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Effects of Corticosterone on Activity and Home-Range Size of Free-Ranging Male Lizards

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The purpose of our study was to examine whether corticosterone (B) affects the spacing behavior of free-ranging male side-blotched lizards (*Uta stansburiana*). Furthermore, we wanted to determine if the density, reflected in seasonal changes in population size, or behavior, as a result of hormonal manipulation, of "neighboring" males influences these effects. Field studies were conducted on four naturally isolated "neighborhoods" of lizards. Half of the males on three of the sites were randomly implanted with either saline or B, while on the fourth site all males were implanted with B. Pre- and postimplant home-ranges and activity levels were determined. Home-range size and activity level were significantly reduced by corticosterone if normally aggressive saline-implanted males were also present in the neighborhood. However, B had no effect on home-range if all males in the neighborhood were implanted with B. Space lost by B-implanted males was incorporated into the home-ranges of saline-implanted males so that the sum of all the male home-ranges in a neighborhood remained unchanged after implantation. These results suggest that elevated B levels put male lizards at a competitive disadvantage and, therefore, force these lizards to reduce their home-range. © 1994 Academic Press, Inc.

Stress induces a complicated neuroendocrine response involving numerous neural pathways and a suite of hormones (see Axelrod and Reisine, 1984; and Rivier and Rivest, 1991, for review). The adrenal corticoids play a prominent role in the stress response. Increases in plasma corticosterone (B) have been measured in reptiles during various stressful situations including handling (Lance and Lauren, 1985), 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).

Experimentally increasing plasma B of male lizards in the laboratory reduces agonistic behavior toward other males (Tokarz, 1987, using *Anolis;* DeNardo and Licht, 1993, using *Uta*) but has no effect on courtship

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behavior (DeNardo and Licht, 1993). Agonistic behavior is especially critical to male lizards of territorial species, since aggressive conflicts between neighboring males impacts territory location, size, and shape. It is these parameters of a male's territory that govern the number of females that are accessible to the male (Stamps, 1977; Ruby, 1984). Males with larger home-ranges tend to have access to more females. Less aggressive male lizards, if in competition with other males, should be less likely to maintain a quality territory, and therefore may have reduced reproductive success.

Experiments directly studying the effects of corticosterone on territory or home-range size are best conducted in the field. The side-blotched lizard, *Uta stansburiana,* is an ideal species for such studies since it is common, occurs in high density, aggressively defends its home-ranges from conspecific males, can thrive in simple environments which are optimal for studies on home-range, and has been the subject of many previous studies on lizard ecology and behavior (Tinkle, 1967; Ferguson and Bohlen, 1978; Nagy, 1983; Sinervo, Doughty, Huey, and Zamudio, 1992; DeNardo and Licht, 1993).

The goal of the studies reported here was to determine the effect of B on various home-range parameters of male *U. stansburiana.* We hypothesized that the decrease in agonistic behavior of B-implanted males that has been reported in laboratory studies would translate into a decreased ability to defend a home-range from conspecific males and, therefore, a reduced home-range size of free-ranging B-implanted males. If any decrease in home-range was indeed a result of reduced aggression toward neighbors, then we would expect the presence of control males as neighbors to be critical for forcing a reduction in home-range of B-implanted males.

To test our hypotheses, we studied four "neighborhoods" of *U. stansburiana,* on which either half or all of the males were implanted with B. We expected that B-implanted males in neighborhoods where saline-implanted males also existed would have reduced home-ranges. However, we predicted B-implanted males in a neighborhood free of competition from saline-implanted males would not show a decrease in home-range, but, instead, would either maintain home-ranges similar in size to the home-ranges they had prior to implantation or show dramatic overlap of activity areas.

MATERIALS AND METHODS

Study Site and Lizards

A population of the side-blotched lizards, *U. stansburiana,* was studied on the east side of California's coast range. The study site, located on Billy Wright Road near Los Banos Grandes, Merced County, California, 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 at low density 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.

Isolated outcrops or outcrop groups were selected for each of four studies. Studies 1 and 2 utilized relatively small outcrops (9 and 8 males initially on outcrop, respectively) during the early breeding season (March–April 1991); study 3 involved a larger outcrop group (18 males) during the latter stage of the breeding season (May–June 1991); while study 4 was conducted on a moderately sized outcrop group (14 males) during the latter stage of the breeding season (May–June 1992). Climatically 1991 and 1992 were similar in that they were characterized by below normal rainfall in winter, but above normal rainfall in early spring.

