TERRITORIAL BEHAVIOUR IN THE WALL LIZARD LACERTA MURALIS

By

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Some Wall Lizards of the species Lacerta muralis and L. sicula were released in 1960 in a walled enclosure some 25 feet square in my garden. Most remained there, but an occasional specimen of Lacerta muralis, which is a better climber than L. sicula, has managed to negotiate the overhanging edge of the wall and escape. One such specimen, a male L. m. brüggemanni, took up residence in the spring of 1962 in a small rockery immediately outside the wall, and I allowed him (personal pronouns will be used for ease of reference later) to remain there in the hope that he would stay long enough to provide some observations on a free-living specimen of this species. He actually remained free in the garden until August 1964, since when he has not been seen.

During the winters of 1962/3 and 1963/4 he hibernated under a fairly large rock in the centre of the small rockery (Point "A" in Sketch 1). For two or three weeks after first emerging in spring, he remained near the rock, retiring under it after sunset and during dull weather. As the days became warmer, he commenced a long series of perambulations away from and back to the rock, and it was noticeable from the start that these sallies were rigidly limited to a precise route. This was at first confined to the flat top of the enclosure wall along the east and north sides (Route 1 on the sketch). In early summer 1962, he extended the route by climbing a distance of about 18 inches through a bush on to a fence running parallel with the north wall of the enclosure. This fence is of conventional construction with overlapping vertical boards nailed to two long runners supported at intervals by posts. The posts and runners are on my side of the fence, and the lizard invariably climbed up to the higher runner, about 9 inches below the top of the fence, and used it as a runway along the fence. He progressively extended his journeys in both directions along the fence until he had reached both ends (Route 2), but did not descend from the runner at any point other than that immediately adjacent to the enclosure wall where he crossed from the one to the other.

In early June, 1963, an additional extension was made, in that when he reached the east end of the fence he climbed down and ran part of the way along a very low wall bordering the east edge of the lawn. Over the next week or two he gradually extended this route until he had reached the opposite fence at the south end of the low wall (Route 3). By late June he had found his way over this fence and between then and early August, on almost every sunny day when observation was possible, he was seen to make a regular journey along Routes 1, 2 and 3 to disappear into the next garden. Towards late afternoon he would return and retrace the same path back to point "A".



Sketch 1



Sketch 2

One day in early August, 1963, I was surprised to see a strange wall lizard on top of the south wall of the enclosure. This proved to be a female *Lacerta m. muralis*, and I assumed it to be one which escaped from a cage in the house during the summer of 1962. She disappeared into a crack under a loose brick in the wall at point "B", and it was obvious after a few days that this was her normal retiring place for the night. Similar development of routes was observed. The first was along the south wall of the enclosure as far as the small rockery (Route 4). Within a few days, she was seen in company with the male lizard, who started to accompany her along Route 4, which he had not before been seen to use. This accompaniment consisted of keeping close to the female but a little behind her.

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When she stopped, so did he, and when she moved on, he followed. They still retained their individual retiring places at points "A" and "B", and met somewhere along Route 4 in the mornings, the female at such times showing the normal reaction of shaking the front feet up and down.

During the next week or so, the female kept to Route 4, and the male did likewise but with the occasional excursions along Route 1, though no further. By early September, 1963, however, they had mutually developed a new route, leading from the small rockery obliquely across a narrow path to a tall rose-covered trellis (Route 5). This short additional route was probably chosen because at that time of the year the west side of the trellis caught the last rays of the sun, and it became customary for both to climb up into the trellis during the afternoons and bask together. The male, more active at all times than the female, would sometimes go for a walk along Route 1, but always returned after a short while, crossing the small path at exactly the same place each time, to rejoin the female.

By the middle of October, both had disappeared into hibernation, the male presumably under his rock at point "A" (next to which he reappeared the following spring), but the whereabouts of the female were unknown. The small exposed cranny at point "B" did not seem a suitable place for hibernation and examination showed that she was, in fact, not there. When she reappeared next spring, it was inside the enclosure, and she must have climbed down into it to hibernate under the rocks there. After emerging in April, 1964, she remained inside the enclosure for about a week, and was then seen back on the south wall of the enclosure.

