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Source: *Copeia*, Feb. 26, 2003, Vol. 2003, No. 1 (Feb. 26, 2003), pp. 99-112

Published by: American Society of Ichthyologists and Herpetologists (ASIH)

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# Home-Range Analysis in *Sceloporus undulatus* (Eastern Fence Lizard).

## I. Spacing Patterns and the Context of Territorial Behavior

GREGORY J. HAENEL, LINDA C. SMITH, AND HENRY B. JOHN-ALDER

Understanding the spacing patterns of individuals in a population of animals is important for establishing the specific functions of territorial behavior. Here, we couple a comprehensive analysis of home range with demographic information and focal behavioral observations of *Sceloporus undulatus* (eastern fence lizard) to investigate (1) spacing patterns, (2) the determinants of home range, and (3) the functional significance of territorial behavior and traits related to territorial behavior (body size, color). Male home-range area is an order of magnitude larger in the New Jersey population of *S. undulatus* described here than in other populations, whereas female home ranges are comparable in area to other populations of this species. Home-range area is positively correlated with body size in adult males, although this relationship is not found within age classes, and males share about 50% of their home range with other males. After removal of the effect of body size, residual home-range area is smaller in two-year olds (first breeding season) than in older males. Home-range area increases as a function of the number of overlapped females, even after the effect of body size is statistically removed, and the sightings of males within their home ranges are tightly clustered in and near the home ranges of females. Males courted females in 60% of focal behavioral observations and contested other males in 14%, always in close proximity to a female. Relative body size, color, and behavior were displayed by contest “winners” and “losers” in the same manner as previously characterized in captive lizards. Of the three status traits examined, only body size explained variation in home-range area, apparently reflecting the ability of males to court increasing numbers of females as they get older and larger. The winners of contests gained access to the nearby female, but contests had no lasting influence on the locations where males subsequently were sighted. Thus, the size and shape of male home ranges are determined largely by the number and locations of females with whom males interact. Females themselves and not specific sites or home-range area are the contested resources. Plasma corticosterone was correlated with the area of a male’s home range overlapped by female home ranges. Because this measure of overlap may reflect the frequency of interactions between lizards and assuming that elevated corticosterone reflects a stress response, social interactions including contests between males and courtship of females appear to be stressful in free-living male *S. undulatus*.

**S**PATIAL distributions of lizards have typically been described in terms of “home range,” indicating the area traversed by an individual in its daily activities (Burt, 1943) and “territory,” traditionally indicating an area defended for exclusive use (Nobel, 1939; Brown and Orians, 1970). Despite their widespread acceptance, however, these terms imply an overly dichotomous notion of a species’ spatial behavior. More recently, Stamps (1977) detailed the concept of territory by noting that lizards defend (1) all or part of a home range, (2) specific site(s) within the home range, or (3) no particular area other than an animal’s “personal space” in its immediate vicinity. Within this framework, lizards can occupy nonexclusive home ranges while exhibiting territorial behavior in a number of different contexts.

How is the context of territorial behavior determined? To test hypotheses about the ecological function of territorial behavior, Stamps and Krishnan (1995) noted that different criteria must be used to separately define the outcome of contests between individuals from competition for space. Martins (1994) categorized territorial behavior by focusing on the relationship between an observed “spatially relevant aggressive behavior” (i.e., territorial behavior) and the proposed defended resource, which may or may not be space itself. Thus, the ecological context of territorial behavior cannot be understood without knowledge of the contested resource, and this requires an understanding of how space is partitioned among individuals in the population. In the present study, we develop a detailed analysis of home ranges in an eastern

population of *Sceloporus undulatus*. We use this information together with focal behavioral observations to identify the main determinants of home range and to establish the ecological context of territorial behavior and related traits associated with the winning of dyadic contests between males in a natural population.

Three primary hypotheses have been proposed for the function of territorial behavior in lizards (Martins, 1994): (1) defense of food and/or water, (2) defense of mates, and (3) defense of basking sites. If contests between males determine the acquisition of space for control of resources, a common assumption in the behavioral literature (reviewed in Stamps, 1994), then one of the contestants should ultimately be excluded from the site of the contest (see Stamps and Krishnan, 1995, 2001). In cases where the contest winner controls the contested space, traits exhibited by contest winners should be associated with territory acquisition and control. However, when males occupy broadly overlapping home ranges, space itself is unlikely to be the contested resource, and focal behavioral observations of the contestants are needed to reveal the alternative function of territoriality. For example, a male's use of space may specifically reflect his efforts to locate and court females, and contests may ensue when two males encounter one another near females (Smith, 1985). If females are the contested resource, then male home-range parameters should be associated with the locations of females, and traits of contest winners should be displayed by males who gain access to females.

*Sceloporus undulatus* is a nominally territorial species (see Stamps, 1983; Martins, 1994) which forms dominance hierarchies in captivity (Carpenter, 1962) and possibly in some natural populations (Ferner, 1974; Jones and Droge, 1980). In a prior study, we characterized three traits of captive males (hereafter designated as "status traits") that are associated with the establishment of social dominance through the winning of dyadic contests (Seitz and John-Alder, 1994, 1995; Smith and John-Alder, 1999). First, as in contests between males of many species (Stamps, 1983; Ruby, 1984; Tokarz, 1985), winning male *S. undulatus* are larger than losers. Second, winners can be recognized by relative dorsal color (Zucker, 1989; Thompson and Moore, 1991; Olsson, 1994). In contests between captive pairs of *S. undulatus* from New Jersey, winners display a "lighter," yellowish red hue (Munsell Soil Color Charts, 1994, GreytageMacbeth, New Windsor, NY) than the dark brown of losers (Smith and John-Alder, 1999), opposite the pattern in other popula-

tions (Carpenter, 1962). Third, winning males exhibit a higher intensity of ritualized behavior and higher levels of general activity than losers during contests. It should be noted, however, that behaviors and other traits expressed during social interactions in captivity may not be expressed in the same manner under natural conditions (see Creel et al., 1997; Smith and John-Alder, 1999; Creel, 2001).

In addition to our documentation of status traits in experiments on captive lizards, we previously found that plasma testosterone (T) increased transiently in resident males following staged territorial intrusion by other males. Also, plasma corticosterone (B) increased transiently in response to intrusion by males or females during the breeding season (Smith and John-Alder, 1999). Here, we present evidence that plasma corticosterone may be a useful index of the frequency and intensity, thus stressfulness, of social interactions in the wild.

