HOME RANGE AND ACTIVITY IN A VIRGINIA POPULATION

OF SCELOPORUS UNDULATUS

by

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Introduction

Home range is the "area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt, 1943). The size of this area can be expected to vary with the availability and distribution of critical resources such as food, shelter, and mates. To reduce direct competition for resources, all or part of a home range is often defended against intrusion by certain classes of conspecifics; in lizards, this type of territoriality is called "home range defense" (Stamps, 1977).

Home range defense may allow a lizard to monopolize one or more of the above resources. Where defense is elicited primarily by competition for food, home ranges tend to increase in size as food abundance decreases (Simon, 1975; Krekorian, 1976). Home range also tends to increase with body size across lizard species (Turner, Jennrich, and Weintraub, 1969) and within species (Simon, 1975; Krekorian, 1976), reflecting the increase in energy requirements with increasing body size (Turner, Jennrich, and Weintraub, 1969; McNab, 1963). However, if the quality or density of food (or other resources) varies from place to place, some home ranges will be "better" than others. If larger individuals in a population are more likely to gain control of superior habitats than smaller individuals, then a negative correlation between body size and home range size may result (Jones and Droge, 1980).

A mate (or mates) is often a resource that influences home range size, location, or both. The mating system influences the social relationships among members of a population, and these, in turn influence the way lizards select and maintain home ranges. Iguanid lizards typically have polygynous mating systems (Stamps, 1977; Rand, 1967). Therefore, in many iguanid species, the size and arrangement of a lizard home ranges should reflect the requirements of the polygynous mating system.

Polygyny may result in different home range sizes for males and females. While a female generally needs only one mate, polygynous males can increase their reproductive success by multiple matings (Orians,1969). If a larger home range increases the chance of finding more than one mate, selection should favor larger home ranges for males than for females (Rand, 1967). Species for which the home ranges of males are larger than those of females include *Sceloporus virgatus* (Rose, 1981), *S. olivaceus* (Blair, 1960), *S.*

jarrovi (Simon, 1975), Holbrookia maculata (Jones and Droge, 1980), and Uta stansburiana (Tinkle, 1967). A Colorado population of S. undulatus followed this pattern (Ferner, 1974), but in a Nebraska population, males and females had similar home range sizes (Jones and Droge, 1980). This geographic variation in behavior suggests that additional factors are involved in determining home range size in this species.

If a male is to benefit from a polygynous system, he must be able to limit the access of other males to his mates. Dominance of or exclusion of rivals are strategies commonly used by males to monopolize females (Emlen and Oring, 1977). When it is economically feasible, exclusion is probably the more effective strategy. Therefore, polygynous males should commonly show strong home range defense directed toward other males; this is frequently seen in iguanid lizards (Stamps, 1977). The tendency for home ranges to overlap should be lower among males than among females, unless some other severely limited resource encourages strong home range defense among females as well (e. g. S. merriami- see Milstead, 1961). In contrast, overlap between males and females should be high.

Higher levels of activity by males than by females should be associated with a polygynous mating system (Rose, 1981). In particular, behaviors involved in finding and attracting mates, or repelling rivals of the same sex, should be more frequent in males than in females. For lizards, such behaviors would include locomotion, aggressive and courtship displays, and touching the tongue to the ground. Behaviors not directly involved with mating, such as predatory and maintenance behaviors, should have the same frequency in both sexes, assuming the sexes are about the same size.

A field study of the iguanid lizard Sceloporus undulatus was designed to ascertain whether home range size, location, and lizard activity levels reflect differences in the reproductive strategies of males and females. My objectives for the study were: 1) to determine if sex influences home range size in S. undulatus, 2) to determine what other factors may be involved, 3) to determine the spatial overlap of home ranges and 4) to compare the frequencies of various activities in male and female lizards.

Although the term "home range" does not automatically imply defense, S. undulatus typically shows home range defense, although subordinate males may be tolerated

(Ferner, 1974; Jones and Droge, 1980; Noble, 1934). For the purposes of this paper, home ranges should be considered defended areas. I use the term "home range" rather than "territory" because the mark-recapture method used did not take defense- or the lack of it- into account.

Materials and Methods

Subject

The fence lizard, *Sceloporus undulatus*, is a small grey or brown iguanid lizard that ranges from New Jersey to Arizona. Adult males have vivid blue or greenish blue markings along the sides of the belly and throat that are exposed by lateral compression of the body during vigorous display behavior (Noble, 1934). This coloration is pale or absent in females and juveniles. Males of any age can be identified by the presence of enlarged post-anal scales. Fence lizards communicate by means of stereotyped push-up displays and "jiggling," a rapid head nodding usually performed while the lizard is moving forward (Rothblum and Jenssen, 1978).

The fence lizards in southwestern Virginia belong to the subspecies *S. u. hyacinthinus*. In the population I studied, snout-vent lengths (SVL) of adult males ranged from 59 - 70 mm (mean=65 mm) and body weights ranged from 8.75 - 14.56 g (mean=11.44 g). SVLs of adult females ranged from 62 - 78 mm (mean=70 mm) and body weights ranged from 9.12 - 16.55 g (mean=13.18 g). The lizards mate in the spring; females apparently produce only one clutch per year.

Hatchlings (approx. 25 mm SVL) appear from late July through September. Hatchlings that survive hibernation reappear the following spring as "juveniles." These animals begin reaching adult size by mid-summer and probably participate in breeding for the first time in the following spring, at which time they are classified as adults. A lizard was classified as an adult if its SVL exceeded 59 mm throughout the year or a juvenile if its SVL was less than 50 mm before mid-May (Figs. 1 and 2). Hatchlings were not included in the study.

Study Site

Field studies were conducted at an abandoned coal mine near McCoy, VA, approximately 10 km west of Blacksburg, VA. Natural features included low mountains and hills forested by pine (especially around disturbed areas), yellow poplar, maple, ash, and oak. Where exposed, the ground consisted of black coal gravel. Abundant man-made features included unpaved roads, paths, wood boards and sheet metal roofing from collapsed buildings, and other debris.

The field site was divided for convenience into two areas known as the "Upper" and "Lower Wrecks," measuring approximately 1400 and 2200 m^2, respectively (Figs. 3 and 4). These areas were essentially "islands" of open ground separated by about 30 m of forest. Both areas had one large collapsed building, some smaller piles of debris, and some isolated trees (mainly yellow poplar saplings and sumac). A stream ran from a point below the Upper Wreck through the Lower Wreck.

Methods

A mark-recapture study of home range was carried out April 19 - October 17, 1981 and March 12 - September 11, 1982. Data collection was concentrated from June through September. In 1981, the Upper and Lower Wrecks were censused on alternate days; both areas were censused daily in 1982. Since lizards were seen less often during morning hours, most censuses were conducted in the afternoon between 1300 and 1600 h.

Lizards were captured with a monofilament noose attached to a pole, and occasionally by hand. Naive lizards were easy to catch, but recapture of experienced individuals was increasingly difficult and time consuming.

At first capture, animals were permanently marked by toe-clipping. No more than one toe per foot was clipped. In addition, the identification number of each individual was marked along its dorsum with acrylic paint. Animals were captured and repainted when their paint spots were lost. Data collected at each capture included: sex, snout-vent length, tail length and length of regenerated portions, body weight to the nearest 0.01 g (using an Ohaus Dial-a-Gram balance), the date, the time, and the location where the lizard was first seen. Animals with clearly visible paint markings were left undisturbed, and only the ID number, date, time, and location were recorded.

Lizard locations were recorded relative to marked trees or other prominent features. Once maps of the site and landmark references had been drawn from aerial photos (Figs. 1 and 2), the locations were translated into X-Y coordinates. Because the subsequent movements of a lizard can be affected by the presence of an observer, only the first sighting per day of an individual was used for home range measurement.

In order to estimate home range sizes, minimum convex polygons (MCP) (Schoener, 1981; Jennrich and Turner, 1969; Rose, 1982) were drawn and measured on a Numonics Graphics Calculator model 237 for each lizard having five or more observations in one area in one year. Lizards that met this criterion were considered home range owners; all others were considered transients. For lizards that were seen both years, separate estimates of home range were made for each year. Because the MCP method can be strongly biased by small sample sizes, I also calculated the mean squared recapture radius (r^2), a statistic that is largely free of sample size bias (Schoener, 1981). The value of r^2 is obtained using the formulas:

$$r^2 = (1/n-1)\ \Sigma r_i^{\ 2}$$

$$r_i = [(x_i - \bar{x})^2 + (y_i - \bar{y})^2]^{1/2}$$

$$\bar{x} = x_i/n \qquad \bar{y} = y_i/n$$

where n is the sample size, r_i is the distance from the i^{th} observation to the geometric center of the observations $(\bar{x},\bar{y})$, and x and y are the map coordinates of the locations where lizards were seen. To estimate the area of a home range, r^2 must be multiplied by a constant determined by the assumed underlying distribution. Schoener (1981) suggests that constants based on a uniform distribution are more useful than those based on a normal distribution and gives the following constants for uniform distributions of various shapes: circular, 6.28; hexagonal, 6.24; square, 6.00; and equilateral triangle, 5.20. As the fence lizards at my field site were restricted by the availability of cover (mainly the irregularly-shaped debris piles), no single distribution adequately describes their home ranges. Therefore, I arbitrarily chose the constant for the circular uniform distribution for my calculations.

I had originally planned to include two variables, sex and ageclass, in an analysis of home range size. However, because all but 4 of the 33 lizards for whom home ranges were measured were clearly attached to a single pile of debris, I also included the size of the debris pile in the analysis. The Upper and Lower Wrecks each had one large collapsed building; lizards having a majority of sightings on one of these structures were classified as "large pile" residents. Lizards having a majority of sightings on one of the several smaller debris piles in either area were classified as "small pile" residents. The small debris piles were generally less than 1/3 the size of the large ones (see Figs. 1 and 2). The four lizards that did not fit into either category were not included in analysis.

In order to make the estimates in the present study comparable to those of other investigators, mean home range sizes for adult males and females were based on data for all adult home ranges regardless of the size of the debris pile, and an additional type of estimate, the adjusted MCP (Jennrich and Turner, 1969), was added.

