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Spatial Relationships among Members of a Population of Wall Lizards

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Summary. Wall lizards occupied overlapping territories, the size of which seemed to vary directly with the dominance level of the individual. Average territories of both males and females encompassed about 25 square meters. The overlap in territories among males was about 8 percent, and among females, about 18 percent. When both sexes were considered, overlap was 100 percent. This spacing mechanism appeared to be effective in governing the number of resident males but less so in governing number of resident females.

In each of three years, females outnumbered males by 3.5 to one, probably because, among non-resident individuals, males were forced to move about more than females in order to avoid resident males, and as a consequence were subjected to greater predation pressure. Of 47 lizards marked on the study area, 60 percent were resident; the remainder were apparently wandering in search of unoccupied habitat.

The number of resident lizards increased over the 5-year period of study from 10 to 21 individuals. Over the same period the average snout-to-vent length of this population decreased from 70.7 mm to 68.2 mm among males and 63.2 mm to 57.3 mm among females, probably reflecting a younger age structure. Correlated with these changes in population size was an increase in predation pressure from feral cats as reflected in the incidence of caudal autotomy among lizards.

Introduction

Studies of iguanid lizards have recorded differences among species in intrapopulational spatial arrangements. Some species, such as *Uta stansburiana,* seem to be "highly territorial" (Tinkle, 1965, 25); members of each sex divide up the habitat into discrete units which overlap only those of the opposite sex. Other species, for example *Sceloporus graciosus* (Stebbins and Robinson, 1946) and *S. olivaceus* (Blair, 1960), apparently have home ranges which freely overlap one another both within and between sexes. Such differences have led to speculation about the role these spatial relationships have on population regulation (Blair, 1960; Rand, 1965).

This report documents the spatial relationships among members of a population of Italian wall lizards (*Lacerta muralis*: Lacertidae), observed during the summer months of 1967, 1969, and 1971. The significance of these relationships is discussed.

Methods

Wall lizards were studied in part of a private garden within the Villa Floridiana, a public park in Naples, Italy. That part of the garden in which the lizards were observed was surrounded on two sides by rough plaster walls against which grew numerous climbing plants. The third side was bordered by the ends of two greenhouses, with a space between them, and the fourth was open into a vivarium in which grew perennial herbaceous and woody plants. Within this area were a variety of potted plants, small flower beds, and two wild orange trees. Thus, an abundance of habitat requirements for lizards (Rand, 1967) such as lookouts, sunning locations, foraging areas, and escape cover were available. A grid system superimposed over a scale drawing of the area permitted the positions of any marked lizards resighted to be plotted accurately (Fig. 1). This area encompassed a horizontal surface of 151 square meters that was utilized to varying degrees by the lizards under study. Vertical surfaces were not included because they were not used by lizards unless sufficiently rough to provide horizontal perches. Only the wall below the stairs, on the right of Fig. 1, provided such surfaces. Even here the lizards spent more of their time on horizontal branches of the plants than on the wall.

Lizards were caught with a light noose on the end of a slender bamboo switch. The sex and snout-to-vent length were recorded for all lizards caught. In

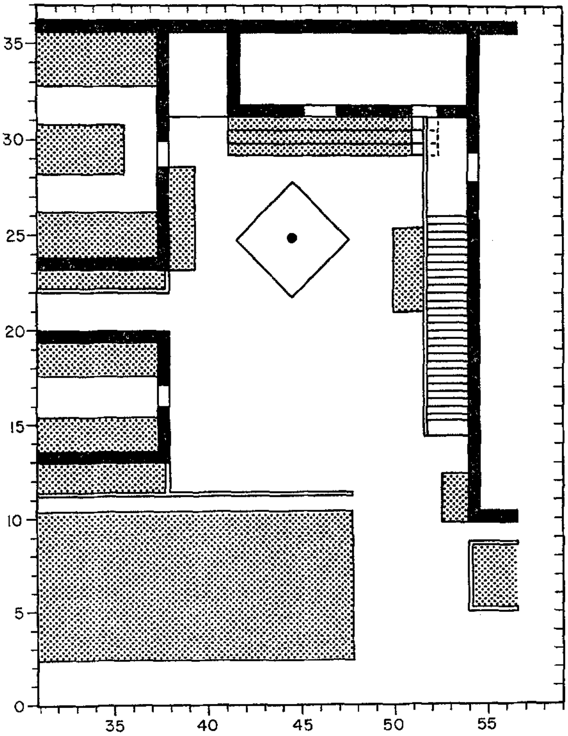

Fig. 1. A diagram of the study area with a grid system at 0.5 m intervals. Stippled areas represent flower beds or potted plants, thick black lines are walls of buildings, the square in center is a fountain