#### MATERIALS AND METHODS

*Study animal.*—*Sceloporus undulatus* is a widely distributed species in the eastern and southern two-thirds of the United States (Conant, 1975). This species has been the subject of numerous ecological and physiological studies (see for example Dunham et al., 1988; Niewiarowski and Roosenburg, 1993; John-Alder et al., 1996 and references therein). Detailed home-range studies have been reported for *S. u. erythrocheilus* (Ferner, 1974) and *S. u. garmani* (Jones and Droge, 1980). In the population of *S. undulatus*, we studied in the pinelands of New Jersey, lizards are seasonally active from mid-March until mid-October, and the breeding season occurs in April and May. Behavioral interactions of all kinds are most apparent during these months, and plasma testosterone (T) and corticosterone (B) both reach higher levels during this period than at other times during the activity season (Seitz, 1998; unpubl.).

Male *S. undulatus* invoke ritualized displays during agonistic encounters and courtship (Rothblum and Jenssen, 1978; Martins, 1993; Smith and John-Alder, 1999). The most common display is the push-up, in which the head and trunk of a lizard are raised and lowered by extension and flexion of the front legs. Push-ups themselves are not sex-specific, being displayed to other males and to females. However, in female-specific displays, males intersperse push-ups with nod-sets (head shudders), in which the head is held low and moved rapidly from side to side (Carpenter, 1962). In male-specific displays, males sometimes arch their

backs and compress their sides during push-ups, a display pattern described as a full-show (Martins, 1993).

*Study site.*—The population of *S. undulatus* described here is located in Lebanon State Forest at the Rutgers University Pinelands Research Station, Burlington County, NJ (approximately 40° north latitude and 74° 35' west longitude). The site is an upland oak-pine forest. The understory is mostly open because of a history of controlled burns in the area, and numerous fallen trees are used as perches by *S. undulatus*. The study site is approximately 100,000 m<sup>2</sup> marked in 15 × 15 m intervals to designate X-Y coordinates. For further information on this population, see Haenel and John-Alder (2002).

We collected lizards under permit from the New Jersey Department of Environmental Protection and with the approval of the Animal Care and Facilities Committee of Rutgers University (documentation available upon request). We intensely monitored the study site for lizards in April and May (the breeding season) of 1996 to (1) record repeated observations of individuals for estimating home-range areas, and (2) observe behavioral patterns through focal observations of individuals. Fieldworkers were present at the field site on 35 of the approximately 50 days of the study.

The first time each lizard was seen on the study site, it was captured for collection of a blood sample (used for extraction of DNA; Haenel et al., 2003) and for measurements of body size. Each individual was given a permanent, unique toe clip for identification and was painted with a unique symbol on the dorsal surface for identification in the field. All male lizards were held one night in cloth bags and were run on a treadmill the following morning to measure exercise endurance for a separate study. We returned males to their site of capture within approximately 24 h.

During daily censuses, two to six workers moved slowly through the site either following grid lines or moving sporadically in search of lizards. On most census days, all parts of the study site were surveyed by at least two workers. Daily censuses were begun as lizards became active between approximately 0830 and 0930 h and continued until late afternoon. Every time we started a new census period, a different course was taken through the field site. When we sighted a lizard, we noted its location to the nearest meter.

Because of the short time period of our study (i.e., the breeding season), we needed to make repeated sightings as frequently as possible to

maximize our sample sizes. This operational requirement increased the risk of serial autocorrelation in our data, which occurs when successive sightings are not independent. Serial autocorrelation of animal location data is a biological reality, and the collection of statistically independent location data may actually be undesirable for correct estimation of range sizes (Harris et al., 1990). Nonetheless, we sought to minimize serial autocorrelation in our data by requiring a minimum of 2 h between consecutive sightings for any given lizard. We subsequently tested for autocorrelation of sighting data using the method of Swihart and Slade (1985) in the computer program "Home Range" (Ackerman et al., 1990). We found only a small amount of autocorrelation in our data (see Results), indicating that the time between sightings for most lizards was sufficient to achieve independence.

*Home range.*—Home-range areas were estimated using the minimum convex polygon (MCP) method (Homerange Analysis and Graphics Package, vers. 6.07.91, P. Niewiarowski and A. Dunham, unpubl.). Numerous methods are available for calculating home-range area, each with its own strengths and weaknesses (reviewed in White and Garrott, 1990, Harris et al., 1990). We used the minimum convex polygon method (MCP) because of our interest in also determining the significance of spatial arrangements vis-à-vis reproductive success (Haenel et al., 2003). The MCP method specifically met our goals of determining whether two lizards were located in areas near each other and, if so, how much area they shared. MCPs provide outlines that enclose all of a lizard's locations. MCPs do not provide specific information about how the individual used the area, and the lizard will often not have traveled throughout the whole area enclosed by the MCP. However, an advantage of MCPs is that they do not depend on an underlying statistical distribution, as do some other estimates of home range. Related to this, MCPs tend to be relatively conservative in their estimates of home-range areas. Statistical methods (e.g., Fixed or Adaptive Kernel, Bivariate Normal, Fourier) often require 100 to over 200 sightings for reliable estimates of home-range area, and they tend to overestimate home-range areas by two- or threefold at substantially lower sample sizes (Worton, 1989, 1995; Seaman and Powell, 1996). These lower sample sizes are exactly those necessitated by studies such as ours that focus on shorter critical time periods (Rose, 1982; Ruby and Dunham, 1987).

To assure that home-range estimates were in-

dependent of the number of sightings, we regressed area on number of sightings. We started by calculating areas based on the first three sightings for each individual. We repeated the analysis by adding the next sighting for each individual and recalculating area (Smith, 1995). We continued this process until there was no relationship between number of sightings and area, and we subsequently used that number of sightings as our lower limit for including lizards in this home-range analysis.

We also examined the relationship between male body size and home-range area and used body-size adjusted residuals where appropriate. The relationship between male body size and number of sightings was also calculated to ensure that bias was not introduced by larger lizards being more noticeable in the environment.

We used three methods to calculate overlap between neighboring lizards. First, we counted the number of neighboring males and females whose home ranges fell within or abutted each individual's home range. Second, we calculated the total area ( $m^2$ ) of overlap shared by neighboring lizards. Third, we calculated the ratio of shared (area overlapped with males or females) to total home-range size.

We compared our estimates of home-range size with those of other populations and other species of lizards by examining home-range area as a function of population density for nominally territorial lizards. Data were taken from tables 2 and 3 in Rose (1982), tables 9.1 and 9.2 in Stamps (1983), Alberts (1993), Griffiths (1999), and the present study. For data from Stamps (1983), density and home-range area were calculated using sex ratio, home-range ratio, female density, and female home-range area.