To estimate the degree of home range overlap, MCPs were plotted on the same map and the regions held in common were measured. Overlap was expressed as the percentage of the home range of each individual that was shared by lizards of each of four sex/age groups: adult male(AM), juvenile male(JM), adult female(AF), and juvenile female(JF). The average overlap (observed) for a pair of sex/age groups was obtained by calculating the mean, weighted by sample size, of two values: 1) the mean amount that lizards in the first sex/age group overlapped the ranges of lizards in the second sex/age group, and 2) the mean amount that lizards in the second sex/age group overlapped ranges of lizards in the first sex/age group. For pairs where both sex/age groups are the same (e.g. AM AM), the average percent overlap is simply the mean overlap among members of that sex/age group.

The degree of overlap between any two sex/age groups should be indicative of the kind of social interactions which occur between members of those two groups. A large amount of overlap would be expected if members of the two sex/age groups are attracted to each other; little or no overlap would be expected if members of the two groups avoid each other. However, as the degree of overlap is, in part, a function of the abundance and density of each sex/age group, overlap must be evaluated relative to some "expected" value. For each individual, the probability of overlap between that individual and any members of a given sex/age group was calculated as:

$$p = 1 - \{[1-(a_1 + a_2)]\ [1-(a_1 + a_3)]\ \ldots\ [1-(a_1 + a_n)]\}$$

where a_1 is the area of the individual's home range relative to the area of the study area, and a_2, a_3,..., a_n are the relative areas of the home ranges of each member of the given sex/age group. This calculation assumes that the distribution of home ranges within a study area is random, such that the probability of any two individuals overlapping depends only on the size of each home range relative to the size of the study area. The lizards' preference for debris piles violated this assumption, but at the Upper Wreck, there was enough movement between debris piles and a high enough density of lizards (11.4 residents/hectare in 1981 and 6.4 residents/hectare in 1982) to make the calculations useful. Lizard density at the Lower Wreck was only 2.3

residents/hectare both years. Therefore, the probability values were calculated only for the Upper Wreck.

The average probability of overlap (expected) for each pair of sex/age groups is the weighted mean of two values: 1) the mean probability that lizards in the first sex/age group will overlap with any member of the second sex/age group, and 2) the mean probability that lizards in the second sex/age group will overlap with any member of the first sex/age group. The observed overlap values were compared to the expected values by comparing their ranks.

Activity patterns of adult lizards were studied from April 18 through September 11, 1982. Continuous 20 min observations were carried out on marked individuals that had not been visibly disturbed by my approach. Most lizards could be observed from distances of only a few meters. Activities during observation were recorded with a shorthand code for common types of behavior, including push-up displays, jiggling, prey capture, licking the substrate, running, and resting. More unusual behaviors were described in longhand. Data were discarded when lizards appeared to move in response to a change in my position or if they were lost to view before the 20 minute period ended. At the conclusion of the observation period, total distance moved was measured as nearly as possible along the route taken by the lizard.

The reactions of resident lizards to tethered "intruders" of the same or opposite sex were observed in August and September, 1981. Intruders were harnessed and attached to the end of a 1' monofilament line anchored to a fist-sized rock. The rock and lizard were placed approximately 1 m from a resident lizard, in plain view of the resident. Behaviors of residents were recorded for 10 to 20 min. after intruders were introduced.

Results

Home Range Size

A total of 91 adult and juvenile lizards were marked during the two-year study. Of these, only 33 lizards, 14 males and 19 females, were considered home range owners. Two home range estimates were made for each of two females that were home range owners both years; thus the total number of estimates was 35. For both of these females, the 1982 home ranges were in the same location as the 1981 home ranges.

Lizards were sighted most often on the wood boards and beams in the debris piles; elevated perches were preferred by both sexes. If approached closely, lizards disappeared into the depths of the debris almost instantly.

Lizards living on large piles of debris had larger home ranges than those living on the small piles (Table 1). No other independent variable analyzed had a significant independent effect on home range size. However, the significant three-way interaction term indicated that sex and age influenced the response of lizards to the size of the debris pile (Table 1). Juvenile females tended to have small home ranges on large or small debris piles; Adult females and juvenile males tended to have small home ranges on small piles and large home ranges on large piles; Adult males tended to have large home ranges on large or small piles (Figs. 5 and 6). The single male (#355) that lived on a small debris pile was seen in places other than his "home pile" often enough to have a large home range estimate even though he was seen most often on the small pile. Another male (#32), whose data were not used in analysis because his sightings were divided between a large and a small pile, had a large home range (MCP estimate= 131 m^2). The behavior of these lizards supports the idea that movements of adult males may be less confined to areas of suitable habitat than those of other sex/age groups.

For both the MCP and r^2 estimates, home ranges of adult females and juvenile males on large piles were significantly different from home ranges of juvenile females and adult females on small piles; all other comparisons were not significant (Table 2).

MCP and r^2 values were highly correlated for all sex/age groups except adult males (Table 3). Neither MCP nor r^2 estimates were significantly correlated with sample sizes of 5 or more, except within the adult male group (Table 3).

The home ranges of S. undulatus at the coal mine are smaller than those observed at other sites (Table 4). This is true for both sexes and for either adjusted or unadjusted MCP estimates.

Home Range Overlap

The areas of greatest overlap among all residents of each study area were always located on debris piles and within the home range of an adult male (Figs. 7-10). Each adult male was was associated with 1-3 adult females (Figs. 10-13). Only two of the six adult males were associated with a single female; both were residents of the Lower Wreck area where lizard density was very low (Fig. 10). Two adult male-female associations present in one area (Figs. 10 and 11) did not overlap. The ranges of adult females within these associations frequently overlapped.

In general, the degree of overlap decreased with overall lizard density, expressed as the number of home range owners per hectare of study area. (Tables 5-7). However, the average percent overlap between adult males and adult females remained consistently high (48-66%) despite density differences between areas and years. The average overlap among adult females ranged from 0 to 62%; the zero value for the Lower Wreck in 1982 was probably due to the fact that the two females were in different male-female associations located at opposite ends of the area (see Fig. 10). Ranges of adult males never overlapped.

Observed overlap ranked higher than the corresponding expected overlap for the adult female-adult male sex/age pair in both 1981 and 1982 (Tables 5 and 6). In 1981, the observed overlap among the 6 juvenile males ranked lower than the corresponding expected overlap. Similarly, the observed overlap among the 5 adult females ranked lower than the corresponding expected overlap. In 1982, when there were 4 adult females and only one juvenile male present, the ranks of observed and expected overlap did not differ for either of these among-groups. (Obviously, the single juvenile male could not overlap with any others.)

In 1982, the observed overlap between adult and juvenile males ranked lower than the corresponding expected overlap (Table 6). However, there is only one individual in each of these sex/age groups, and the lower rank may be an artifact. This relationship is not found in the 1981 data where there were 2 adult and 6 juvenile males.

Activity

Male fence lizards became active earlier in the year than females. Males were first seen in mid-March and females were first seen in mid-April.

Whether or not an adult male established a home range seemed dependent on the date of his first appearance on the field site. Surprisingly, those that became home range owners were usually late arrivals. Of the nine adult males first captured in March and April of 1981 and 1982 (early males), only four were seen again, and of those only one established a home range. Of the six adult males first captured after May 1 (late males), five established home ranges.

Early males were usually lizards that had had previous experience with the areas in which they appeared. The four early adult males seen at the Upper Wreck in 1982 had all been seen there in 1981, and three of them had had home ranges in 1981. (Two of the three were juveniles in 1981.) The single adult male that established a home range at the Upper Wreck in 1982 had not been captured prior to June 21, 1982.

Date of appearance did not seem to influence the establishment of home ranges by adult female lizards. All three of the adult females first captured in April established home ranges. Of the 12 adult females first captured after May 1, 11 were seen again and 10 of these established home ranges.

Female home range owners frequently had prior experience with the areas in which they established home ranges. Of the four adult females at the Upper Wreck in 1982 (all with home ranges), three had been seen there in 1981, and one of these three had had a home range in 1981. The two that did not have home ranges in 1981 were juveniles that year.

Thirteen 20 min observations on 8 males and 24 observations on 15 females were recorded. Of the behaviors observed, only the frequency of display and the total distance moved were significantly greater in males than in females (Table 8). Frequency of prey capture, frequency of substrate licking, and the proportion of one minute intervals in which the individual moved, displayed, etc., were not related to the sex of the lizard. Since males tended to move greater distances, this latter observation suggests that male lizards moved more rapidly than females. As jiggling was observed infrequently and was only performed by males, it was not included in Table 8.

Only the frequency of subtrate licking by males changed with time, decreasing after the period in which females emerge (late April- early May). A single male, on May 4, licked the substrate 16 times; all other males, observed between May 22 and Aug. 26, licked 0-7 times, with most counts being 3 or less (Fig. 14). Linear regression of lick frequency as a function of date indicated a significant downward trend in lick frequency ($p = 0.0271$).

Although only one 20 min observation was made on a male during the period of female emergence in 1982, casual observations of lizards in the spring of both years indicated that males were much more active during this early period than later in the year. In the early spring, most of my effort was devoted to marking lizards in preparation for study; Males were more difficult to catch than females because of their ceaseless motion. If more quantitative observations had been made on early males, the distance moved and the display rate may have been significantly higher in males during the spring than during the rest of the year.

Response to intruders

Both adult male residents presented with a tethered male displayed vigorously at, and eventually attacked, the intruder. The intruder initially attempted to flee when the resident first approached and displayed. Since escape was impossible, the resident began chasing the intruder around the limits of its tether. One resident actually bit the struggling intruder several times. The fights continued until the intruder was removed. One resident continued to display vigorously after the intruder was removed.

The reactions of adult females to a female intruder were varied but generally less aggressive than the reactions of males to male intruders. In six out of 10 female-female encounters, residents displayed at intruders but usually moved away from them. No female resident attacked an intruder, although one resident displayed at and approached an intruder. At this point, an adult male interrupted the encounter.

Three female-female encounters were interrupted by the arrival of resident males. In each case the male jiggled while making short, rapid advances toward the females, alternating this behavior with push-up displays. The male always approached the resident female first. The resident female moved away from the male, occasionally performing an arched-back push-up display and a movement called "sidlehopping," which has been interpreted as a rejection display (Carpenter, 1962). The male then approached the tethered female, which tried to move away. Once the tethered female tried to bite the male, after which the male retreated.

One adult female was presented with an adult male intruder. She performed an arched display and remained in an elevated, arched posture until the tethered male was removed, even though the male did not display or try to approach her.