Determination of Home-Range Size and Activity

All lizards on a study outcrop were captured by either 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 postanal 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 and survival (unpublished observations).

Home-ranges were determined by making repeated passes of the study plots. The route by which an outcrop was surveyed was varied, but each pass involved coverage of the entire outcrop. 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 documented with a flag which was labeled with the date, time, and lizard identification number. The location of each flag was later 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 m using a hip chain). Passes of outcrops were continued until sightings from three consecutive passes failed to enlarge any individual's home-range. An average of 21 passes were made over a time course of 14–21 days. The number of passes of an outcrop before and after implantation were similar. Minimal convex polygons (Tinkle, 1967) were created from the sightings data using a custom computer program (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 measurement 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, thermoregulating).

Experimental Manipulation

Once initial home-ranges were determined, male lizards were recaptured and implanted with either a saline or a B Silastic implant. For studies 1, 2 and 3, males were randomly implanted with either saline or B, while in study 4 all males were implanted with B. Implants consisted of a 3-mm length of 0.078-in (inside diameter) Silastic brand medical grade tubing (Dow Corning No. 602–305) sealed at each end with 1 mm of silicone sealant. These implants thus provided 1-mm length of fillable tubing. Implants were soaked in sterile saline for 24 hr prior to implantation. Similar implants have been used previously in *U. stansburiana* to create plasma levels of B of 30–50 ng/ml (DeNardo and Licht, 1993). This range approximates maximal levels recorded in *U. stansburiana* post capture in the wild (Wilson, 1990). These implants are known to keep B levels in both captive and free-ranging lizards elevated in excess of 3 months (DeNardo and Licht, 1993), which far exceeds the length of these studies (maximum of 1.5 months). Therefore, it is relatively safe to assume that our B implants provided elevated levels of B for the entire length of our study. These lizards were not blood sampled for determination of hormone levels since they are 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 behavior or survivorship 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 provided appropriate anesthesia and allowed 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 in a study were performed in either 1 (studies 1, 2, and 4) or 2 days (study 3). The lizards were given approximately 7 days to recover from surgery and interact with neighbors before redetermination of their home-ranges as described above.

TABLE 1
Average Home-Range Size of a Male *U. stansburiana* after Implantation with B as a Percentage of either (a) the Average Preimplant Home-Range Size or (b) the Average Saline-Implanted Male Home-Range Size

Study no.	a (%)	b (%)
1 (n = 5)	22*	23*
2 (n = 3)	62*	50*
3 (n = 7)	11*	11*
4 (n = 14)	100	N/A

* Significant decrease in home-range size, $P \leq 0.05$; significance determined on absolute values using paired t tests for (a) and Mann–Whitney U tests for (b); N/A, no saline implanted males in study 4.

Statistics

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

RESULTS

A few males disappeared prior to the completion of the study, including one saline-implanted and one B-implanted male from outcrop 2 and three saline-implanted and two B-implanted males from outcrop 3. Statistical analysis utilized only the data from males that survived the entire study of a given outcrop (n = 4 saline-implanted and 5 B-implanted males for outcrop 1; n = 3 saline-implanted and 3 B-implanted males for outcrop 2; n = 6 saline-implanted and 7 B-implanted males for outcrop 3; n = 14 B-implanted males for outcrop 4). Preimplant home-ranges varied considerably among individuals (0–713 m^2), and the average home-range for each outcrop also varied (48, 69, 148, and 46 m^2 for studies 1–4, respectively). Because of this great variation, home-ranges of B-implanted lizards in individual neighborhoods are reported as percentages of either preimplant home-range size of the same lizards or postimplant home-range size of saline-implanted lizards.

For studies 1, 2, and 3 (outcrops where both saline and B were used), the home-ranges of B-implanted lizards were significantly smaller than either the preimplant home-ranges of the same lizards or the home-ranges of saline-implanted lizards (Table 1, Fig. 1). Figure 2 illustrates the effects of treatment on home-range size for one of the three studies. Many of