**Behavior and coloration.**—Fifteen-minute focal observations of male lizards were made by three observers during April and May of 1996. The observers had been trained in previous experiments on captive lizards (Smith and John-Alder, 1999), and the behaviors recorded in the present study were unambiguous, precluding any possibility of observer bias in making qualitative decisions. Likewise, the possibility of observer bias in our color observations was eliminated because we simply recorded the lighter and darker of two interacting lizards instead of attempting to match dorsal color to particular Munsell color chips (see below). Observations were conducted opportunistically each time an observer sighted an adult male on the gridded study site. As such, observations of our focal animals were interpreted relative to three behav-

ioral contexts (see Results): lone males (26%), male-male contestants (14%), and male-female courtships (60%). The activity level of *S. undulatus* in New Jersey is unimodal and fairly uniform from about 0900 until 1700 h during April and May (Niewiarowski, 2001), a finding that is supported by the temporal distribution of our X-Y sightings. Furthermore, the likelihood of social activity when lizards encounter one another and the kinds of behavioral interactions that occur in social encounters appear to be independent of the time of day. Thus, we conducted focal observations throughout the day. The distance moved by a lizard and the number of behavioral displays were recorded during each focal observation. Estimates of distance moved were aided by the regular placement of flags on the X-Y coordinate system of the study site. The prominent displays during social interactions were push-ups, nod sets, and full-shows. These displays occurred in discrete sets, and the beginning and ending of each set was unambiguous. We considered a social interaction to have commenced when a period devoid of social interaction was followed by a period of social activity in which displays were performed, all during a 15-min focal observation period. We considered a social interaction to have stopped when interacting lizards halted their display behavior and moved at least 10 m away from each other.

When observing contests between two males, we recorded the social status and dorsal color of each contestant, and we surveyed the immediate vicinity of the contest for females. Social status was determined by which lizard chased (winner) the other into retreat (loser; see Stamps and Krishnan, 1994), where a retreat was marked by withdrawal from the site of the contest and out of sight of the observer. Dorsal color was estimated by visual examination as either dark brown (darker) or yellowish red (lighter). Quantification of these colors was established in previous experiments by comparison to the Munsell Color Notation System (Munsell Soil Color Charts, 1994, GreytageMacbeth, New Windsor, NY, hue series 5 yr).

To minimize investigator interference in social interactions, we opted not to catch the lizards for comparison of the dorsal hue to a Munsell color chip. To further reduce our influence on social dynamics, we remained approximately 7–11 m. from any focal male. The majority of lizards appeared to be unaffected by our presence.

**Hormone levels.**—Blood samples from all adult males were used to assay plasma levels of testos-



terone and corticosterone (21–24 April), during the peak period of reproductive activity. Blood was collected from the postorbital sinus into a heparinized 75  $\mu$ l micro-hematocrit capillary tube within 2 min of capture. Blood samples were immediately placed on ice and were centrifuged within 5 h. Plasma was stored at  $-20^{\circ}\text{C}$  for hormone assays, and the cellular fraction was used for DNA extraction in other studies (Haenel et al., 2003).

**Radioimmunoassay.**—Plasma levels of testosterone and corticosterone were measured by radioimmunoassay (RIA) following published procedures (Wingfield and Farner, 1975; Moore, 1986; Smith and John-Alder, 1999). Briefly, plasma samples of approximately 30  $\mu$ l were extracted twice in diethyl ether and dried under a stream of ultrafiltered air. Steroids were separated via Celite (Sigma-Aldrich) chromatography after samples had been reconstituted in 10% ethyl acetate: 90% isooctane (v/v). Recovery of testosterone and corticosterone was measured for each sample. After chromatographic separation, samples were dried, reconstituted in assay buffer, and allowed to equilibrate overnight prior to radioimmunoassays.

For RIAs, tritiated hormones were obtained from Dupont, NEN (Wilmington, DE), testosterone antiserum from Wien Laboratories (Sucasunna, NJ) and corticosterone antiserum from Endocrine Sciences (Calabasas, CA). All samples were analyzed in one assay with an intraassay coefficient of variation of 7.1% and 8.9% for testosterone and corticosterone, respectively.

**Statistical analyses.**—We used SAS-PC (SAS/STAT, Guide for personal computers, vers. 6 ed., SAS Institute, Inc., Cary, NC, 1985) for our statistical analyses. Initially, we investigated the size-dependence of home-range parameters, status traits, and hormone levels using snout-vent length as our measure of body size (see Calder, 1996). For variables that were significantly dependent on body size (i.e., those that had significant size exponents in allometric equations), we used size-independent residuals for further analyses. We used an arcsine-transformation (Cohen, 1988) for analysis of ratios (e.g., proportion of HR overlapped by neighboring males or females).

For our analyses of behavior, we divided the total number of each behavior performed during focal observations by 15 min to calculate a standardized descriptive statistic of the overall intensity of behavior. We assigned numerical scores to relative dorsal color, where the lighter

lizard was indicated by a 1 and the darker lizard by a 2. Similarly, we assigned numerical scores to social status, where the “winner” was indicated by a 1 and the “loser” by a  $-1$ . To control for the variable number of observations per male, we calculated a mean score over all observation periods in the study for each male in the behavioral analyses. We performed paired analyses of the behaviors, size, and integumental color exhibited by winners and losers in male-male contests. We analyzed log-transformed snout-vent, distance moved, push-ups, and full-shows (to which 1 was added to eliminate 0) in paired analyses. A score for chase versus retreat (1 = chase; 2 = retreat; 0 = remain) was calculated for winners and losers, and a score for dorsal color was analyzed with the non-parametric procedure in SAS (SAS/STAT, Guide for personal computers, vers. 6 ed., SAS Institute, Inc., Cary, NC, 1985).

We used a multiple regression model to investigate whether plasma hormone levels were correlated with home-range parameters. We used principle components analysis (PCA) as an intermediate step to reduce the dimensionality of the home-range parameters, and we then entered the PCA factors as independent variables in the multiple regression model.

## RESULTS

**Home-range parameters and body size.**—Forty-two adult males and 54 adult females were sighted on the study site from 21 April to 31 May. We recorded a total of 878 sightings of adult lizards during the breeding season, of which 55% of sightings were of females. On any given day prior to 13 May, the midpoint of our study, males comprised  $67 \pm 5\%$  of the sightings compared to  $39 \pm 2\%$  in the latter half of the study ( $P = 0.0001$ ). For any individual male,  $42 \pm 6\%$  of his sightings were made in the first half of the study compared to just  $20 \pm 3\%$  for females ( $P = 0.0002$ ). Nearly all of the males (89%) and females (73%) were located prior to the midpoint of the study. For these females, an average hiatus of 14.5 days elapsed between their early sightings and when they were found again in mid-May. In all cases, these females were observed at essentially the same locations as their original sightings.

Estimates of home-range area calculated via the MCP method are known to depend upon sample size (White and Garrott, 1990). Our estimates of home-range area reached a plateau with 10 sightings per lizard, the same number as required for *S. u. erythrocheilus* (Ferner, 1974). Thus, a minimum of 10 sightings per individual

was required to maintain independence between male home-range size (log-transformed) and number of sightings ( $R^2 = 0.02$ ,  $P = 0.078$ ). The average number of sightings we obtained for males during the breeding season was well above this threshold, and we excluded from further analyses those males with fewer sightings. Thus, we could include 19 males in the home-range calculations.

