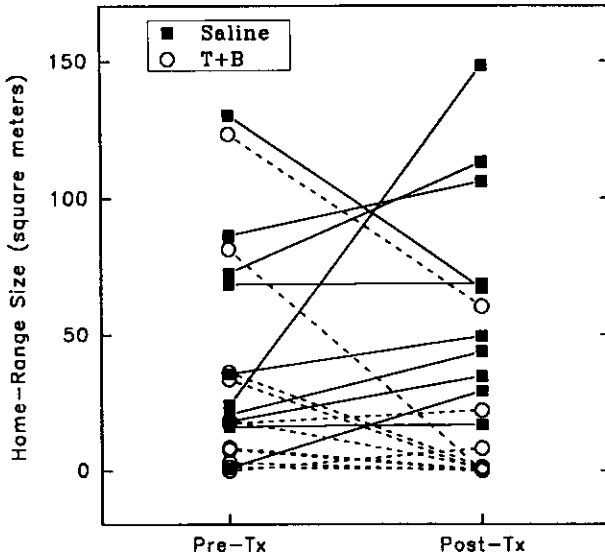


FIG. 4. Effect of S (solid squares and lines) and T + B (open circles and dashed lines) treatment on home-range size. Note that T + B-implanted males decreased home-range size ($P = 0.033$). The decrease in home-range size of S-implanted males is not significant ($P = 0.174$).

interaction between neighboring lizards, and that changes in the behavior of neighboring males may be as critical as changes in the resident male.

Although T plays a major role in regulating aggression, it is not the sole controller of aggression. Male *S. jarrovi* have both reduced plasma T levels and reduced aggression during the non-breeding season. However, the aggression seen in nonbreeding season males is neither affected by castration nor completely restored to breeding season levels with exogenous T (Moore, 1988). These results support the view that T interacts with additional mediators to regulate aggression (Sapolsky, 1987).

One such regulator of aggression is corticosterone, a major component of the stress response. Unlike T which stimulates aggression, the effect of B is inhibitory (Tokarz, 1987a, and DeNardo and Licht, 1993). B works, in part, by reducing circulating levels of T (Tokarz, 1987a; DeNardo and Licht, 1993), but laboratory results show that B also inhibits aggression when plasma T levels are maintained by co-implanting T with B (DeNardo and Licht, 1993). The results of our manipulation of lizards on the T + B vs. S outcrop support these latter laboratory results. Although T has a powerful positive effect on home-range size, B has a dramatic inhibitory effect on home-range size regardless of whether T levels are maintained. Males implanted with both T and B showed a significant reduction in mean home-range size of 72% (Table 1, Figs. 2 and 4). Additionally,

post-implant activity levels of T + B-implanted males were significantly less than the activity levels of S-implanted neighbors.

The reduction in home-range size and activity seen here in T + B-implanted lizards is comparable to that reported for B implantation alone, which reduced home-range size 38–89% and activity levels by 52–59% (DeNardo and Sinervo, 1994). These results suggest that the inhibitory effects of B on aggression are primarily independent of the induced reduction in plasma T levels. Similar reduction in aggressive behavior with no effect on plasma T levels in lizards was reported using the anti-androgen cyproterone acetate which competitively binds T receptors (Tokarz, 1987b). Whether the plasma T-independent effects of B is similarly related to T receptors or totally independent of T has not been elucidated and warrants further investigation.

Corticosterone, in addition to its effects on reproductive behavior, influences numerous other body systems in lizards, including the immune system (see Saad, 1988, for review). Therefore, caution must be used when evaluating the effects of such a diverse-acting hormone. Based on previous results, we propose that the decrease in home-range size seen in T + B-implanted lizards is a result of inhibition of aggressive behavior, not merely a result of "ill health" brought on by the exogenous B. In support of this hypothesis, courtship and copulatory behavior of B-implanted males in the laboratory is similar to that of S-implanted males (DeNardo and Licht, 1993). More convincingly, while B implantation reduces the home-range size of free-ranging males that co-exist with S-implanted males, there is no reduction in home-range size if all males on an outcrop are implanted with B (DeNardo and Sinervo, 1994). Moreover, in females, B implantation increases clutch mass (Sinervo and DeNardo, in preparation), while having no effect on home-range size (DeNardo, 1994).