1967 and 1969, each lizard was individually marked with a small piece of coloured light, but strong plastic. In case this mark was lost, all lizards were individually marked by clipping toes. The plastic was attached to the lizard with a loop of surgical linen threaded between the skin and underlying muscle in the nuchal region. During these two summers, the garden was visited at hourly intervals throughout most days during July and August. All marked lizards seen in the first five minutes of each visit were noted, and their locations and activities when first seen were recorded. Certain lizards were then watched and notes made on behavioural patterns and outcomes of any interactions.

In 1971, all lizards found on the study area were caught and marked by toe-clipping only. All previously marked lizards were recorded and their locations noted.

Results and Discussion

The number and sex of all adult lizards caught and marked within the study area and its immediate surroundings are recorded in Table 1. The population apparently increased over the five-year period. Females consistently outnumbered males.

Table 1. Numbers and sex ratios of marked wall lizards

Year	Males	Females	Females/male	Total
1967	6 (4)[a]	16 (10)	2.7	22
1969	4 (2)	21 (13)	5.3	25
1971	8 (4)	28 (17)	3.5	36
Total	18	65	3.6	83

[a] Number of individuals resident on area in parentheses.

The bimodal distribution of resightings of lizards marked on the study area (Fig. 2) suggests two categories: transient lizards—resighted on less than 11 percent of the days on which observations were made; and resident lizards—resighted on more than 10 percent of the observational days. Based on the combined data for 1967 and 1969, lizards in the first category included 40 percent of males and 43 percent of females. These lizards, usually seen only once, or, if resighted, seen at a considerable distance from the previous sighting, were apparently part of a wandering, non-resident population. Their ephemeral presence on the study area suggested a state of constant mobility, probably in search of unoccupied habitat. Three resident lizards were resighted regularly on the study area for relatively short periods only in 1967, and consequently were seen on less than 30 percent of the observational days. One of these, a male, moved onto the study area to occupy temporarily a place vacated by a resident male which I had caged for 17 days;

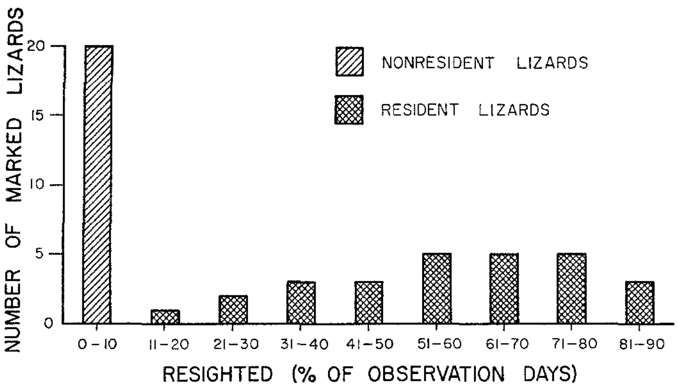

Fig. 2. Distribution of resightings of marked wall lizards

the other two were females that disappeared relatively early in the study, one at least having been killed by a cat. The remaining lizards were resighted regularly. On this basis, 60 percent of the marked males and 57 percent of the marked females were considered resident and part of the breeding population. This population numbered 11 in 1967, after disappearance of three individuals, and 15 in 1969. By 1971 it was estimated to have increased to 21.