Females had much smaller home ranges that showed no significant relationship between number of sightings and area when a minimum of four sightings were included ( $R^2 = 0.04$ ,  $P = 0.185$ ). Thus, we included all 42 females sighted at least four times during the breeding season for calculations involving home-range areas. For our analysis of the number of instances of overlap between male home ranges, we plotted all individuals with four or more sightings. With four sightings, we could be certain of detecting, at a minimum, the existence of home-range overlap even though we could not reliably estimate the area of overlap. For all other analyses involving estimates of home-range area, we plotted males with 10 or more sightings to ensure that home-range area was independent of the number of sightings. All the males included had a similar number of sightings ( $n = 10$ –23).

Overall, there were 60 pairs of observations made during a single day on any particular lizard. These were evenly distributed among different individuals with an average of three pairs of same-day observations for a single lizard (STD = 1.9). Only five males showed significant levels of serial autocorrelation ( $P < 0.05$ , Swihart and Slade 1985). Three of these males had two sightings on the same day, one male had four and another had five. This was no different from the mean of three pairs of same-day sightings found for those individuals without significant serial autocorrelation. Therefore, we did not correct for autocorrelation in our home-range estimates. Only 1 data point was found to be an outlier. Removal of this point from the MCP calculations did not change the patterns of overlap, and it was retained in the analysis.

In general, home ranges of males were relatively large and extensively overlapped by other males, whereas those of females were much smaller and generally noncontiguous (see Fig. 1). On average,  $49 \pm 6\%$  of a male's home range overlapped with at least one other male's home range, and  $15 \pm 4\%$  overlapped with at least one female's home range. Within their home ranges, the activity of males was heavily concentrated in the vicinity of females. On average,  $83.3 \pm 0.03\%$  (range: 45–100%; median: 86.4%) of each male's sightings were within 5

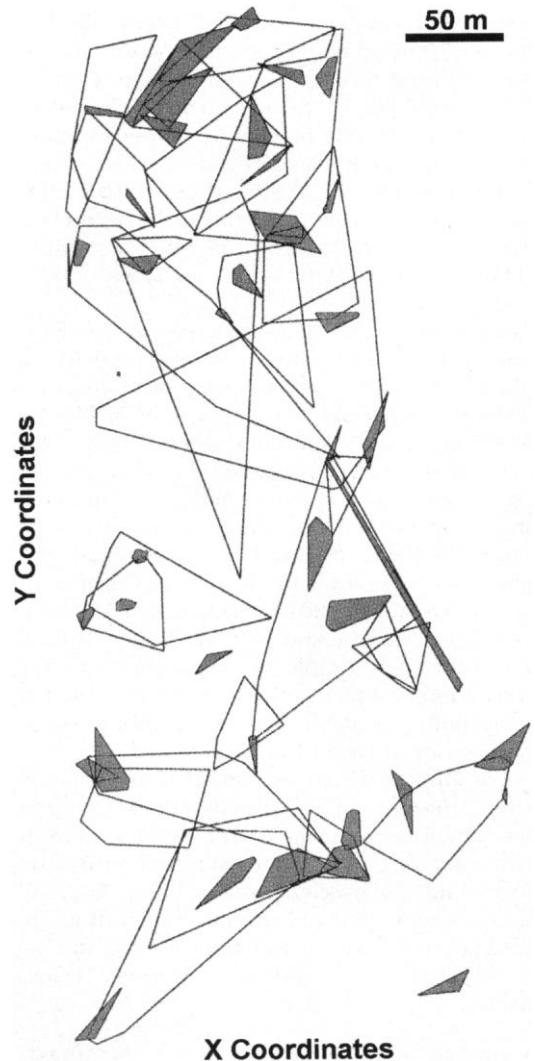


Fig. 1. Minimum convex polygon estimates of adult male (open polygons) and female (shaded polygons) home ranges from April 1996 to June 1996. A minimum of four sightings was used for each female and 10 sightings for each male. Male home ranges are much larger than female home ranges and include extensive overlap with both males and females (see text for details). Female home ranges are widely spaced and display little overlap with other female home ranges.

m of where a female had been seen at least once. The total number of males and females overlapped and abutted by a male's home range were  $3.9 \pm 0.38$  males (range: 2–9) and  $3.4 \pm 0.33$  females (range: 2–12).

In contrast to the distribution of male territories, the percentage of a female's home range overlapped by other female home ranges was on average only  $4 \pm 2\%$  (mean  $\pm 1$  SE area of