The reduction in home-range size induced by T + B-implantation virtually eliminated access of these males to females (only 1 of 10 T + B-implanted males had a female in his home range). As a result, the reduction in home-range size induced by B is probably reproductively costly. However, it is also energy-saving. Home-range maintenance requires high energy output (Nagy, 1983). During the breeding season, energy output and energy intake are closely balanced, with little or no fat bodies present at this time in some lizard species (Derickson, 1976 for review), including *U. stansburiana* (Wilson and Wingfield, in preparation; DeNardo and Sinervo, unpublished data). Therefore, any increase in energy demands or decrease in energy supply may prove fatal. Male *S. jarrovi* implanted with T show increased aggression and decreased survivorship (Marler and Moore, 1988). However, if these lizards are diet supplemented, the negative effect on survivorship is removed (Marler and Moore, 1991). In

nature, diet supplementation is unlikely, and therefore the only means of correcting an energy imbalance is by reducing energy expenditure.

Changes in circulating B may provide a relatively quick adjustment in aggressive behavior that, regardless of the influence of T, reduces the energy expenditure on home-range defense. Such an adjustment may be critical during certain stressful situations such as food resource reduction. While the immediate effects of corticosterone are probably inhibitory on reproductive success (since home-range size dictates female availability), the possible increase in survivorship may greatly enhance future reproduction. While *U. stansburiana* on our site is primarily an annual species, the breeding season is relatively long (March–July). Therefore, reducing current reproductive effort in response to stress may still enhance lifetime reproductive effort (Wingfield, 1988). In the course of a single breeding season, the make-up of a “neighborhood” of *U. stansburiana* is dynamic. Male mortality can be quite high, and abandoned home ranges are taken up by other males on the outcrop. Males that are at a competitive disadvantage may opt to forego highly aggressive interactions with other males during the onset of the breeding season, and, instead, behave as “sneaker” males (Caro and Bateson, 1986), cryptically foraging and searching for females without confronting the resident male. As the season progresses and density is reduced, these sneaker males may then attempt to maintain a distinct home range and actively court females (Sinervo, unpublished data).

Whether or not there is an adaptive significance to the reduced aggression associated with B is still unknown. However, the importance of B as a regulator of reproductive behavior has become more evident. Further investigations into both hormonal and non-hormonal regulators of reproduction are necessary to better understand the complexity of reproductive strategies.

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REFERENCES

- Caro, T. M., and Bateson, P. (1986). Organization and ontogeny of alternative tactics. *Anim. Behav.* **34**, 1483–1499.
- DeNardo, D. F. (1994). *The influence of steroids on the reproductive behavior and physiology of the side-blotched lizard, Uta stansburiana*. Unpublished Ph.D. dissertation, University of California, Berkeley, CA.
- DeNardo, D. F., and Licht, P. (1993). Effects of corticosterone on social behavior of male lizards. *Horm. Behav.* **27**, 184–199.