Expressing these numbers on a per hectare basis, the density of lizards in this man-made habitat rose from 662 to 1391 which is much in excess of reported densities of comparable-sized lizards in natural habitats of North America (cf. Tinkle, 1965). These differences may reflect ecological versus crude densities, the former being worked out on very small areas of optimum habitat, as in this study, and the latter being based on larger study areas (Tinkle, 1965) where much of the area may have been uninhabitable. Other possibilities include differences in the biomass of the lizards involved and availability of food and shelter to support them, differences between areas in productivity, differences in the spacing mechanisms among members of different species, or any combination of the above.

Spatial relationships among members of the resident population were determined from hourly sightings, on most days, of marked individuals. The area used by each lizard was assessed after all locations of sightings were connected by known routes of travel between these locations. Since lizards spent most of their time at sunning locations with only short and rapid forays to catch prey or to move to other sunning locations, most sightings during the 5-minute hourly recording period were at these sunning places. Nevertheless, routes of travel were recorded whenever

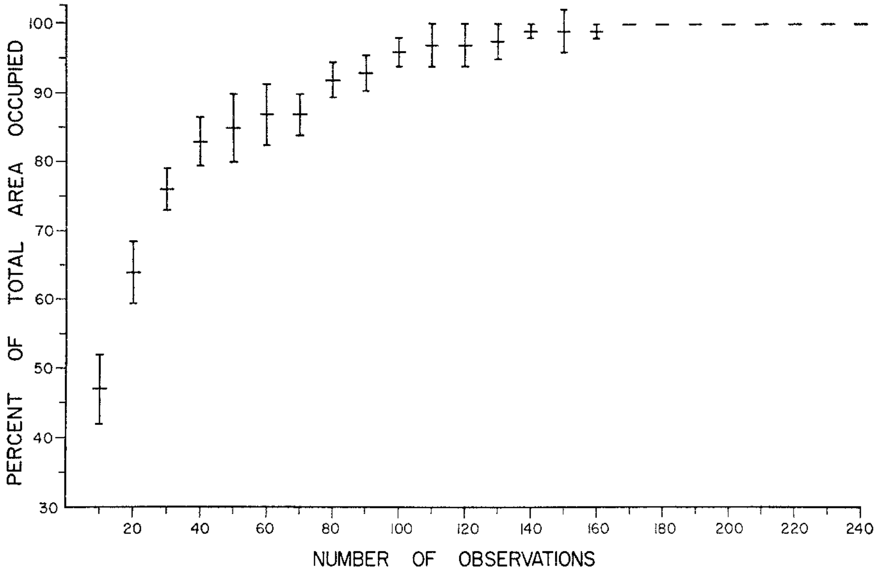

Fig. 3. Relationship between the number of sightings and the percent of the total area occupied. Vertical lines indicate one standard error of the mean

observed. The assumption that the calculated area represented the total area used by a given lizard was investigated by determining the relationship between the percentage of calculated total area used and each successive series of ten observations (Fig. 3). Only lizards for which there were more than 50 observations were considered in this analysis. The size of the area encompassed continued to increased until 170 observations were recorded. The area used by lizards, for which there were less than 170 sightings, could be estimated by applying a correction factor from the curve in Fig. 3.

As is implied by the data on density, the size of areas occupied by individual resident wall lizards is small relative to those reported for some North American lizards. Males occupied areas that averaged 26 square meters (range of 10 to 52); females occupied areas that averaged 23 square meters (range of 6 to 42). Tinkle (1965) estimated the area occupied by male *Uta stansburiana* to lie between 0.06 and 0.49 acres (243 to 1982 square meters) and females, 0.03 to 0.15 acres (121 to 607 square meters). Blair (1960) reported areas used by male *Sceloporus olivaceus* measured 85.5 feet to a side (680 square meters) and females 56 feet (292 square meters). In both studies of North American lizards the size of areas occupied by males exceeded those of females.

Table 2. Overlap of areas occupied by all resident wall lizards of the same sex

Year	Number of comparisons among		Range in overlap of occupied areas (%)		Average overlap in occupied areas (%)	
	Males	Females	Males	Females	Males	Females
1967	6	72	0–27	0–71	8	21
1969	2	132	5–15	0–67	10	17
Total	212		range 0–71		average 18	

Such was not the case in this study. Male and female wall lizards occupied areas of approximately equal size. The degree to which the area occupied by a male overlapped areas occupied by each other male on the study area is presented, along with similar data for females, in Table 2.