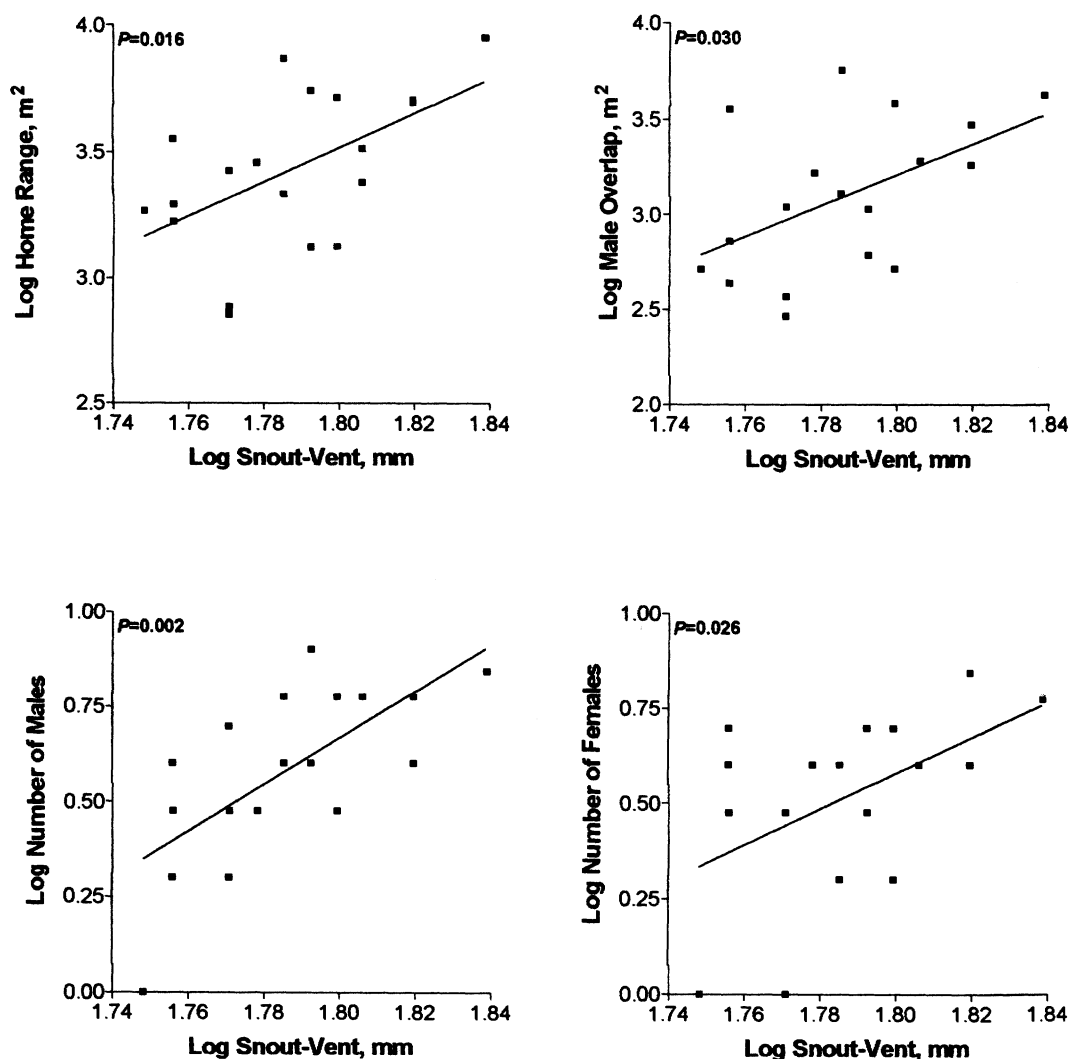


Fig. 2. Home-range parameters as functions of body size (snout-vent length, millimeters). Home-range area and male overlap are reported in  $\text{m}^2$ . All values were  $\log_{10}$ -transformed for allometric analyses. Numbers of males and females include all individuals whose home ranges overlapped or abutted a male's home range. See text for details of statistical analysis.

overlap =  $13.1 \pm 5.98 \text{ m}^2$ ; range 0 to  $181 \text{ m}^2$ ). The total number of females overlapped or abutted by a female's home range was close to 0 (mean  $\pm 1 \text{ SE}$ ,  $0.4 \pm 0.13$ ; range: 0 to 4) and of neighboring males, from 1 to 4 (mean  $\pm 1 \text{ SE}$ ,  $2.3 \pm 0.13$ ).

As shown in Figure 2, male body size (snout-vent length) explained 25% of the variation in home-range area ( $R^2 = 0.25$ ,  $F_{1,17} = 7.153$ ,  $P = 0.016$ ), 21.5% of the variation in home range overlapped by other males ( $F_{1,16} = 5.660$ ,  $P = 0.030$ ), and 43% and 22%, respectively, of the variation in the number of males and females overlapped or abutted by a male's home range ( $F_{1,16} = 13.721$ ,  $P = 0.002$ ;  $F_{1,17} = 5.991$ ,  $P =$

$0.026$ ). Thus, body size itself had to be statistically removed prior to further analyses of home-range attributes. The number of sightings per male was not correlated with body size (snout-vent length:  $r = -0.045$ ,  $P = 0.856$ ; body mass:  $r = -0.043$ ,  $P = 0.862$ ).

Based on repeated captures over multiple years, we were able to determine the age of many lizards in the population (Table 1). In a multiple regression model in which body size and male age class (2 yr vs > 2 yr of age; Haenel and John-Alder [2002] reported that very few males were > 3 yr of age in this population) were entered as independent variables to explain variation in home-range area, only age



TABLE 1. AGE DISTRIBUTIONS OF LIZARDS WHOSE AGES WERE KNOWN BECAUSE OF REPEATED CENSUSES. These lizards are a subset of all individuals sighted and include all those entered into the home-range analysis. Based on the SVL distributions of known-aged lizards, seven males and four females were inferred to be 2-yr olds, and two males and three females were inferred to be  $\geq 3$ -yr olds. The SVLs of five males and 12 females fell within the ranges of overlap of known 2- and  $\geq 3$ -yr olds; thus, their ages were neither known nor inferred.

Age class	Male		Female	
	N	SVL (mean $\pm$ 1 SE)	N	SVL (mean $\pm$ 1 SE)
Known 2-Year olds	7	57.7 $\pm$ 0.51 mm	24	63.8 $\pm$ 0.78 mm
Known $\geq 3$ -Year olds	4	63.7 $\pm$ 1.17 mm	10	70.9 $\pm$ 0.87 mm

class entered the model as a significant independent variable ( $F_{1,17} = 11.77$ ,  $P = 0.003$ ). In an analysis of residual home-range area from the regression analysis presented in Figure 2, size-independent home-range area was smaller in two-year-old males (first breeding season) than in older males (Fig. 3). A stepwise multiple regression model using the number of overlapped females and body size to explain variation in home-range area found that only the number of overlapped females was a statistically significant independent variable ( $R^2 = 0.44$ ;  $F_{1,17} = 13.587$ ,  $P = 0.002$ ). Female home-range area was not dependent on body size ( $F_{1,40} = 0.487$ ,  $P = 0.489$ ).

Area of overlap between neighboring male home ranges increased proportionately with home-range area (slope =  $1.00 \pm 0.21$ ,  $F_{1,16} = 22.872$ ,  $P = 0.001$ ), even after the effects of body size had been removed (Fig. 4). Consequently, the percentage of a male's home range overlapped by other males ( $49 \pm 6\%$ ) was independent of home-range area ( $R^2 = 0.03$ ,  $F_{1,17} = 0.524$ ,  $P = 0.479$ ). The area of overlap between neighboring male and female home

ranges tended to increase with male home-range area after the statistical removal of the effects of male body size, but this association failed to achieve statistical significance ( $F_{1,17} = 4.016$ ,  $P = 0.061$ ). Again, the percentage of a male's home range overlapped by neighboring



Fig. 3. Comparison of size-independent residual home-range area of males during their first breeding season (two-year olds) to those in their second and later breeding seasons. Older males have significantly larger home ranges (see text for details).