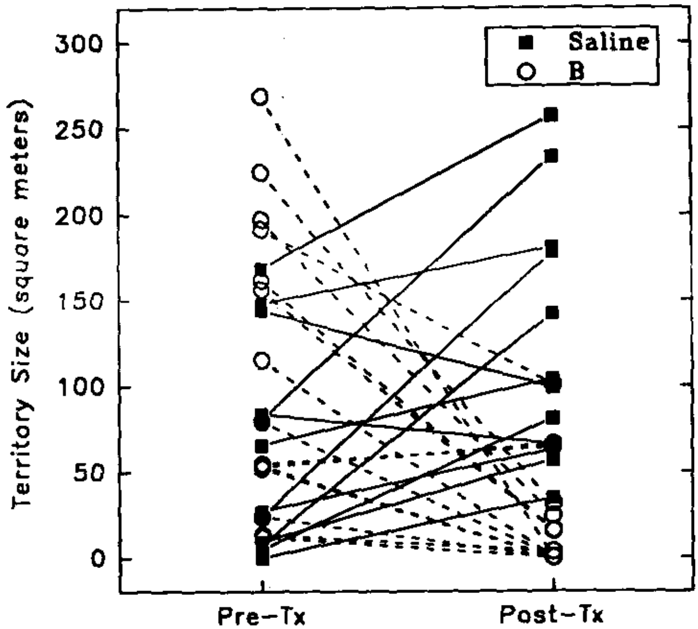

FIG. 1. Effect of saline (solid squares and lines) and B (open circles and dashed lines) treatment on home-range size. Data includes all males from neighborhoods where both saline-implanted and B-implanted males occurred (studies 1–3). Note that B-implanted males decreased home-range size ($P = 0.001$) and saline-implanted males increased home-range size ($P = 0.006$).

the B-implanted lizards had extremely small home-ranges. This was not the result of an insufficient number of sightings or the complete disappearance of a lizard from the outcrop, but reflects lizards that were repeatedly sighted on the same or adjacent rocks. Moreover, the average postimplant home-range of the B-implanted lizards in study 4 (where all males were implanted with B) was no different than the average home-range of the same lizards prior to implantation (Table 1, Fig. 3).

In studies 1, 2, and 3, where saline implants were used, the average home-range of saline-implanted males increased 210, 342, and 244%, respectively (Fig. 1). The increase in saline-implanted male home-range coincides with the decrease seen in B-implanted male home-ranges so that the sum of the home-ranges of all males postimplantation was similar to the sum of all male home-ranges preimplantation (Table 2). Similarly, the sum of the male home-ranges in study 4 was unchanged after implantation (postimplant sum of the home-ranges was 99% of the preimplant sum).

The number of times a male was sighted decreased after B-implantation, regardless of whether saline-implanted males were present in the popu-

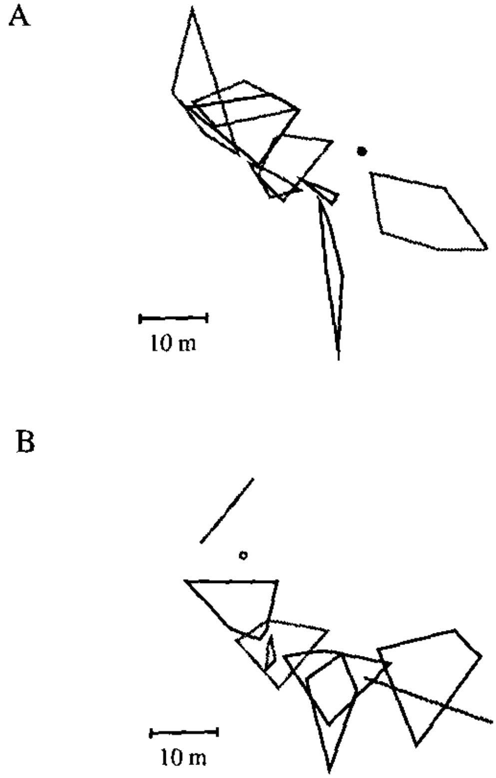

FIG. 2. Map of home-ranges of male *U. stansburiana* in study 1 (A) preimplantation and (B) postimplantation with either corticosterone (dashed lines) or saline (solid lines). Note the dramatic decrease in home-range of B-implanted males and the concomitant increase in home-range of saline-implanted males.

lation or not. However, the decline in activity recorded in study 4 where all lizards were implanted with B was less than that recorded on the outcrops where both saline-implanted and B-implanted males existed (postimplant activity was reduced to 85% of preimplantation activity for study 4 vs a reduction to 41–48% of preimplant activity for B-implanted males in studies 1–3; Table 3). In studies 1 and 2, saline-implanted males showed no difference in activity after implantation, while activity increased in saline-implanted males in study 3.

There was no consistent effect of B-implantation on home-range overlap between males; however, it is noteworthy that the average home-range overlap in study 4 (where all males were implanted with B) actually decreased after implantation (from an average of 13% of a male's home-range overlapping with another male's home-range to an average of 1% overlap after B-implantation).