Discussion

Home Range Size and Overlap

The home ranges of adult males and females at the Virginia coal mine did not differ significantly in size. This is not inconsistent with polygyny if males do not necessarily increase their chances of finding mates by enlarging their ranges. Since most adult males associated with two or three adult females despite the similarity in male and female home range sizes, polygyny is still a reasonable mating strategy for this population.

Male and female home ranges were also similar in size in a Nebraska population of *S. undulatus*, where the lizards selected erroded terrain ("blowouts") and yucca plants as suitable habitats. Males of the species *Holbrookia maculata*, living in the same area but not associated with such structures, had larger home ranges than females. The number of female home ranges that overlapped the range of each male did not differ significantly between the two species. The investigators concluded that, in *S. undulatus*, the association of lizards with blowouts and yucca make it unnecessary for males to expand their home ranges in order to find several mates (Jones and Droge, 1980).

A similar situation seems to exist at the Virginia coal mine. Whereas sex as an independent variable had little effect on home range size, the size of the debris pile had a strong influence. As in the Nebraska population, fence lizards at the mine preferred structurally complex habitats (debris piles), which is typical of the species (e. g. Ferner, 1974; Tinkle, 1972). In the Nebraska and Virginia populations, the females may have been distributed such that home range expansion by males is unprofitable.

In contrast, males of a Colorado population of _S. undulatus_ had home ranges two to three times larger than those of females, despite an association with rocky habitat (Ferner, 1974). In this population, the females may have been distributed such that home range expansion by males is profitable.

An apparent inverse relationship between female-female overlap and male-male overlap values in Colorado, Nebraska, and Virginia may explain the geographic differences in male behavior (Table 9). High overlap among females may allow a male to associate with several females while maintaining a home range no larger than that of a female. Where overlap among females is low, males may need to expand their ranges in order to associate with several females. Male-female overlap was high where female-female overlap was high, suggesting that males can overlap female ranges more completely if female ranges overlap.

If small home ranges are defended more economically than large ones, males in the Colorado population should be less likely to show strong home range defense than those in the Nebraska and Virginia populations. This is supported by the high degree of overlap among males in the Colorado population, and by behavioral observations which suggested the existence of a dominance heirarchy among males (Ferner, 1974). Observations suggested home range defense in the Nebraska population (Jones and Droge, 1980). The lack of overlap among adult males and the aggressive attack of male intruders by male residents also suggested home range defense in the Virginia population.

At the coal mine, debris was a clumped resource which seemed to encourage a clumped distribution of females as well as high overlap among females. In order to monopolize mates, males may simply have taken advantage of a natural clumping of females (Emlen and Oring, 1977). In the other populations, the distribution of suitable habitat may also have influenced female distribution, which then in turn influenced the distribution of males.

The comparison of observed to expected home range overlap indicated that the consistent association of males and females was unlikely to result from random home range selection. Both sexes may have been attracted by the same habitat characteristics, or one sex may have been attracted to the habitat while the other sex was attracted to the first.

Overlap analysis also suggested that, when many adult females or juvenile males were present in one area, there was some avoidance within these sex/age groups. Competition for food should be most acute among individuals with the most similar food requirements, i.e. lizards of the same sex and size (Rand, 1967). If competition for food increases with the density of lizards of the same sex and size, lizards may try to avoid sharing their ranges with more than a certain number of competitors. No adult female overlapped with more than two other adult females, and only one juvenile male overlapped as many as 3 other juvenile males.

The comparison of observed and expected overlap among adult males did not indicate that males avoid each other even though no overlap among adult males was observed. This was due to the fact that there were only one or two adult males present in any area at one time, which caused the expected overlap to receive a low rank. The observed overlap of zero also received a low rank; it could not rank any lower than the expected overlap. This rank comparison technique would fail whenever avoidance exists within the sex/age group pair with the lowest ranking expected overlap, or whenever attraction exists within the sex/age group pair with the highest ranking expected overlap. The technique is also deficient where sample sizes of some sex/age groups are low (less than 4).

Activity and Response to Intruders

The frequencies of social behaviors of lizards at the coal mine did not appear to decrease after the reproductive season, with the possible exception of substrate licking by males. There was some evidence that male fence lizards touch the substrate with their tongues more often during the mating season than during the rest of the year. Licking the substrate may aid in the recognition of the sex of conspecifics. During the mating season, male *S. jarrovi* increase tongue touching behavior when entering an area recently occupied by a female (Bissinger and Simon, 1981). A similar function for *S. undulatus* is suggested. More extensive sampling in the spring might have found increased activity associated with courtship and mating, since casual observations indicate that males are extremely active in the spring.

Although most of the data were collected after the mating season, males displayed more often and moved greater distances than females. Push-up displays are associated with the attraction of mates and the repulsion of rivals (Rothblum and Jenssen, 1978; Noble, 1934). The greater distances moved by males than females suggested that males were patrolling their home ranges to guard against intruders, to seek females, or both.

Jiggling was usually performed by males while approaching females. Most investigators associate this behavior with courtship (Carpenter, 1962; Ferguson, 1971), although it has been observed in females and in non-sexual contexts (Rothblum and Jenssen, 1978). The latter authors suggest that jiggling may be more indicative of general arousal than a desire to mate. As few social interactions, other than between the sexes, were observed in the field, no definite conclusions as to the function of jiggling were possible.

The frequency of prey capture was unrelated to the sex of the lizard. Since iguanid lizards are generally "sit-and-wait" predators (Stamps, 1977), feeding frequency is probably most dependent on the rate at which insects appear within easy capture distance.

Many males seen during the period of female emergence (early males) disappeared within a few weeks without qualifying as home range owners. Whether these lizards die or are driven away is unknown; none of them were found in areas adjacent to the study site. Male S. undulatus in a Kansas population have a high mortality rate from April through June (Ferguson, Bohlen, and Woolley, 1980), and in a Utah population, survivorship was lower for males than for females (Tinkle, 1972), so it is possible that early males at the mine have a high mortality rate.

Male fence lizards at the coal mine maintained home ranges in close association with females throughout the year. Even in August and September, males approached females as if courting, and vigorously attacked intruding males. Post-reproductive courtship and defense in S. undulatus were also reported by Ferguson (1971). Additional information from my field study suggested that such behavior may be adaptive. Most home ranges were established by males that appeared later in the year. These residents were likely to become the early males of the following year. Therefore, males with home ranges may have an advantage over transient males in finding and mating with females the following spring. During the season of home range ownership, males have the opportunity to become familiar with the locations of females and to become familiar with individual females through social interactions. This may explain why males expend energy in courtship and defense activities after the mating season (Ferguson, 1971). When males emerge in the early spring, former home range owners may be better at predicting where females will emerge. Range-owners may even select hibernacula close to areas where females are likely to appear. Thus, due to familiarity or hibernaculum selection, former home range owners are the first to arrive at choice sites on the debris piles and have an increased chance of mating with newly-emerged females.

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Table 1. Three-way AVOVA on factors affecting home range size, as estimated by MCP and r^2 methods.

	MCP	r^2
Variable	p value	p value
sex	0.12	0.08
ageclass	0.21	0.14
pile size	0.06	0.01*
sex*ageclass	0.55	0.83
sex*pile size	0.58	0.38
ageclass*pile size	0.89	0.16
sex*ageclass*pile size	0.03*	0.01*

*significant at the 0.05 level.

Table 2. Comparison of mean home range sizes (m^2) for sex/age groups on small and large piles. A=adult, J=juvenile, F=female, M=male, L=large pile, S=small pile. Means with the same letter are not significanly different (alpha =0.05, Student Newman-Kuels test). Sex/age/pile size combinations where N=1 were not included in this analysis.

MCP			r^2		
AF, L	82.4	a	JM, L	232.6	a
JM, L	80.9	a	AF, L	203.4	a
AM, L	53.8	ab	AM, L	146.3	ab
JF, L	19.5	ab	JF, L	110.3	ab
JF, S	12.7	b	JF, S	38.2	b
AF, S	9.4	b	AF, S	34.6	b

Table 3. Correlation between home range estimators and between each estimator and sample size (N≥5). A=adult, J=juvenile.

r^2 as a function of MCP

sex/age class	R^2	p value
J female	0.68	0.01*
A female	0.84	<0.001*
J male	0.58	0.03*
A male	0.54	0.09

MCP as a function of N

sex/age class	R^2	p value
J female	0.06	0.55
A female	0.07	0.38
J male	0.03	0.69
A male	0.75	0.03*

r^2 as a function of N

sex/age class	R^2	p value
J female	0.01	0.80
A female	0.01	0.80
J male	0.40	0.09
A male	0.61	0.07

*significant at the 0.05 level.

Table 4. Comparison of home range sizes for *S. undulatus* in three geographic locations. Values are mean areas in m^2 (± 2 SE, when available). Adjusted MCP (MCP-JT) are calculated according to Jennrich and Turner, 1969. Nebraska data are from Jones and Droge, 1980; Colorado data are from Ferner, 1974.

	present study		Nebraska		Colorado
	MCP	MCP-JT	MCP	MCP-JT	MCP-JT
Adult females					
	59.9	172.1	101.1	851.5	363
	(±22.4)	(±66.8)	(±315.7)	(±977.3)	
Adult males					
	69.3	189.6	121.1	717.2	826
	(±32.0)	(±61.7)	(±235.3)	(±723.2)	

Table 5. Expected and observed overlap (%) for all pairs of sex/age groups, Upper Wreck 1981. Lizard density: 11.4 residents/hectare. N is the number of lizards in each sex/age group. Numbers in parentheses are rank values. H=sex/age pair where observed overlap is greater than expected, L=sex/age pair where observed overlap is less than expected. Ranks differing by 2 or less were not considered different.

sex/age group pairs	N	Expected Overlap		Observed Overlap		
(AM AM)	2	24	(2)	0	(1.5)	
(AM JM)	2/6	53	(7)	55	(8)	
(AM AE)	2/5	47	(5)	58	(9)	H
(AM JF)	2/3	33	(3)	22	(3)	
(JM JM)	6	76	(10)	42	(7)	L
(JM AF)	6/5	72	(9)	60	(10)	
(JM JF)	6/3	49	(6)	25	(4.5)	
(AF AF)	5	56	(8)	25	(4.5)	L
(AF JF)	5/3	39	(4)	30	(6)	
(JF JF)	3	14	(1)	0	(1.5)	