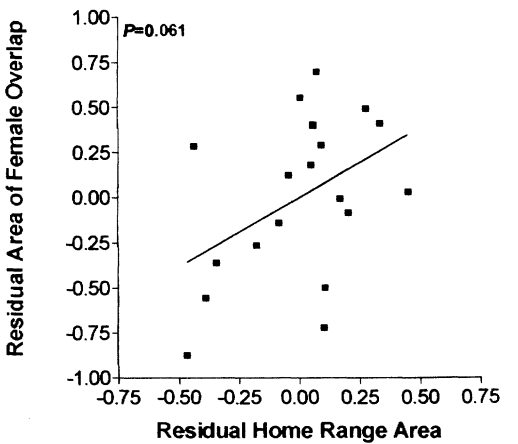
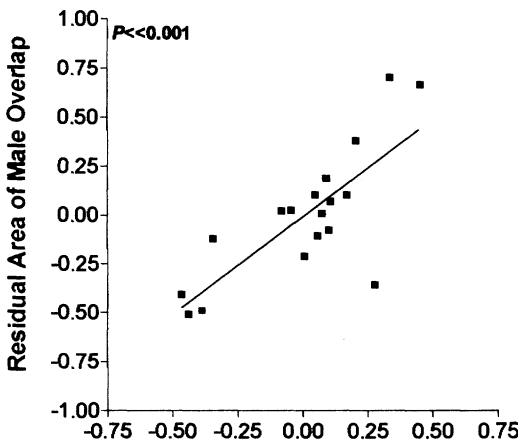


Fig. 4. Residual correlations between home-range area and areas of male and female overlap after the statistical removal of the effects of body size. See text for details of statistical analysis.

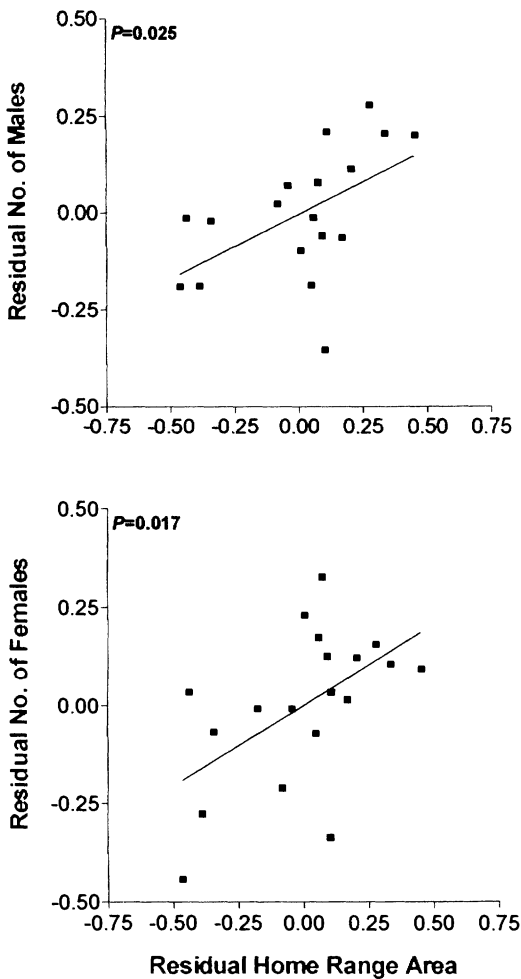


Fig. 5. Residual correlations between home-range area and the numbers of males and females overlapped or abutted by a male's home range after the statistical removal of the effects of body size. See text for details of statistical analysis.

females ( $15 \pm 4\%$ ) did not increase with home-range area ( $R^2 = 0.07$ ,  $F_{1,17} = 2.416$ ,  $P = 0.139$ ). Additionally, the larger a male's home range the greater the number of females and males that fell within or abutted his convex polygon estimate of home range even after the effects of body size were removed from the analysis (Fig. 5; females:  $F_{1,16} = 6.953$ ,  $P = 0.017$ ; males:  $F_{1,16} = 6.077$ ,  $P = 0.025$ ).

Home-range area in different populations and across species was strongly dependent on population density (i.e., home-range area was significantly correlated with population density, Fig. 6), and *S. undulatus* cannot be distinguished from the overall patterns (Fig. 6A [males]:  $R^2 = 0.768$ ,  $F_{1,25} = 82.65$ ,  $P = 0.001$ ; Fig. 6B [females]:  $R^2 = 0.720$ ,  $F_{1,25} = 64.16$ ,  $P$

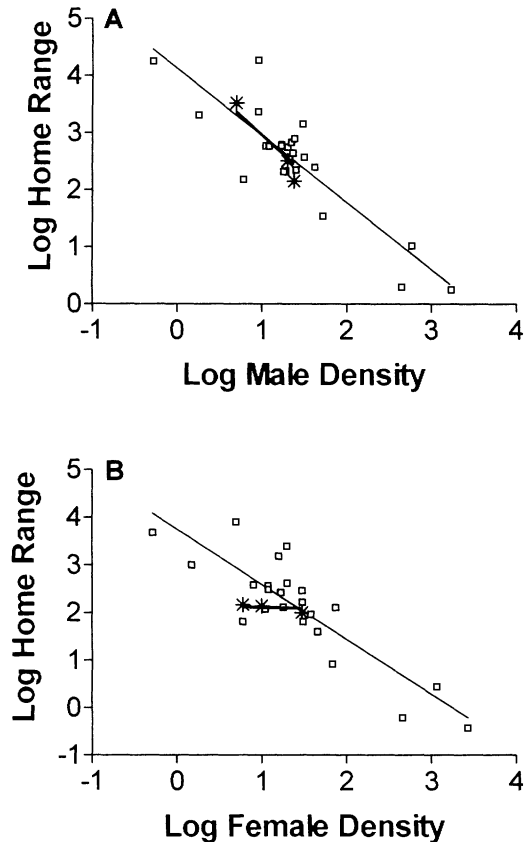


Fig. 6. Home-range area as a function of population density for nominally territorial male (A) and female (B) lizards. Data were taken from tables 2 and 3 in Rose (1982), tables 9.1 and 9.2 in Stamps (1983), Alberts (1993), Griffiths (1999), and the present study. Large asterisks (\*) and the short, thick lines represent three populations (subspecies) of *Sceloporus undulatus* (Ferner, 1974; Jones and Droge, 1980; present study). In analyses of all data, home-range area is strongly dependent on population density, and *S. undulatus* cannot be distinguished from the overall patterns (A [males]:  $R^2 = 0.768$ ,  $F_{1,25} = 82.65$ ,  $P < 0.001$ ; B [females]:  $R^2 = 0.720$ ,  $F_{1,25} = 64.16$ ,  $P < 0.001$ ). In an analysis just on the three populations of *S. undulatus*, home-range area is dependent on population density in males ( $P = 0.028$ ) but not in females ( $P = 0.364$ ).

$= 0.001$ . In an analysis on three populations of *S. undulatus* for which data were available, home-range area is dependent on population density in males ( $P = 0.028$ ) but not in females ( $P = 0.364$ ).

**Behavior and color.**—Of the 19 males included in the home-range analysis, seven were excluded from the analysis of social behaviors based on the absence of behavioral focal observations for these individuals. On average, each of the other

TABLE 2. DISTANCE MOVED, NUMBERS OF BEHAVIORAL DISPLAYS, AND DORSAL COLOR OBSERVED DURING 15-MIN SOCIAL INTERACTIONS.