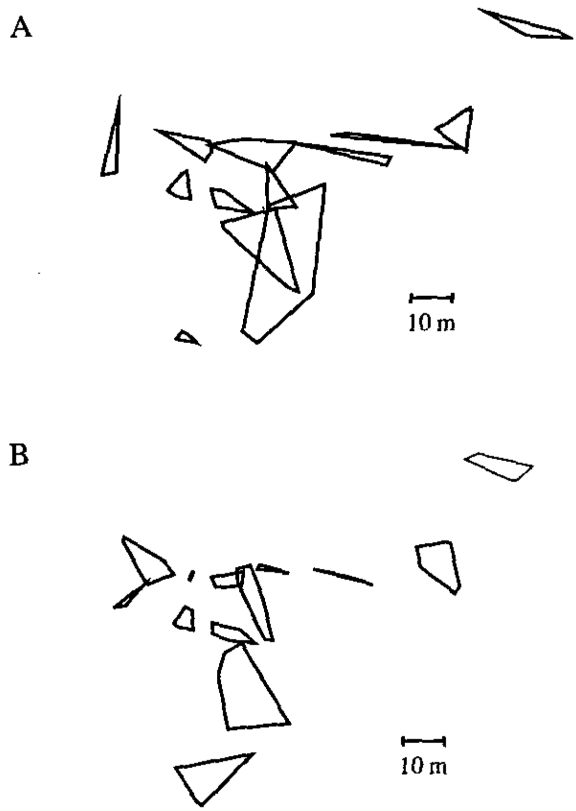

FIG. 3. Map of home-ranges of male *U. stansburiana* in study 4 (A) preimplantation and (B) postimplantation with corticosterone. Note that all males on this site were implanted with corticosterone and that home-range size was maintained after implantation.

DISCUSSION

Studying stress in a natural setting is a monumental task. The stress response is not a simple physiological reaction to a single stimuli, but

TABLE 2
Total Space Occupied by All Lizards in a Neighborhood Pre- and Postimplants

Study no.	Total space used preimplant (m^2)	Total space used postimplant (m^2)	Percentage of preimplant space[a]
1 (n = 9)	431	438	102
2 (n = 6)	554	521	94
3 (n = 13)	3559	4067	114
4 (n = 14)	639	632	99

[a] Total space used postimplantation divided by total space used preimplantation.

TABLE 3
Average Postimplant Sightings of Male *U. stansburiana* as a Percentage of Preimplant Sightings

Study no.	S-implanted ♂♂ (%)	B-implanted ♂♂ (%)
1 (n = 4S,5B)	104	41* ↓
2 (n = 3S,3B)	86	48* ↓
3 (n = 6S,7B)	137* ↑	41* ↓
4 (n = 14B)	N/A	85* ↓

* ↑, Significant increase in sightings, $P \leq 0.05$; * ↓, significant decrease in sightings, $P \leq 0.05$; significance determined conducting paired t tests on absolute values; N/A, no saline implanted males in study 4.

rather a complex interaction through numerous neural and endocrine pathways in response to any of a countless number of negative situations perceived by an individual (Axelrod and Reisine, 1984; Dukelow and Dukelow, 1989; Rivier and Rivest, 1991). In addition, the natural environment of an organism, even in the simplest of habitats, is a complicated mosaic of niches with numerous variables that can influence the choices that an individual makes.

Therefore, it is not surprising that most studies pertaining to stress or corticosterone in lizards have been conducted in the laboratory (Chan and Callard, 1972; Daugherty and Callard, 1972; Greenburg *et al.*, 1984; Dauphin-Villemant and Xavier, 1985, 1987; Tokarz, 1987; Summers, 1988; Summers and Norman, 1988; Grassman and Hess, 1992a; DeNardo and Licht, 1993). The few studies that have addressed stress in the field have focused on correlations between circulating levels of corticosterone and various other physiological parameters (Moore and Thompson, 1990; Moore *et al.,* 1991; Wilson and Wingfield, 1992; Grassman and Hess, 1992b). While such information is extremely valuable toward understanding the role of corticosterone in the stress response, there is clearly also a need for a more interactive approach.

In an effort to reduce the complexity in addressing questions concerning stress, B-implantation can be used to eliminate the perceptual component of the stress response. While B-implantation is not a true mimic of stress, it provides a valuable tool to examine a key constituent of the stress response, namely, the rise in circulating glucocorticoid levels (DeNardo and Licht, 1993).