- DeNardo, D. F., and Sinervo, B. (1994). Effects of corticosterone on activity and home-range size of free-ranging male lizards. *Horm. Behav.* **28**, 53-65.
- Derickson, W. K. (1976). Lipid storage and utilization in reptiles. *Am. Zool.* **16**, 711-723.
- Fox, S. F. (1983). Fitness, home-range quality, and aggression in *Uta stansburiana*. In R. B. Huey, E. R. Pianka, and T. W. Schoener (Eds.), *Lizard Ecology: Studies on a Model Organism*, pp. 149-168.
- Grassman, M., and Hess, D. L. (1992). Sex differences in adrenal function in the lizard *Cnemidophorus sexlineatus*. II. Responses to acute stress in the laboratory. *J. Exp. Zool.* **264**, 183-88.
- Greenberg, N., Chen, T., and Crews, D. (1984). Social status, gonadal state and the adrenal stress response in the lizard *Anolis carolinensis*. *Horm. Behav.* **18**, 1-11.
- Greenberg, N., and Crews, D. (1983). Physiological ethology of aggression in amphibians and reptiles. In Svare, B. B. (Ed.), *Hormones and Aggressive Behavior*, pp. 469-506.
- Harding, C. F. (1981). Social modulation of circulating hormone levels in the male. *Am. Zool.* **21**, 223-231.
- Hews, D. K. (1990). Examining hypotheses generated by field measures of sexual selection on male lizards, *Uta palmeri*. *Evolution* **44**, 1956-66.
- Marler, C. A., and Moore, M. C. (1988). Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. *Behav. Ecol. Sociobiol.* **23**, 21-26.
- Marler, C. A., and Moore, M. C. (1991). Supplementary feeding compensates for testosterone-induced costs of aggression in male mountain spiny lizards, *Sceloporus jarrovi*. *Anim. Behav.* **42**, 209-219.
- Moore, F. L., and Zoeller, R. T. (1985). Stress-induced inhibition of reproduction: Evidence of suppressed secretion of LH-RH in an amphibian. *Gen. Comp. Endocr.* **60**, 252-258.
- Moore, M. C. (1986). Elevated testosterone levels during nonbreeding season territoriality in a fall-breeding lizard, *Sceloporus jarrovi*. *J. Comp. Physiol.* **A158**, 159-163.
- Moore, M. C. (1987). Castration effects territorial and sexual behavior of free-living male lizard, *Sceloporus jarrovi*. *Anim. Behav.* **35**, 1193-1199.
- Moore, M. C. (1988). Testosterone control of territorial behavior: Tonic-release implants fully restore seasonal and short-term aggressive responses in free-living castrated lizards. *Gen. Comp. Endocr.* **70**, 450-459.
- Moore, M. C., and Marler, C. A. (1987). Effects of testosterone manipulations on non-breeding season territorial aggression in free-living male lizards, *Sceloporus jarrovi*. *Gen. Comp. Endocr.* **65**, 225-232.
- Moore, M. C., Thompson, C. W., and Marler, C. A. (1991). Reciprocal changes in corticosterone and testosterone levels following acute and chronic handling stress in the tree lizard, *Urosaurus ornatus*. *Gen. Comp. Endocr.* **81**, 217-226.
- Nagy, K. A. (1983). Ecological energetics. In R. B. Huey, E. R. Pianka, and T. W. Schoener (Eds.), *Lizard Ecology: Studies on a Model Organism*, pp. 24-54.
- Orr, T. E., and Mann, D. R. (1992). Role of glucocorticoids in the stress-induced suppression of testicular steroidogenesis in adult male rats. *Horm. Behav.* **26**, 350-363.
- Ramenofsky, M. (1984). Endogenous plasma hormones and agonistic behavior in male Japanese quail, *Coturnix coturnix*. *Anim. Behav.* **32**, 698-708.
- Ruby, D. E. (1984). Male breeding success and differential access to females in *Anolis carolinensis*. *Herpetologica* **40**, 272-280.
- Saad, A. H. (1988). Corticosteroids and immune systems of non-mammalian vertebrates: a review. *Dev. Comp. Immunol.* **12**, 481-494.
- Sapolsky, R. M. (1987). Stress, social status, and reproductive physiology in free-living baboons. In D. Crews (Ed.), *Psychobiology of Reproductive Behavior: An Evolutionary Perspective*, pp. 291-322.

- Sinervo, B., and DeNardo, D. F. (in preparation). Costs of reproduction in the wild: a mechanistic analysis of natural selection on reproductive effort.
- Stamps, J. A. (1977). The relationship between resource competition, risk and aggression in a tropical territorial lizard. *Ecology* **58**, 349–358.
- Tinkle, D. W. (1967). The life and demography of the side-blotched lizard, *Uta stansburiana*. *Misc. Pub. Mus. Zool.* (Univ. of Michigan), No. 132.
- Tokarz, R. (1987a). Effects of corticosterone treatment on male aggressive behavior in a lizard (*Anolis sagrei*). *Horm. Behav.* **21**, 358–370.
- Tokarz, R. (1987b). Effects of the antiandrogens cyproterone acetate and flutamide on male reproductive behavior in a lizard (*Anolis sagrei*). *Horm. Behav.* **21**, 1–16.
- Wilson, B., and Wingfield, J. C. Seasonal and interpopulational variation in plasma levels of corticosterone in the side-blotched lizard (*Uta stansburiana*). In preparation.
- Wingfield, J. C. (1985). Short-term changes in plasma levels of hormones during establishment and defense of a breeding territory in male song sparrows, *Melospiza melodia*. *Horm. Behav.* **19**, 174–187.
- Wingfield, J. C. (1988). Changes in reproductive function of free-living birds in direct response to environmental perturbations. In M. H. Stetson (Ed.), *Processing of Environmental Information in Vertebrates*, pp. 121–148.
- Wingfield, J. C., Ball, G. F., Dufty, A. M., Hegner, R. E., and Ramenofsky, M. (1987). Testosterone and aggression in birds. *Am. Sci.* **75**, 602–608.
- Wingfield, J. C., and Moore, M. C. (1987). Hormonal, social and environmental factors in the reproductive biology of free-living male birds. In D. Crews (Ed.), *Psychobiology of Reproductive Behavior: An Evolutionary Perspective*, pp. 149–175.
- Wingfield, J. C., and Silverin, B. (1986). Effects of corticosterone on territorial behavior of free-living male song sparrows *Melospiza melodia*. *Horm. Behav.* **20**, 405–417.