Table 6. Expected and observed overlap (%) for all pairs of sex/age groups, Upper Wreck 1982. Lizard density: 6.4 residents/hectare. See Table 4 for explanations.

sex/age group pairs	N	Expected Overlap		Observed Overlap		
(AM AM)	1	0	(1.5)	0	(2.5)	
(AM JM)	1/1	24	(6)	0	(2.5)	L
(AM AF)	1/4	30	(7.5)	55	(10)	H
(AM JF)	1/3	20	(4.5)	16	(7)	H
(JM JM)	1	0	(1.5)	0	(2.5)	
(JM AF)	1/4	30	(7.5)	8	(5.5)	
(JM JF)	1/3	20	(4.5)	8	(5.5)	
(AF AF)	4	48	(10)	43	(9)	
(AF JF)	4/3	35	(9)	30	(8)	
(JF JF)	3	10	(3)	0	(2.5)	

Table 7. Observed overlap for 5 pairs of sex/age groups at the Lower Wreck. Lizard density was 2.3 residents/hectare both years. Sex/age groups pairs that had zero overlap both years were not included in this table.

sex/age	1981		1982	
group pairs	N	Observed Overlap	N	Observed Overlap
(AM AM)	1	--	2	0
(AM JM)	1/1	24	2/0	--
(AM AF)	1/2	66	2/2	48
(JM AF)	1/2	42	0/2	--
(AF AF)	2	62	2	0

Table 8. Frequency of six activities of adult males and females. Comparisons were made with one-tailed Fisher's exact tests. "Activity (min)" is the proportion of one-minute intervals in which the individual moved, displayed, etc.

		Males		Females	
Behavior	p-value	median	range	median	range
substrate licking	0.16	1.7	0-16	0	0-4
prey captures	0.75	0	0-2	0	0-1
prey items missed	0.89	0	0-0.3	0	0-1
activity (min)	0.25	3.7	0-10	3.5	0-10
push-up displays	0.03*	3.3	0-9.5	0.5	0-3
total distance (m)	0.04*	4.1	0-14.5	2.6	0-6.7

*significant at the 0.05 level.

Table 9. Comparison of adult intrasexual and intersexual overlap (%) in three populationsof *S. undulatus*. Nebraska data are from Jones and Droge, 1980; Colorado data are from Ferner, 1974.

	present study	Nebraska	Colorado
among males	0	27	52
among females	32	18.9	9.5
male-female	56	11.7	--

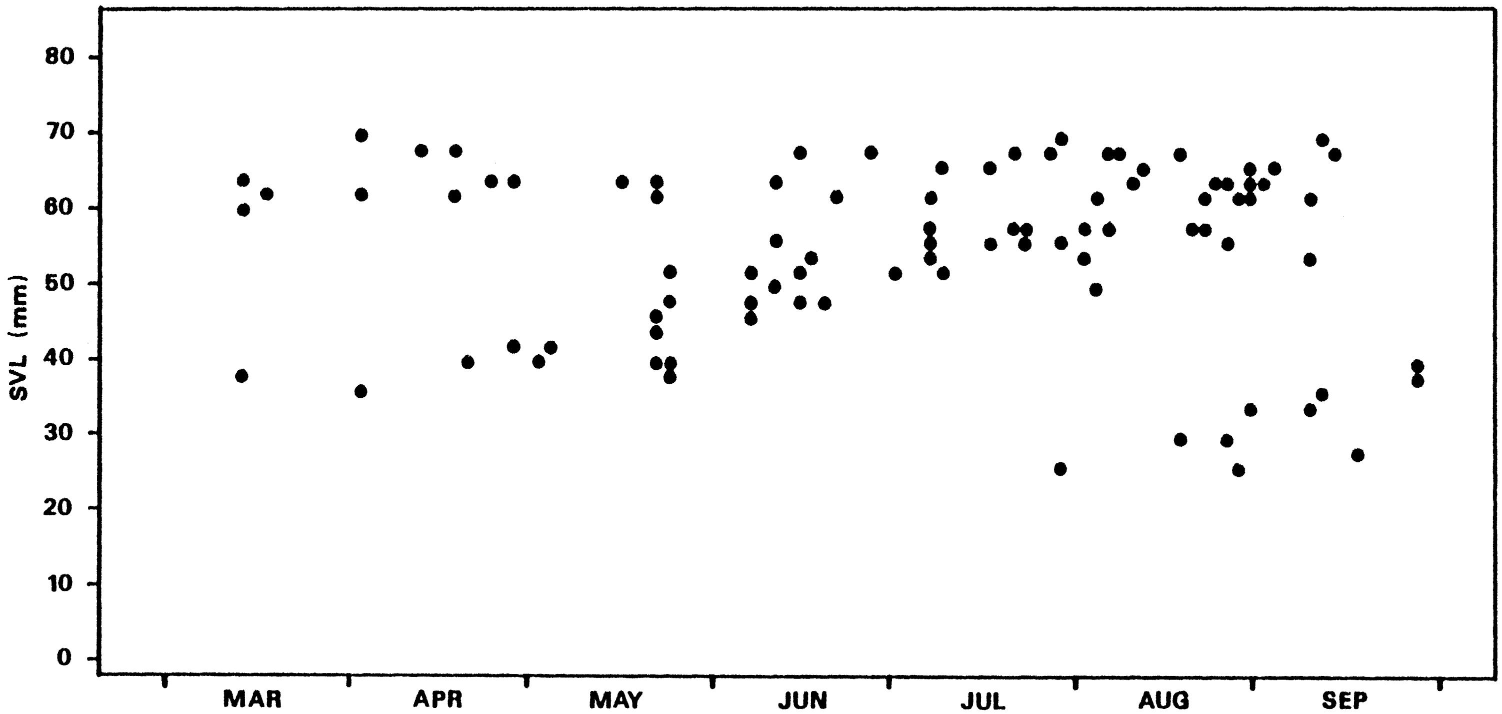

Figure 1. SVL as a function of date for male S. undulatus at the coal mine. Includes 1981 and 1982 data.

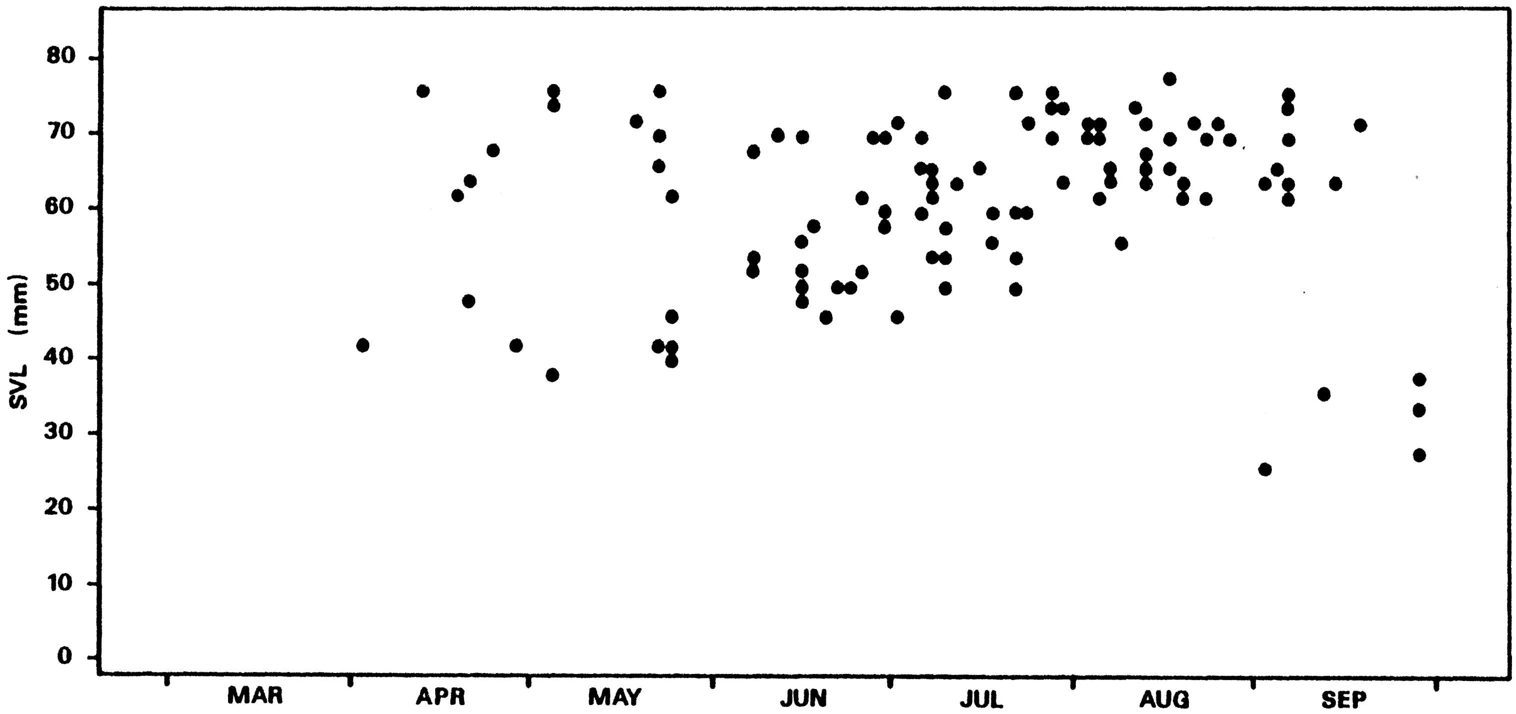

Figure 2. SVL as a function of date for female S. undulatus at the coal mine. Includes 1981 and 1982 data.