B-implantation is known to reduce both circulating testosterone (T) levels and aggression in captive lizards (Tokarz, 1987; DeNardo and Licht, 1993). T is known to play an important role in agonistic behavior of lizards

(Fox, 1983; Moore, 1987; Moore and Marler, 1987; Moore, 1988), and no doubt the resultant reduction in T contributes to the reduced aggression seen in B-implanted lizards. Additionally, however, B-implantation can inhibit aggression even when T levels are maintained by coimplantation of B and T (DeNardo and Licht, 1993).

Wingfield and Silverin (1986) used B-implants to study the potential behavioral consequences of stress in free-ranging song sparrows, *Melospiza melodia,* and here we used similar B-implants to study the potential effects of stress on home-range size and activity in the side-blotched lizard, *U. stansburiana.* Our results, when combined with previously reported laboratory results (DeNardo and Licht, 1993), suggest that increased B levels, possibly brought on by a stressful situation, may have drastic negative effects on a lizard's aggressive behavior, and therefore its ability to compete with conspecifics for space.

Implantation with B caused a reduction in home-range in populations where "normal," saline-implanted males were present (studies 1, 2, and 3) (Table 1, Figs. 1 and 2). This effect was quite strong, occurring regardless of whether initial average male home-range overlap (a measure of pressure on an individual's home-range) was high or low. Studies 1 and 2 were conducted on outcrops during the early breeding season when lizard density is high. As a result, the initial average male home-range overlaps were quite prominent at 17 and 35%, respectively. Study 3 was conducted later in the breeding season after significant male mortality had occurred. Typically, 25–40% of the males on our entire study site perish by the late breeding season (unpublished data). Hence, the average male home-range overlap initially in study 3 was only 5%, yet competition was significant enough to inhibit B-implanted males from maintaining their original home-ranges.

The space surrendered by the B-implanted males was not left unoccupied but rather was incorporated into the home-range of the saline-implanted males (Figs. 1 and 2). Saline-implanted males, on average, more than doubled their home-range size after cohorts were implanted with B, leaving the total space occupied by male lizards on each outcrop after experimental manipulations similar to the total space occupied prior to manipulations (postmanipulation total occupied space ranged from 94 to 114% of premanipulation total occupied space for the four studies) (Table 2).

While it is unknown whether the B-implanted males in studies 1–3 reduced their home-range size independently or as a result of competitive pressure from their saline-implanted cohorts, the latter is more probable since B-implanted males in study 4, where all males were implanted with B, maintained the same or similar sized home-ranges (Table 1, Fig. 3). These B-implanted males most likely continued to defend their home-ranges from conspecific males since overlap actually decreased from 13 to 1%.

The results from study 4 also weaken the possibility that the reduction in home-range induced by elevated B levels (as seen in studies 1–3) is a function of poor health brought on by the B-implant. The B-implanted males in this study were capable of defending large territories in the absence of more aggressive saline-implanted males. Similarly, laboratory findings show that B-implanted lizards not only survive extended periods (greater than one year), but also exhibit courtship and copulatory behavior comparable to that of saline-implanted lizards (DeNardo and Licht, 1993).

B-implantation reduced activity levels of lizards regardless of whether saline-implanted males were present in the population (Table 3). The reduced activity levels may contribute to the inability to maintain a home-range by reducing patrol time and may also affect such critical parameters as survival, growth, and reproductive success (Rose, 1981). Unfortunately any effect that reduced activity has on these additional components cannot be addressed with the data available here. The reduced activity may also contribute to reduced measures of home-range size due to sampling errors. While this possibility cannot be ruled out, the existence of a true reduction in home-range size is supported by the fact that B-implanted males on study 4 showed reduced activity, but not reduced home-range size. Additionally, many of the small home-ranges were a result of repeated sightings of an individual on only one or two rocks.

Increased corticosterone levels, with the resultant decrease in aggression, home-range, and activity, may dictate an individual to assume a particular behavioral strategy that concentrates on minimizing present costs in order to survive a stressful period. Territory maintenance requires high-energy output (Nagy, 1983), which if maintained during stressful times may jeopardize survival. Reducing one's home-range and activity, and therefore one's energy demand, may aid in survival during unfavorable times. Further studies in both the laboratory and the field are necessary not only to further understand the mechanisms involved in the stress response, but also to explore the trade-offs between the potential short- and long-term costs and benefits of the stress response. Only with such an integrative approach will the adaptive significance of the stress response be unveiled.

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