The range in overlap indicates a wide variation from no overlap where areas occupied were in different parts of the garden to approximately 75 percent overlap where lizards were occupying areas in similar parts of the garden. However, mean overlap of occupied areas among resident males was consistently less than among females, although the differences in any one year were not statistically significant. Blair (1960) reports a similar situation among *Sceloporus olivaceus* in which males averaged 24 percent overlap and females 35.

These results raise several questions: What were the dominance relationships among lizards that led to transient and resident status, and the varying degree of common usage of habitat? Did the spatial relationship among individuals limit their numbers on the study area? What was the difference between males and females that led to such an unbalanced sex ratio? And if the population did increase over the five-year period, how was this possible?

I examined the first question by considering separately the spatial relationships among members of each sex, the behavioural interactions among them, and the fidelity they showed to respective areas. In both years resident males evidently divided up the available area minimizing overlap among them (Fig. 4). Locations at which each male was seen most frequently were more equally spaced in 1967 than in 1969, when they were closer together and within sight of one another.

Whenever wall lizards approached one another they began threatening by pulling down their chins, swelling their necks, extending their forelegs, and twitching the tips of their tails. The greater the size difference between individuals the less threatening occurred as the smaller individual invariably withdrew as soon as the larger began to threaten. Among residents none was overtly dominant over the other; at points where

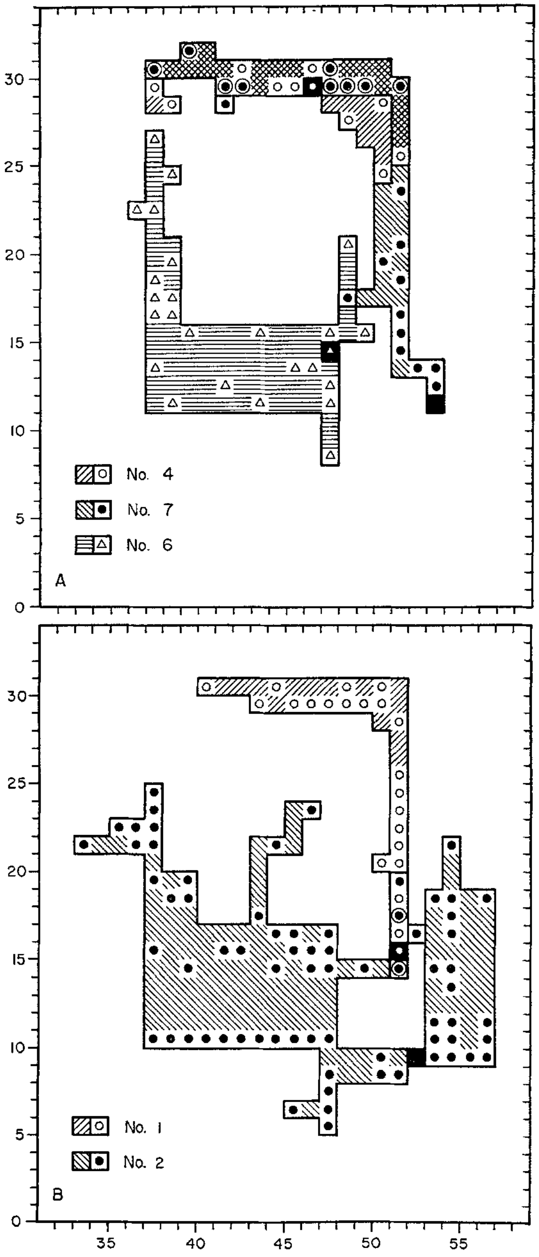

Fig. 4A and B. Spatial relationships among 3 male wall lizards resident on the study area in 1967 (A) and 2 males in 1969 (B). Squares containing symbols indicate locations where lizards were actually recorded during observation periods; those blackened were locations most used for sunning by each individual occupied areas overlapped each threatened the other without displacement of either. Nevertheless, the farther an individual was from its favourite sunning location, the more likely it was to retreat upon being threatened. Such a situation seemed to determine the limits of the area occupied.