	Male-Male		Male-Female
	Winner	Loser	
Distance moved (m)	15.1 ± 2.39*	7.1 ± 1.77**	10.7 ± 1.81*
No. Push-ups	43.3 ± 7.95*	2.2 ± 1.52**	41.8 ± 5.85*
No. Full-shows	16.2 ± 5.50**	2.9 ± 1.35*	0*
No. Nod sets	0*	0*	26.9 ± 12.92**
Dorsal color	1.1 ± 0.11*	1.7 ± 0.13**	1.1 ± 0.12*

Values are mean ± 1 SE. Dorsal color, designated as light = 1 and dark = 2, is represented by a mean score for each group. The number of asterisks following each entry indicates statistical groupings within each behavioral or color category. See text for corresponding probability levels.

12 males was observed eight times (range: 6–11) for a total of 96 observation periods. Overall, males were observed in 19 social interactions with other males and in 57 with females. In addition, 20 observations were made of solitary males.

Of 19 male-male contests, males that established social dominance by winning their contests were significantly larger than the losing males (Table 2;  $P = 0.001$ ). Furthermore, winners displayed more push-ups ( $P = 0.001$ ) and full-shows ( $P = 0.010$ ) and moved a greater distance during contests ( $P = 0.005$ ) than losers (all paired analyses). Finally, winners exhibited a lighter yellowish red than the dark brown of losers ( $P = 0.003$ ).

In a direct test of the relationship between home-range area and status traits presented in Table 2, the outcome of male contests was not associated with home-range size: winners did not have larger home ranges than losers ( $P = 0.310$ ). Instead, the male who had been sighted within a few meters of a female prior to a contest was the winner ( $P = 0.001$ ). Furthermore, this “attending” male prohibited the intruding male from gaining access to the female by defeating him in a contest and often chasing him completely away from the site.

Female-specific behaviors for the males in the 57 female-male interactions are shown in Table 2. The intensity of push-ups ( $P = 0.713$ ), distance moved ( $P = 0.126$ ), and dorsal color ( $P = 0.643$ ) did not differ between males courting females and males who prevailed in contests with other males. However, males exhibited nod sets only when courting females and full-shows only when contesting other males.

**Hormones.**—Plasma levels of testosterone ( $F_{1,15} = 3.829$ ,  $P = 0.069$ ) and corticosterone ( $F_{1,15} = 0.270$ ,  $P = 0.611$ ) were not significantly dependent on body size (snout-vent length) in the sample of males for which we have at least 10 X-Y sightings. In the larger sample for which we assayed plasma hormones, T was significantly dependent on body size ( $T \propto \text{Mass}^{1.26 \pm 0.39 \text{ SE}}$ ;  $n = 22$ ,  $F = 3.233$ ;  $P = 0.004$ ) but B was independent of size ( $P = 0.327$ ). Table 3 presents the analyses of correlations between home-range parameters and plasma hormones. The results of principle components analysis involving home-range parameters are presented in Table 3A, and the results of the multiple regression model used to explain variation in plasma B in Table 3B. We used a log-transformation to normalize the distribution of values of plasma B.

TABLE 3. (A) FACTOR LOADING PATTERNS AND THE SIGNIFICANCE LEVEL OF EACH VALUE FROM PRINCIPLE COMPONENTS ANALYSIS OF HOME-RANGE PARAMETERS. The first two PCA factors explained 83% of the cumulative variation in the primary variables. Significant correlations are indicated in bold.

	Factor 1	Factor 2
Home Range	0.838, 0.0001	0.373, 0.1279
No. Overlapped Females	0.874, 0.0001	−0.395, 0.1045
No. Overlapped Males	0.773, 0.0002	0.044, 0.8619
Area Female Overlap	0.651, 0.0034	−0.694, 0.0014
Area Male Overlap	0.666, 0.0025	0.677, 0.0020

(B) Results of backward-elimination multiple regression model used to explain  $\log_{10}B$  as a function of and the first two PCA factors (above). Because of the simple loading pattern of home-range parameters on factor 2, this model indicates that log-B increases with increases in area of female overlap and decreases with area of male overlap.

Log B = 1.00 − 0.268 Factor 2  
 $R^2 = 0.542$ ,  $F_{1,14} = 16.59$ ,  $P = 0.0011$

Plasma T was not included in the table because home-range parameters did not explain a significant fraction of the variation in plasma T regardless of the regression model we used. The loading pattern of home-range parameters on the PCA factors was straightforward: factor 1 can be interpreted as a general measure of home-range area, and factor 2 clearly represents a contrast between area of overlap with neighboring males versus neighboring females. The regression model retained only factor 2 through a backward elimination procedure, and factor 2 alone explained more than 54% of the variation in log B. The signs of the loading scores indicate that plasma B increases with area of female overlap and decreases with area of male overlap.

#### DISCUSSION

*Home range.*—Home-range areas of male *S. u. hyacinthinus* in the pinelands of New Jersey are on average an order of magnitude larger than those of male *S. u. erythrocheilus* (Ferner, 1974) and *S. u. garmani* (Jones and Droge, 1980). Female home-range areas are very similar among these three populations. Among small, insectivorous lizards that are ecologically similar to *S. undulatus*, comparable home-range areas have been reported only for male *S. occidentalis* (Tanner and Hopkin, 1972; see Rose, 1982; Stamps, 1983), and Rose (1982) was sufficiently concerned about the validity of those data to exclude them from her analyses. As presented in other sections, we used appropriate computational methodology for our home-range estimates, we verified that our estimates were not influenced by sample size, and after describing the size-dependence of home range in males, we verified that sample size was unrelated to body size.

The average value we report for our population of *S. undulatus* (as well as the value reported by Tanner and Hopkin [1972] for *S. occidentalis*) was almost exactly as predicted based on population density. Indeed, the relationship between male home-range area and population density in the three populations of *S. undulatus* was strikingly similar to the overall interspecific relationship (Fig. 6). We present this interspecific and interpopulation analysis not to confirm the accuracy of our home-range estimates but rather to affirm that our estimates were reasonable and consistent with expectation. Thus, the remarkable feature of our population is not that males have large home ranges but that the population density is much lower in New Jersey than elsewhere.

Home-range area is positively correlated with

body size in males but not females of our population, similar to the pattern found more generally in lizards (Christian and Waldschmidt, 1984; G. Perry and T. Garland Jr., unpubl.). In *S. u. garmani* in the sand hills of Nebraska, however, male home range actually decreases with increasing body size (Jones and Droge, 1980). The authors attributed this phenomenon to the tendency of larger, older males to command areas of high female density, thus relegating smaller, younger males to areas in which they must travel greater distances to locate potential mates. In the following sections, we argue that the positive size-dependence of home-range area for male *S. undulatus* in New Jersey obtains because the size and shape of male home ranges are established largely by the number and locations of females with whom males interact.