During the spring of 1964, both lizards confined themselves to Routes 1 and 4; Route 5 was apparently forgotten. With warmer weather in early summer, they were seen less and less in each other's company, the female still keeping to Routes 1 and 4, but the male once again spending most of his time on Routes 2 and 3. The female was never seen on either of these routes, but one day in July, 1964, was seen on the wall of the house at point "C". The next day she was back on the enclosure wall, and did not seem to leave it again, but from this time on the male, though occasionally seen somewhere on Routes 2 or 3, no longer seemed to return to point "A" at night. If seen late in the afternoon, he was usually heading away from point "A", and the impression was gained that he had established a new retiring place in the next garden.

The last time the male was seen was at the beginning of August, 1964. The female was still around when I went on holiday in the middle of August, but since my return in September has been seen no more.

The main interest of these observations has been the surprising rigidity which the lizards showed in their territorial wanderings. Apart from the two minor aberrations on the part of the female (hibernation in the enclosure and single appearance at point "C"), several hundred sightings of the lizards never once found them anywhere but on one or other of their habitual routes. It would seem that these lizards find their way about their territory entirely by means of such learned routes, and rely very little on any sense of direct orientation. When, for example, the male returned from his trips into the next garden, it could be foreseen that he would finally reach point "A" via Routes 3, 2 and 1, although he could have got there by crossing the lawn in about half the distance. Even the single appearance of the female at point "C" could possibly be put into this picture of remembered routes, since it was immediately next to the door through which she must have originally escaped.

Lizards living in the enclosure showed similar rigidity of movement, each individual maintaining a specific retiring place for long periods and following the same routes day by day, but even though the enclosure is fairly large (some 25 feet square), their movements must have been affected by the overall limitation in area. The observations on the free-living lizards, which as far as I know are unique over such a period of time, showed that the behaviour of the lizards in the enclosure was typical though restricted in space. The free-living lizards followed even more rigid a system of movements, but extended it (in the case of the male) to regular return journeys of well over 120 feet each way.

What also seemed clear was that the choice of route was decided by the facilities available. Having selected their bases at points "A" and "B" (two of the sunniest spots in the garden), the lizards extended their range along routes with certain features in common. These routes were all either along the top of a wall, or along horizontal wooden railings in the fence or trellis. All offered an easy route free from encumbrances, with plenty of cover close to hand from bushes and shrubs but otherwise open to the sun. Open spaces at ground level were almost completely avoided, the only exception being the narrow path between the small rockery and the trellis, and this was always crossed at a fast run.

Feeding took place along the routes, and it almost seemed that one reason for walking the routes was to look for food. Deviations from the route to chase insects were frequent, but rarely exceeded a foot on either side, and were followed by an immediate return to the route proper. Otherwise, the only deviations ever seen were on three occasions when a lizard alarmed by a bird or cat dashed into the nearest cover, and remained there for perhaps 5 to 10 minutes before returning to the route.

The lizards in the enclosure frequently drank from a pond there. The free-living lizards had no water available other than rain and dew. In hot weather, they would readily drink water sprinkled near them, but there was no indication that they ever entered the enclosure to drink or otherwise tried to find water.

Males of Lacerta muralis and L. sicula in the enclosure rarely tolerated each other in close proximity, but one would chase the other away vigorously. It was found in practice that in the 25 feet square area of the enclosure the maximum number of males that could be kept at one time, if constant chasing was to be avoided, was three. Even with this small number, a rough division of territory took some time to achieve, and the introduction of a new male could upset the balance for quite a while. This always surprised me, as local populations of both species in the wild appear to reach much greater concentrations. The system of fixed routes could perhaps provide the explanation. Each lizard, or at least each male, would develop routes which constituted his territory. If a route came to coincide in part with that of another male, in due course the two lizards would meet and a chase would ensue. The dominant lizard would retain the route, the other would have to find another. This would result in a network of routes which might frequently cross each other, but rarely have any lengths in common.