The fidelity of male wall lizards to a particular area and their ability to redominate it was tested in 1967 by removing male No. 7 (Fig. 4) and holding him in captivity away from the study area for a period of 17 days. The day following his removal a male from just outside the study area expanded the area he occupied to include a major part of that vacated by No. 7. Upon release at the edge of the study area, No. 7 immediately reoccupied the area previously held and expelled the encroaching male with threats and a chase.

From these observations I concluded that the areas occupied by resident male wall lizards are best considered overlapping territories (McBride, 1971) in which one or more sunning sites are defended. The dominance of each individual diminished as it moved away from this favoured location(s) and a point in space was reached where its dominance was less than its neighbours and this point marked the limit of its territory. Male wall lizards appeared to demonstrate different levels of dominance. Some resident males approached closely the favoured sunning location(s) of other resident males where they threatened but did not displace the occupants. However, the reverse situation among the same males was never recorded and I concluded that, among resident males, those approaching sunning sites of others were more dominant than those males that did not do this. Correlated with these assumed differences in levels of dominance were differences in size of territory: the most dominant males occupied large territories over which they were able to maintain their dominance at considerable distances from favourite sunning locations (Nos. 2, 6 and 7 in Fig. 4); less dominant males possessed smaller territories as they appeared to lose their dominance status within a short distance of a preferred sunning location (Nos. 3 and 4 in Fig. 4); the least dominant individuals were those which were unable to dominate at any sunning location and which retreated from any threatening male.

Resident females (Figs. 5 and 6) overlapped more in their use of space than did males. Nevertheless, favoured locations tended to be distinct for each female. Numerous interactions were observed among resident females, but unlike males, threats and manifestations of dominance were observed mainly when a trespasser approached an occupant at the latter's favoured sunning spot, whereupon the trespasser retreated.

To test the fidelity of females to their home ranges and the ability to re-establish themselves in the resident population after being displaced,

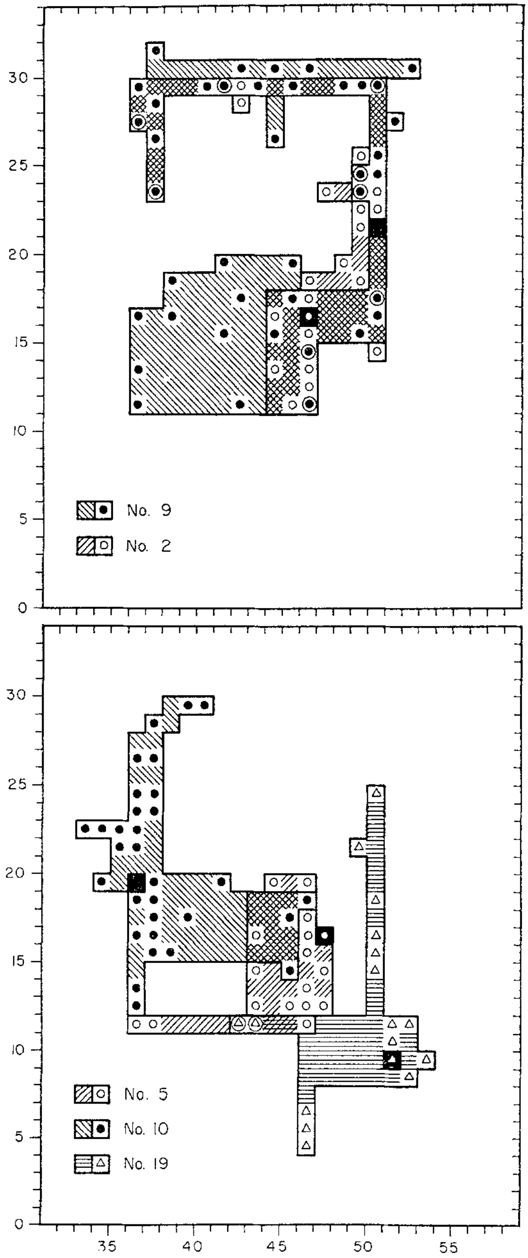

Fig. 5. Spatial relationships among 5 of 10 female wall lizards resident on the study area in 1967. See Fig. 4 for explanation of symbols