*Determinants of home range and the context of territorial behavior.*—Despite large interpopulation differences in male home-range area in *S. undulatus*, the proportion of home range shared by neighboring males is very similar among populations ( $\approx 50\%$ ; see Ferner, 1974). These spatial relationships indicate that males do not defend exclusive territories, and statistical analyses suggest that male home ranges are determined by the distribution of females. First, when the number of overlapped females and body size are used in a stepwise multiple regression model to explain variation in home-range area, only the number of overlapped females is retained as a statistically significant independent variable. Another way of looking at this is through a linear regression model on residual values, in which the number of overlapped females explained a significant fraction of the variation in home range after the effects of body size had been factored out of each variable. Second, the number of overlapped females but not the area of overlap between male and female home ranges is significantly correlated with male home-range area, illustrating that males target their use of space quite precisely on the locations of females rather than female home range itself. These two analyses clearly suggest that males focus on females, not area per se. Finally, male home-range area is correlated with body size alone, but when age class and body size are both entered as independent variables to predict home-range area in a multiple regression model, only age class is retained as a significant independent variable. Alternatively, size-independent home-range area increases with age. Taken together, these analyses lead to two conclusions: (1) that male home range is determined largely by the num-

ber and locations of females with whom males interact; and (2) that home-range area increases with body size because larger, older males visit more females than smaller males, not because large males had used their size to garner more home-range area directly.

In support of our statistical inference, the distribution of females within male home ranges further indicates that the locations of females determine the size and shape of male home ranges. The specific locations of male sightings are concentrated in and near the home ranges of females; Rose, 1982). Furthermore, the temporal sequence of successive sightings indicates that males traveled relatively great distances to visit individual females. Thus, males were only rarely sighted in those areas not occupied by females.

Finally, our focal behavioral observations further strengthen the conclusion that male home-range size and shape are determined largely by the distribution of females. The extensive overlap of neighboring male home ranges suggests that males may compete for social dominance by winning dyadic contests (Jones and Droge, 1982; Davis and Ford, 1983; Stamps, 1994). In previous experiments involving captive *S. undulatus*, males that established social dominance in dyadic contests were larger in size, more aggressive in their behavioral displays, and a "lighter," yellowish red dorsal coloration than their subordinate partners (Seitz and John-Alder, 1994; Smith and John-Alder, 1999). We observed identical status traits in the present study during contests between free-ranging males. However, contests between males were relatively infrequent in the field, being observed in only 14% of all focal observations, and we never observed solitary males performing aggressive assertion displays. Contests always occurred within a few meters of a visible female, which one of the contestants had been courting or near whom he had been basking. These contests lasted approximately 4.5 min on average, and the winner was larger, more aggressive, and lighter in dorsal coloration than the loser. As in their captive counterparts, behavior and dorsal coloration were transient traits in free-living males, as the expression of these traits depended on a male's immediate social circumstances. Our observations are reminiscent of the system described by Zucker (1989, 1994a,b), in which variable dorsal color serves as an indicator of social status in some populations of *Urosaurus ornatus*.

Although status traits showed the expected relationship with winning contests, we found no evidence that males used their social dominance to acquire exclusive use of a territory or

home range. Of primary relevance to this issue, the winners of contests between males were not consistently the holders of larger home-range areas, as would have been expected if contests determined the acquisition of space (see Stamps and Krishnan, 2001). Furthermore, as in other species (see Stamps, 1994), losers did not permanently abandon the site of the contest, sometimes remaining at and often returning to the same place. Moreover, relative dorsal coloration and the overall intensity of ritualized behavior in social contests showed no relationship with home-range area. Of the three traits we analyzed, only body size was positively correlated with home-range area. However, given that each observed contest occurred in close proximity to a female, that each contest winner subsequently directed his attention to the nearby female, and that contests had no lasting effect on occupancy of territory, our observations indicate that males competed to gain access to females, not home-range area.

Rose (1982) and Smith (1985) observed that the locations of females also determined home-range patterns of male *Sceloporus virgatus*, a closely related species. When male *S. virgatus* encountered each other in close proximity to a female, a contest often ensued, and the outcome of that contest determined access to the female. In other words, females were the contested or defended resources. This is also the context of territorial behavior in *S. undulatus*, and it leads to the hypothesis that male reproductive success should increase with the number of overlapped females (see Haenel et al., 2002).

*Testosterone and corticosterone: The stress of social life.*—Recently, Klukowski and Nelson (1998) reported an immediate increase in corticosterone in free-living *S. undulatus* that were engaged in staged male-male contests. Separately, Smith and John-Alder (1999) found a transient rise in testosterone and corticosterone in male *S. undulatus* in response to daily, staged encounters with females or other males in outdoor enclosures. Taken together, these studies suggest that hormones in a blood sample taken from a lizard in its natural habitat during the breeding period could potentially reflect a male's social interactions in the wild.

In our study, plasma levels of testosterone and corticosterone did not differ between the winners and losers of contests. However, the collection of blood samples for hormone analyses was not temporally associated with the contests themselves. Thus, it is not surprising that we found no relationship between the outcome of



particular male contests and hormone levels, and our data do not negate the hypothesis that social interactions cause hormonal responses in the wild. Instead, single hormone measurements, such as we report, may reflect the “time-averaged” intensity of social interactions rather than the outcome of any particular contest (see Creel, 2001).

Plasma corticosterone was negatively correlated with the second axis of our principal components analysis. The second PCA axis clearly contrasts area of overlap with neighboring females (negative loading) from overlap with neighboring males (positive loading). Thus, the correlation between plasma corticosterone and this second axis indicates that plasma corticosterone is strongly associated with the area of overlap between a male and neighboring females. Areas of overlap between male and female home ranges are “high traffic” areas visited frequently by lizards, thus increasing the likelihood of social interactions in these areas. As such, the correlation between plasma corticosterone and the area of overlap may reflect the overall social and energetic stress of interactions, including visitation and courtship of females (see Smith and John-Alder, 1999). Ultimately this issue will need to be resolved through experimental studies on the endocrine significance of social contests in the wild.

#### ACKNOWLEDGMENTS

This project was approved by the Animal Care and Facilities Committee of Rutgers University (Protocol 92-039). Lizards were collected under permit from the New Jersey Department of Environmental Protection. We thank L. Branan, M. Gleba, and R. Tsao for help with behavioral observations and stimulating discussion after long days of fieldwork. For use of the facilities at the Rutgers University Pinelands Field Station, we thank J. Dighton and staff. Thanks to J. Wingfield and L. Erkmann for expert advice about hormone assays. This study was supported by the National Science Foundation (IBN-95-07529).

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