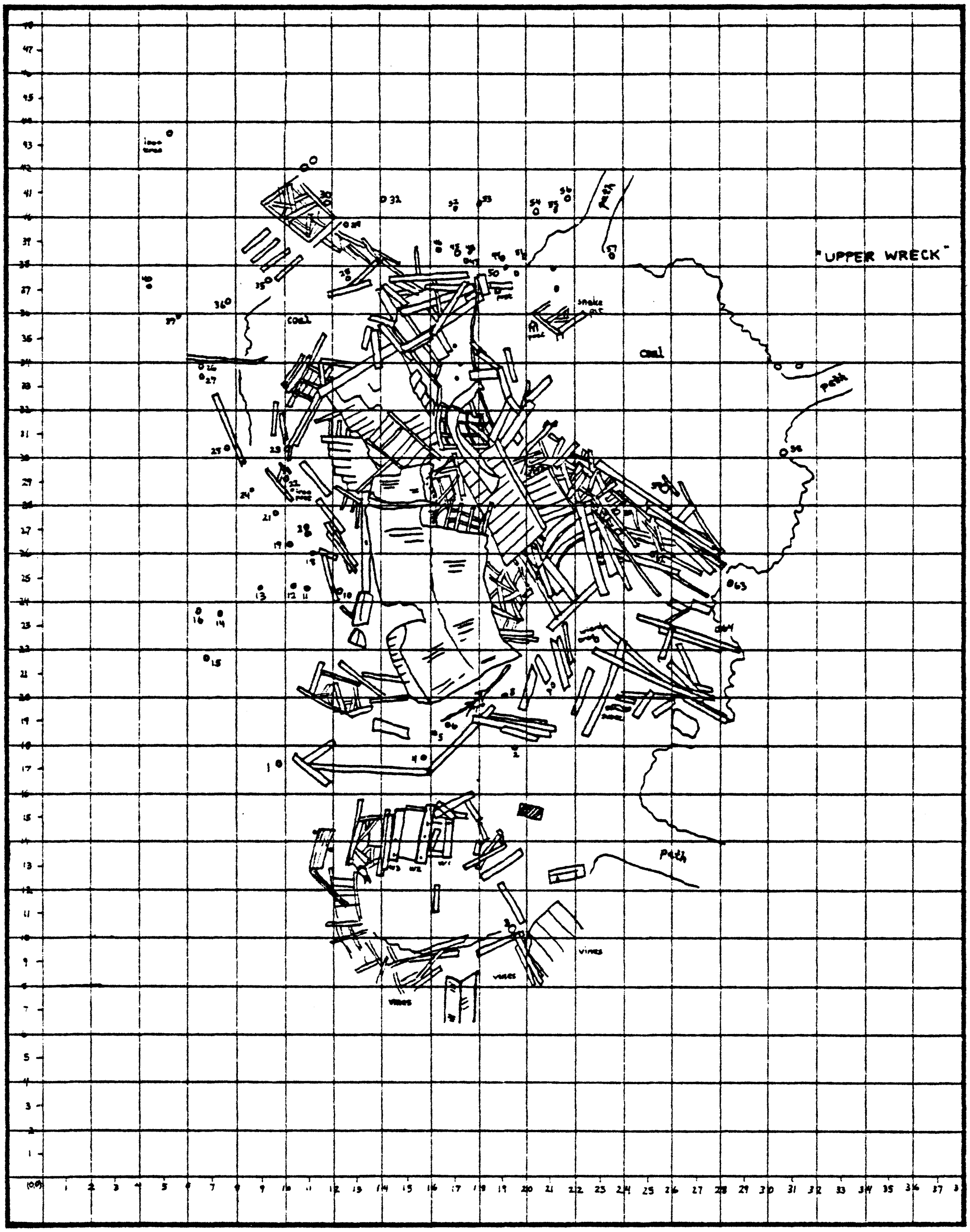

Figure 3. Upper Wreck area. Each square is 2m x 2m. Numbered circles are marked trees.

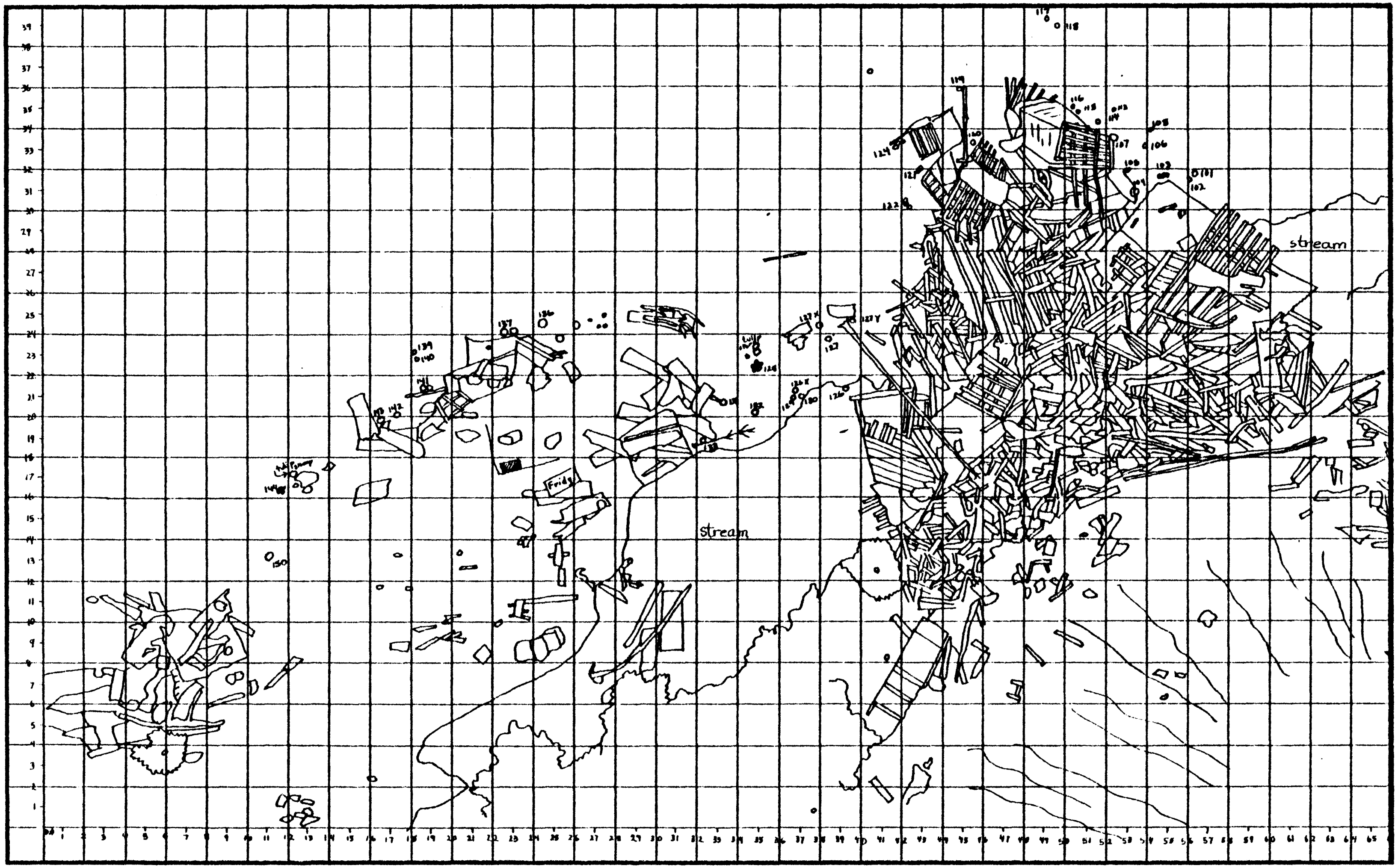

Figure 4. Lower Wreck area. Each square is 2m x 2m. Numbered circles are marked trees.

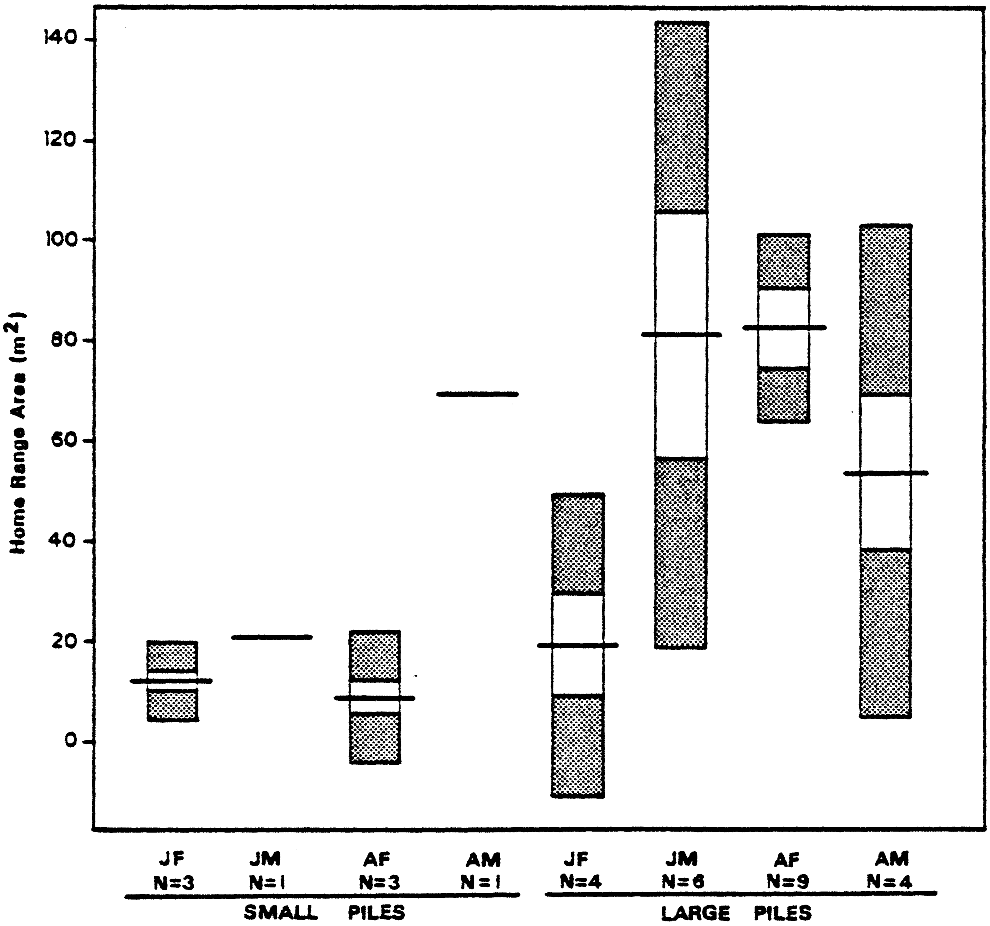

Figure 5. MCP home range estimates. Vertical bars show mean, SE, and 95% confidence limits.