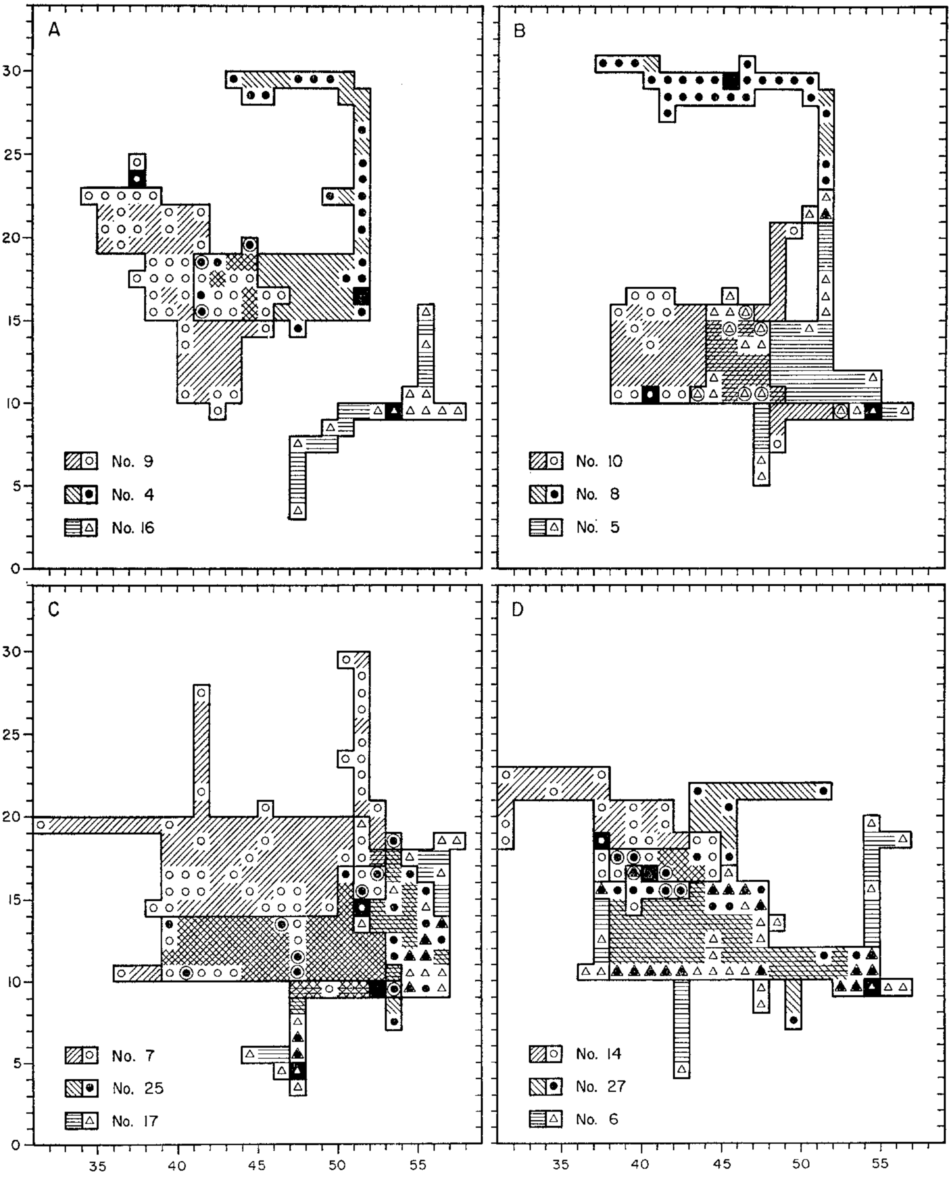

Fig. 6 A—D. Spatial relationships among 12 of 13 female wall lizards resident on the study area in 1969. See Fig. 4 for explanation of symbols

two females, Nos. 5 and 10, were caged for 17 days in 1967. Upon release at the edge of the study area both females immediately re-established themselves in their former areas and each displaced a female that had usurped its favoured sunning location. Thus like males, females apparently occupied overlapping territories and defended sunning locations.