Under certain circumstances, this would enable a number of lizards with otherwise divergent territories to include in them a common local area with some periodic advantage. An obvious example could be a rock face which catches the sun at a certain time of day, or even some local and temporary source of food such as winged ants emerging from a nest or caterpillars dropping from a tree. This suggestion can be put forward all the more readily because it fits in with many observations of wall lizards of various species in the wild. It is in fact quite normal to find that a given rock or wall is visited by a number of lizards each day at about the same time, and this is often what gives the impression of large local populations. It is exceptional, however, to find two male lizards really close to each other, even though many may be present in a small area.

Since these conclusions were based largely on the behaviour of only two lizards, I have endeavoured to check them against behaviour of wall lizards in the wild. The best opportunities were with Lacerta hispanica and Psammodromus algirus in north-east Spain, and the results confirmed that a given lizard could be seen about the same time each day at precisely the same spot. In three cases (two L. hispanica and one P. algirus) it was possible to work out at least part of a regular individual route by plotting the places in which a recognisable lizard appeared repeatedly. Most significant of all was the possibility of confirming that certain small areas were used regularly by more than one lizard, without their ever coming into close contact. The best-observed example involved three specimens of P. algirus which could be seen on most mornings on a group of isolated rocks on a steep slope facing east. The lizards were easily identifiable as individuals-one had a large scar on the back, one had very distinct dorsolateral stripes, and the third was a particularly large specimen with a re-grown tail. The locality was visited on nine days out of fourteen in August/September, 1962, between 7 and 8.30 in the morning and on six days out of the same fourteen at some time during the afternoon. Out of the nine morning visits, on six occasions all three lizards were seen among the group of rocks, on two occasions two were seen, and on one occasion one. In each instance each lizard was occupying the same individual spot -the scar-backed lizard on top of a large boulder, the bright-striped one on a small flat rock about two feet from the boulder, and the very large specimen in a patch of dead grass at the foot of a bush roughly three feet from both the boulder and the flat stone (see Sketch 2). The lizards were watched from a distance through binoculars and not disturbed. On four occasions the first lizard was seen to approach or leave the boulder, three times along a route leading from the boulder to the south-west and once directly north, passing between the flat rock and the bush. The second lizard was twice seen to arrive on the flat rock from the north-west. The third lizard moved twice into the bush but no route could be worked out. During the afternoon visits, only once was one of the lizards seen in position, this being the large lizard by the bush. The general area was carefully searched on several other afternoon visits, but only once was one of the lizards sighted in another spot. This was when the scar-backed lizard was seen basking on a patch of granulated limestone among low vegetation some 35 feet south-west of the boulder, almost exactly in line with the route it took when leaving and approaching it. No other lizards of any kind were at any time seen within 100 feet of the small group of rocks.

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In another place, some dozen lizards (P. algirus) were present each afternoon in a small area of sand-dunes sloping south-west to sea-level, but as the dunes were fairly thickly covered with bushes and tall grass, it was difficult to locate them without disturbing them. It was, however, noticeable that at the most only one or two lizards were to be found in the same area in the mornings.

SUMMARY.

Close observation of two specimens of *Lacerta muralis* living free in a garden over a period of nearly $2\frac{1}{2}$ years, together with more generalised observation of the habits of wall lizards in captivity and the wild, suggests that in this species and probably in other species of wall lizard, individual territories are developed, not as compact areas but as a system of routes built up over a period and kept to more or less rigidly. Males may tolerate females on their routes and even actively accompany them at times, but may be expected to defend their routes against other males. The footshaking reaction of the females when meeting other lizards suppresses antagonism in the males. The system of routes facilitates greater concentration of lizards in periodically favourable areas than would be possible in more compact territories.

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