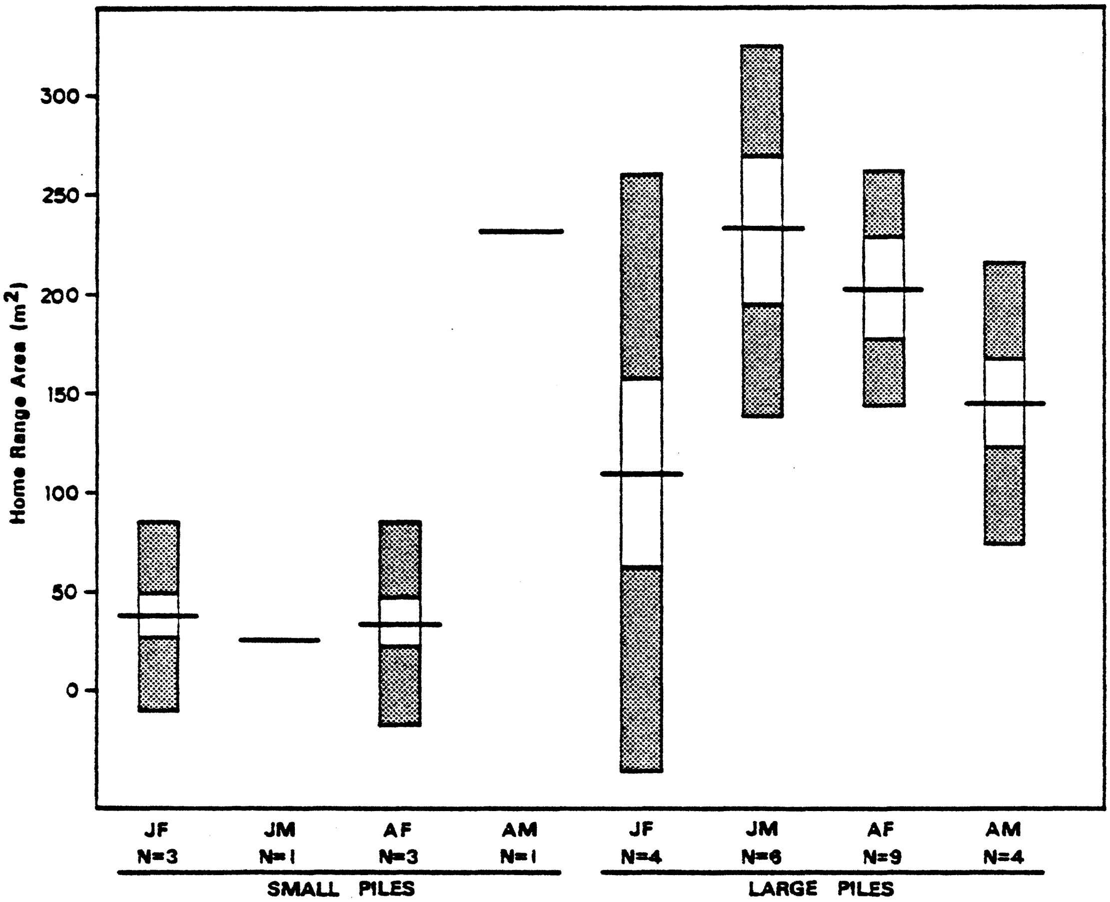

Figure 6. r^2 home range estimates. Vertical bars show mean, SE, and 95% confidence limits.

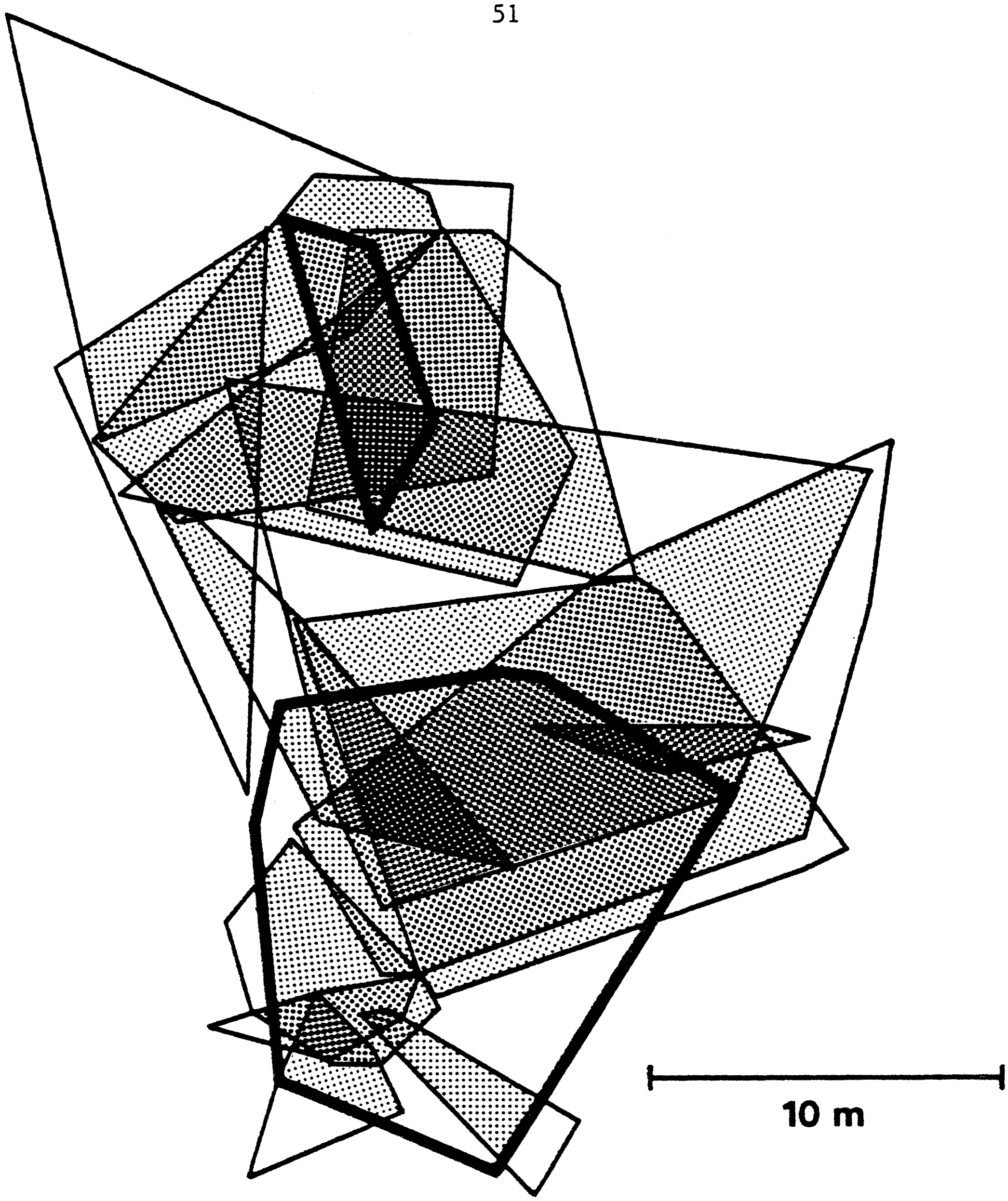

Figure 7. Home ranges of adult and juvenile lizards at the Upper Wreck in 1981. Number of overlapping home ranges increases with density of shading. Ranges of adult males have heavy outlines. Areas of greatest overlap occur within the ranges of adult males and are located on debris piles.

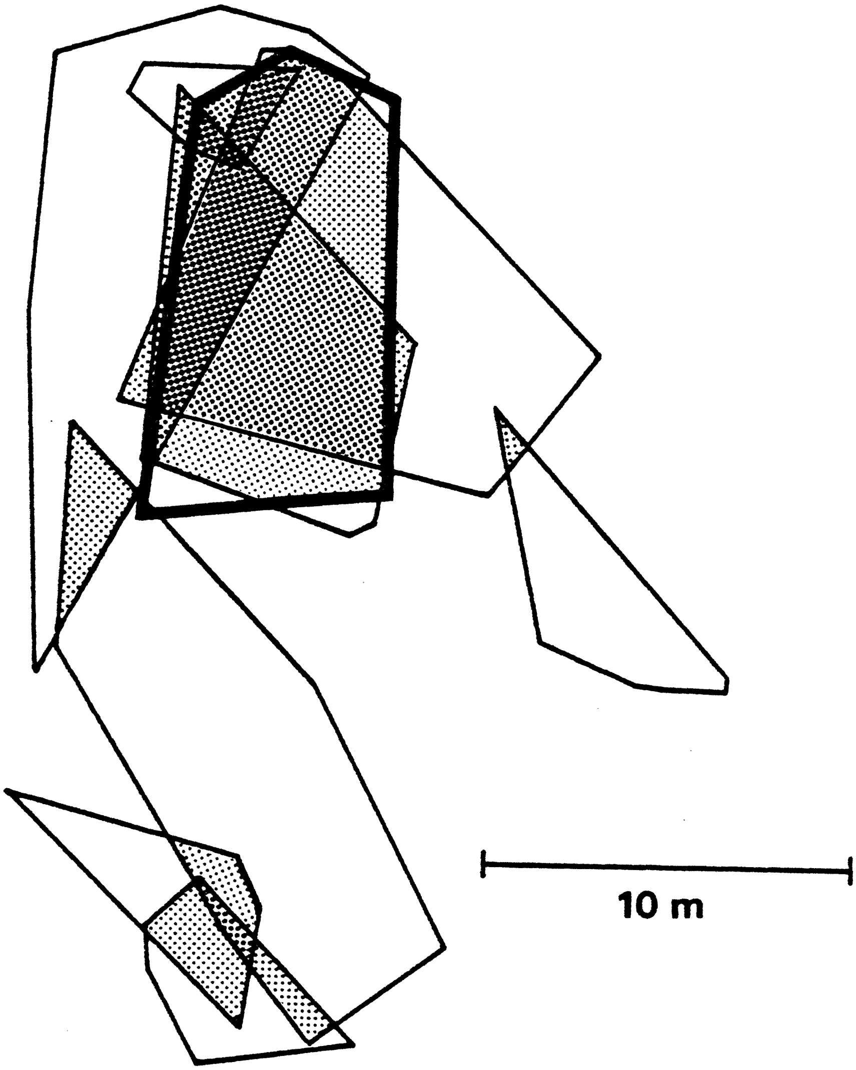

Figure 8. Home ranges of adult and juvenile lizards at the Upper Wreck in 1982. See Fig. 7 for explanations.