Based on the same criterion of dominance as in males, females also exhibited varying degrees of dominance: the most dominant females possessed large home ranges that overlapped their neighbours' (No. 5 in Fig. 5, and No. 6 in Fig. 6) and on which they were dominant over other females at all sunning locations except the favourite one of the neighbour; a second level of dominance was seen in females that possessed a territory, usually small, on which they were dominant only around favoured sunning spots (No. 19 in Fig. 5, and No. 4 in Fig. 6); the least dominant females lacked a territory and were subordinate to other females at all locations.

The territories of males were superimposed on those of females. Favoured sunning locations were often shared between a male and a female. In all interactions observed between sexes, males invariably displaced females when a favoured location was contested. Otherwise females were tolerated at close range and, indeed, were often courted by males.

In general, these results approximate the situation described by Blair (1960, 152) in which "adult males are antagonistic to other adult males" and "adult females appear to be highly tolerant of other adult females".

The extent to which this system of home ranges limited the number of individuals present on a given area seemed different for each sex. Its effectiveness seemed to be greater among males than among females as the number of resident males remained relatively constant, whereas the number of resident females increased over the same period (Table 1). This was probably because males were able to exert their dominance more effectively than females through a greater size differential between residents and non-residents. The former, with a mean snout-to-vent length of 73 mm, were significantly larger ($t_{26df} = 6.47$; $P < 0.001$) than the latter, with a mean snout-to-vent length of 62 mm. Among females this size difference, although statistically significant ($t_{36df} = 2.63$; $P < 0.02$) was not as great, 64 versus 59. Furthermore, resident males threatened other males wherever encountered; this contrasted with females which threatened other females mainly around favoured sunning spots. Consequently, it probably was more difficult for a male to enter the resident population than a female. This could explain the unequal sex ratio seen in this population (Table 1), assuming that non-resident individuals were more subject than residents to mortality.

Table 3. Snout-vent lengths and percentages of wall lizards having experienced caudal autotomy

Year	Males		Females		Total	Snout-vent length			
						Males		Females	
	No.	% with autotomy	No.	% with autotomy		mean	standard error	mean	standard error
1967	20	25	36	39	56	70.7	1.1	63.2	0.7
1969	11	73	32	56	43	68.9	0.8	60.8	0.1
1971	12	58	33	64	45	68.2	2.2	57.3	1.7

The possession of a territory ought to increase an individual's chances of survival through securing for it a familiar foraging area as well as familiar escape cover. The survival rate, over a two-year period, among residents (Table 1) was relatively high; the weighted mean survival for males was 39 percent, and for females, 26 percent. By contrast, no marked individuals in the non-resident category were subsequently found in possession of a territory on the study area or its immediate surroundings. This suggests a much lower survival rate among the non-resident cohort. Increased survival among those individuals possessing a territory should be reflected in a greater mean age, and hence a greater mean size, than among lizards not so established. As a group both resident males and females were indeed significantly larger than their non-resident counterparts.

This population of wall lizards appears to have been subjected to heavy predation pressure from feral house cats, which were observed stalking, killing, and eating lizards on numerous occasion. Evidence based on incidence of readily recognizable caudal autotomy among these lizards, usually evidence of an encounter with a predator, suggests that predation pressure from cats had increased since 1967 (Table 3). In spite of this apparent rise in predation pressure, the resident lizard population continued to grow, mainly through increased numbers of resident females. Additional evidence of increased predation comes from the age structure of the population which, based on mean snout-to-vent lengths, has changed over the same period of time (Table 3).

The mean lengths of both males and females declined over this period suggesting a population of younger age structure and one in which the turnover rate may have increased. With this decline in mean lengths, the difference in body size between resident and non-resident females, at least, also declined. Since the ability to dominate other lizards seemed largely a function of size (most dominant females averaged 68 mm, snout-to-vent, whereas less dominant residents averaged 62.5 mm) an equalization of size could result in an equalization of dominance levels and therefore a greater opportunity for additional lizards to enter the breeding population. In this manner the population may have increased.

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