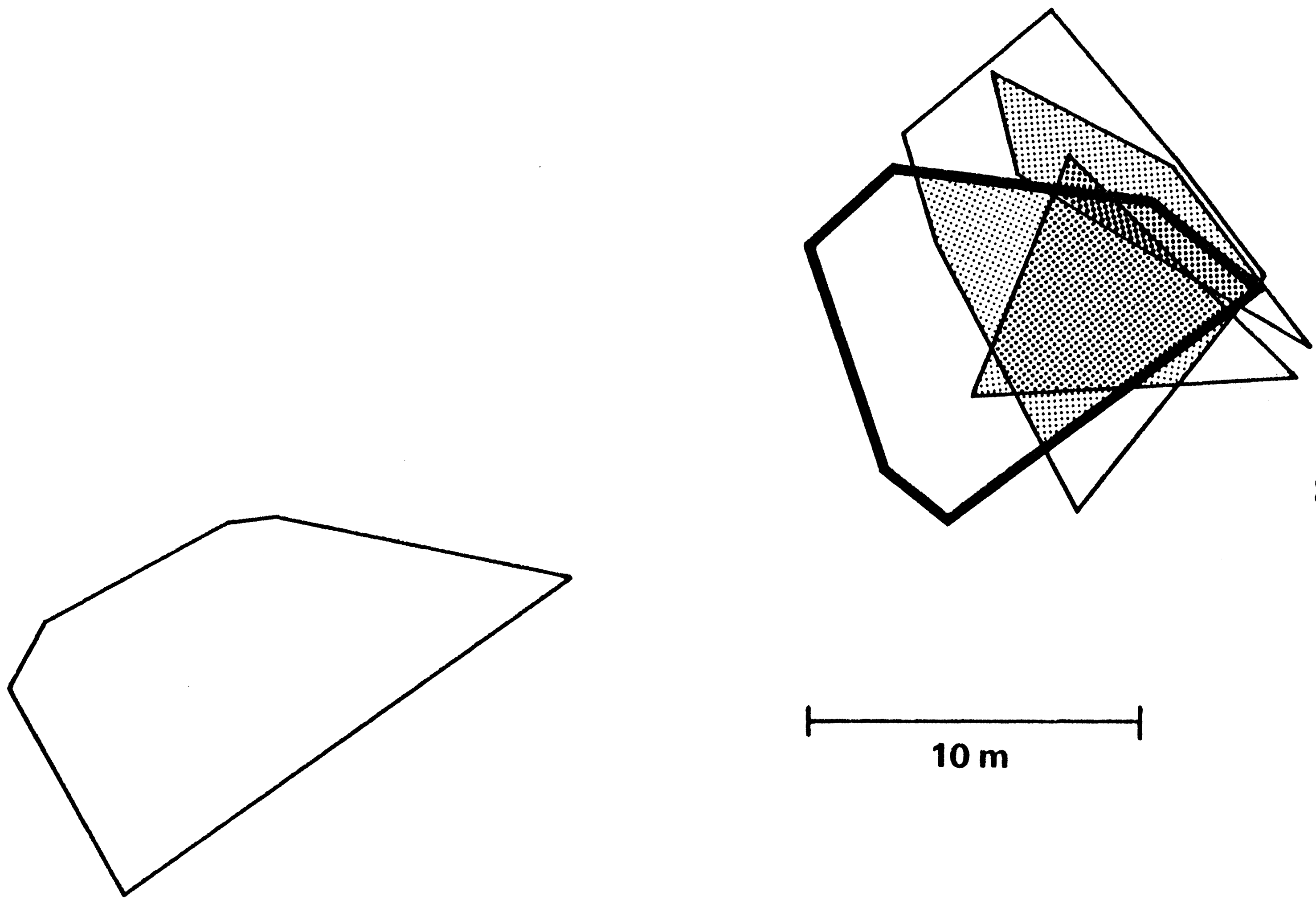

Figure 9. Home ranges of adult and juvenile lizards at the Lower Wreck in 1981. See Fig. 7 for explanations.

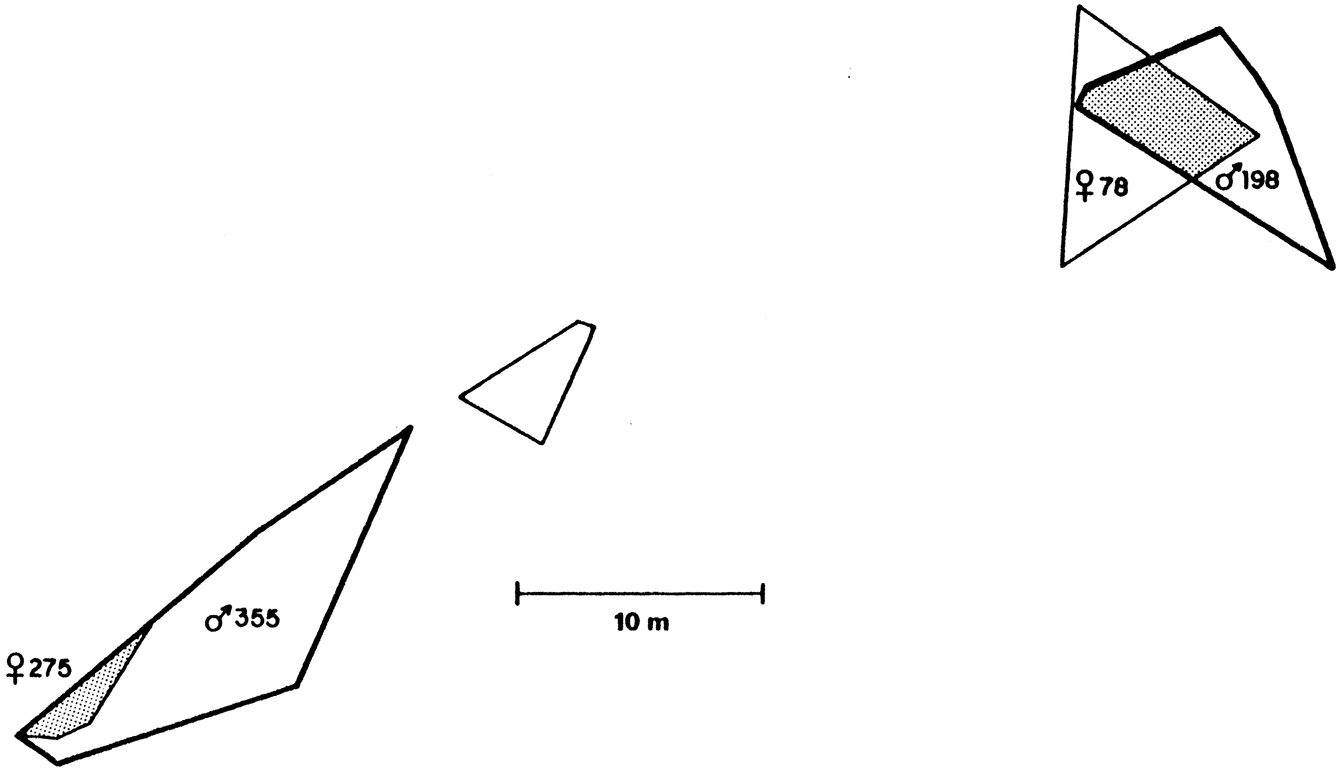

Figure 10. Home ranges of adult and juvenile lizards at the Lower Wreck in 1982. The unlabeled polygon belongs to a juvenile female; all others are adults. Lizards #355 and #275 are "small pile" residents; the male roamed more widely than the female.
Female #78 is in the same area she occupied in 1981.

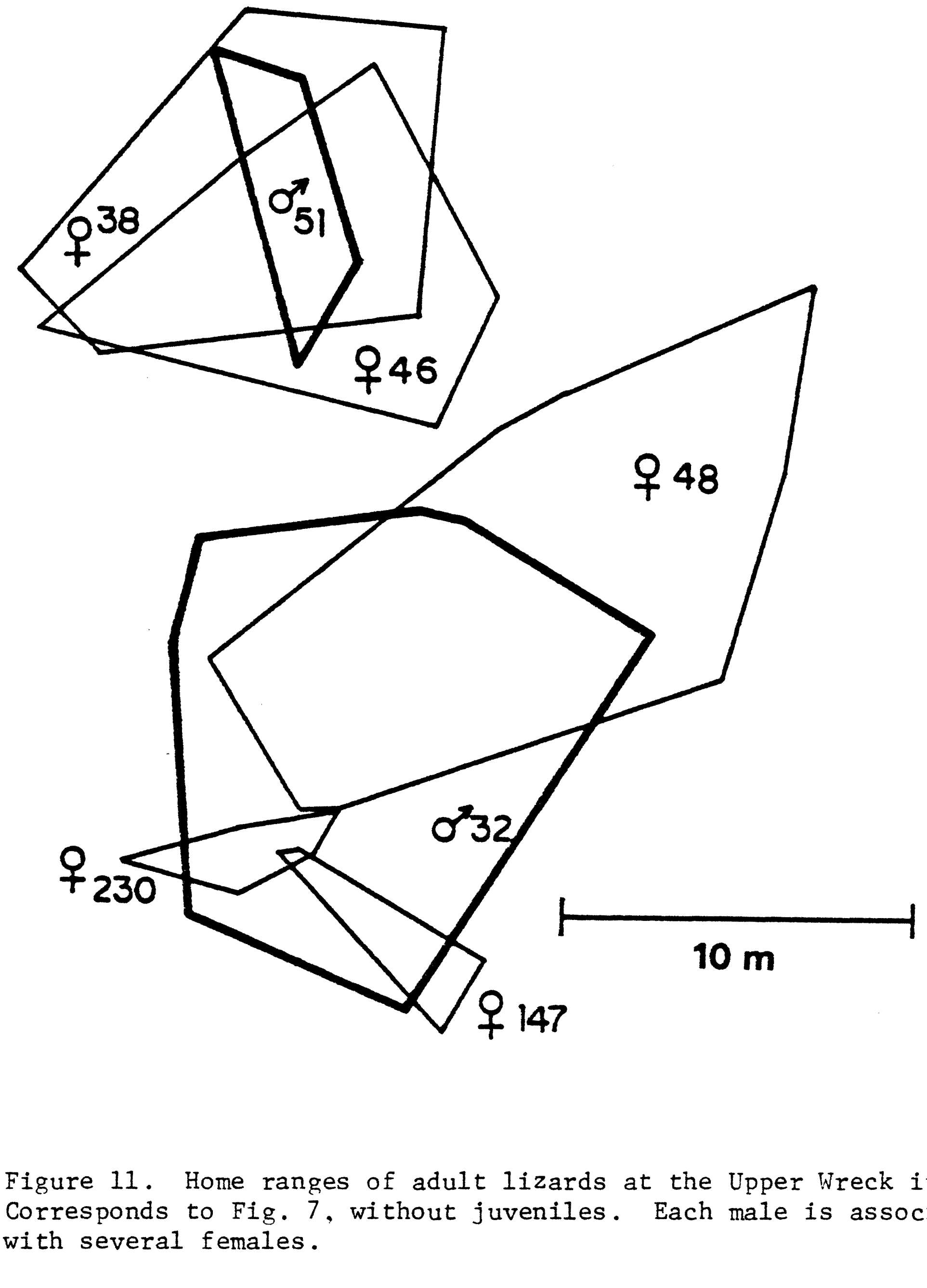

Figure 11. Home ranges of adult lizards at the Upper Wreck in 1981. Corresponds to Fig. 7, without juveniles. Each male is associated with several females.

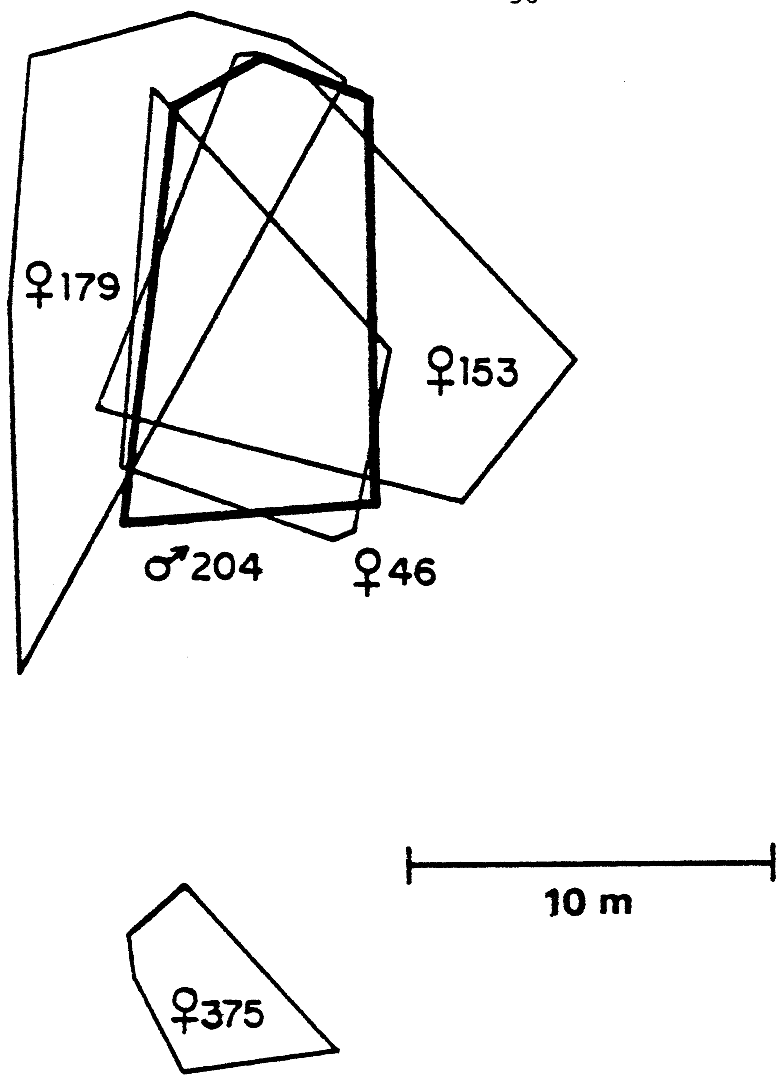

Figure 12. Home ranges of adult lizards at the Upper Wreck in 1982. Corresponds to Fig. 8, without juveniles. The adult male is associated with three females. Female #46 is in the same area she occupied in 1981 (Fig. 11).

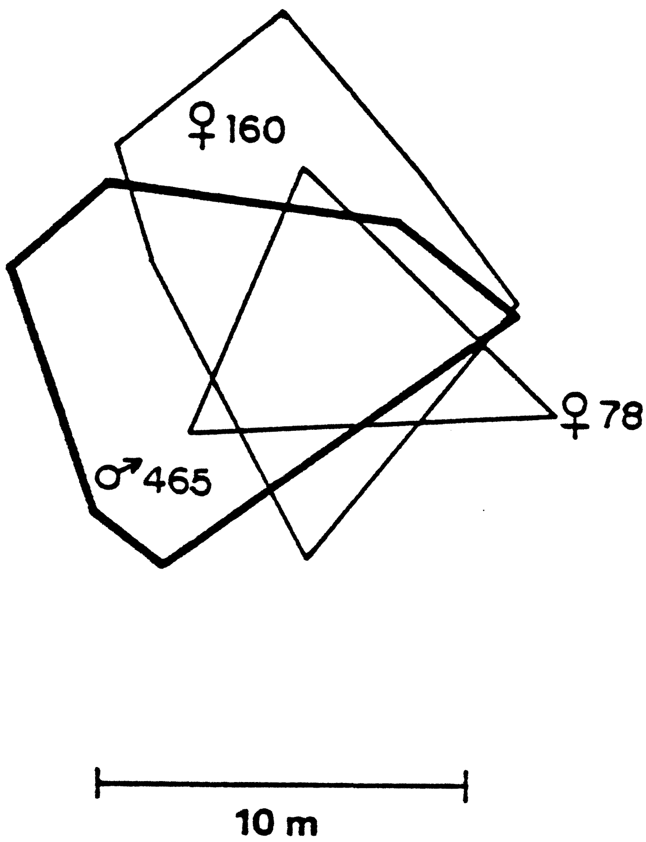

Figure 13. Home ranges of adult lizards at the Lower Wreck in 1981. Corresponds to Fig. 9, without juveniles. The male is associated with two females.

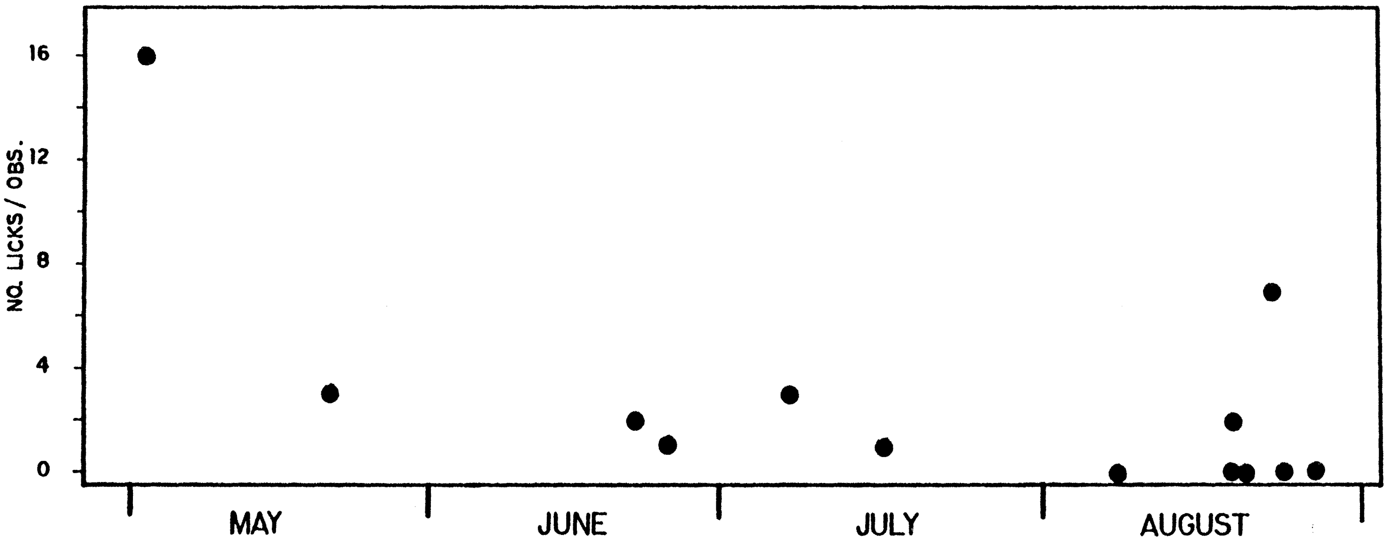

Figure 14. Substrate licking by male fence lizards as a function of date. The highest frequency of licking occurred during the period when females began appearing on the field site. Linear regression indicates a significant downward trend in lick frequency with time (p= 0.03).

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HOME RANGE AND ACTIVITY IN A VIRGINIA POPULATION

OF *SCELOPORUS UNDULATUS*

By

Karen Elizabeth Preston

(ABSTRACT)

A study of the lizard *Sceloporus undulatus*, conducted 1981-82 at an abandoned coal mine in Virginia, was designed to determine whether home range size, home range overlap, and patterns of behavior reflected the requirements of polygyny. The lizards were seen most often on the piles of debris that characterized the study site.

Home range size was most strongly influenced by the debris pile size. Mean home range sizes (MCP, $N \geq 5$) were 69.3 m^2 and 59.9 m^2 for adult males and females, respectively, when data for all debris piles were pooled.

The average overlap of home ranges for both study areas and for both years was 32% among adult females and 56% between adult males and females. No overlap among adult males was observed. Adult males usually associated with more than one female.

Display frequency (push-ups) and total distance moved during 20 min observation periods were higher for adult males than adult females. Jiggling (rapid head nodding) was

observed only in males. The frequencies of other behaviors (e. g. prey capture) did not differ between the sexes. Only one activity, substrate licking by males, seemed to decrease significantly as a function of date.

Male home range owners interacted socially with females during the post-reproductive period. This behavior may increase a male's mating success the following spring, as most adult males that appeared on the study site during the mating season in 1982 had been home range owners in 1981.