HERPETOLOGICAL JOURNAL, Vol. 4, pp.132-135 (1994)

THE 'SURVEY' POSTURE IN WALL LIZARDS, *PODARCIS MURALIS*

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Male, female and juvenile wall lizards *(Podarcis muralis)* observed living on a high, south-facing brick wall in April and August were sometimes (4% of total observation time in adult males) seen immobile, facing downwards in an orientation equivalent to the 'survey' posture of *Anolis* and other Iguanidae. Some aspects of the temporal dynamics of the behaviour were investigated. It was most commonly seen in adult males during August, when there were significant trends for the frequency of the posture to increase towards the base of the wall and for the mean time spent immobile in the posture to be greater than the mean times immobile at other orientations. The 'survey' posture at the middle and higher levels of the wall appeared to be associated with topographical features such as small tufts of vegetation or bricks which stood proud from the remainder. This association could not be tested directly, but fixing a small strip of wood to the wall increased the duration of locomotor pauses and the frequency of 'survey' postures of lizards when they were immediately above it.

INTRODUCTION

Many species of arboreal lizards which have a 'sit-and-wait' foraging strategy, perch on vertical or near-vertical surfaces, such as the trunks of trees, with the longitudinal axis of the body vertical and the head facing downwards. The behaviour is seen particularly commonly in *Anolis* species (Iguanidae), in which it has been called the 'survey' posture (Stamps, 1977).

During a study of the thermoregulatory behaviour of wall lizards {*Podarcis muralis;* Lacertidae) in Italy, it was noticed that the behaviour was sometimes displayed by individuals of this species living on the walls of the city of Lucca. The behaviour has not previously been recorded in Lacertidae, except for a passing reference "... there is scarcely a wall on which these active lizards *(P. muralis)* do not bask or run up and down, often head downwards, in search of insects" (Gadow, 1901). The posture is illustrated (but not described as such) incidentally in a photograph of *P. muralis* by Guttner(1988).

This paper describes some observations on the incidence of the behaviour and gives the results of a simple experiment devised to test the association of 'survey' postures with irregularities on vertical surfaces.

MATERIALS AND METHODS

The city of Lucca, in NW Italy, is surrounded by a massive rampart, 4 km in length, the outer sides of which are near-vertical walls approximately 6.5 m high and faced with small bricks. Wall lizards are abundant on these walls. They were studied at a south-facing part of the wall near the Porta San Pietro; the profile and dimensions of the wall at this site are shown at the right hand side of Fig. 1. The lizards could readily be observed when they were moving on the wall, but not of course, when they disappeared into crevices within it. Sometimes the movements of an individual took it into the grass at the base of the wall. This grass was mown frequently and so provided little cover, but there was a narrow strip of unmown vegetation (mainly annual herbs) immediately adjacent to the wall. Movements off the top of the wall also took place, but these were relatively infrequent. The behaviour of lizards on the wall was recorded using a dictaphone, while individuals were watched though binoculars from distances of 6-10 m, between 1000 and 1600 hr in August 1988 (times are EST, which is about 15 min ahead of solar time at Lucca). Weather conditions were stable, with little cloud; daily maximum shade air temperatures were always greater than 28°C.

The movement pattern of *P. muralis* usually involves an alternation of periods of locomotion with pauses; the latter are of very variable duration (Avery, Mueller, Jones, Smith & Bond, 1987). The orientations of lizards which were stationary for more than 5 s (hereafter referred to simply as 'stationary') were recorded by estimating to the nearest 45° the angle with respect to the vertical of an imaginary line between the middle of the shoulder and pelvic girdles; vertical orientation with the head upwards was defined as 0°. The period of 5 s was arbitrary, and dictated by the practicalities of working in the field without video recording equipment (see also Discussion). The height of a lizard on the wall was easily measured by counting bricks. Heights were recorded in six bands 1 m in width beginning at 0.5-1.5 m. The presence of lizards in the band 0-0.5 m was recorded separately, because the animals were often concentrated there. Lizards in the 180° orientation (in reality between about 157.5 and 202.5°) were considered to be in the 'survey' posture. Lizards were initially

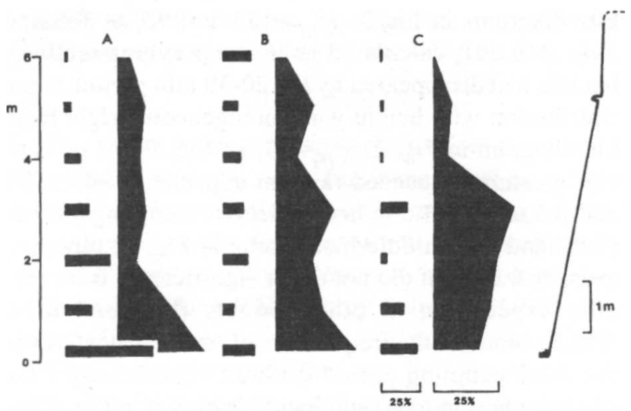

FIG. 1. Kite diagram showing relative frequencies of periods stationary for more than 5 s at different heights on the wall by (A) adult male, (B) adult female and (C) juvenile lizards in August. Horizontal histograms to the left of each kite diagram show the percentage of periods stationary at each height in the 'survey' posture. Note that the width of the lowest sampling band (0-0.5 m) is one half that of the remainder. A profile of the wall is shown at the right hand side of the Figure.

selected at random, and their behaviour (duration of time moving, duration of time stationary when this was >5 s, orientation when stationary, height) recorded until they disappeared from view. Sequences lasting less than 10 min were discarded; the longest continuous sequence of behaviour recorded for any individual was 2.1 hr. After a total of 25.6hr of observations, attention was concentrated exclusively on adult males.

Observations of lizards on the wall were also carried out in April 1989, when the weather was varied and shade air temperatures at mid-day never exceed 21°C. They commenced on the first occasion after 1100 hr on any day (n = 9 days) when the sun reappeared after being obscured by cloud ('start time'). The numbers of lizards which could be counted while stationary along a 200 m length of wall were recorded within the periods 2-5, 7-10 and 20-30 min following each start time; height and orientation of each lizard were also noted.

The impression was gained that 'survey' postures at the middle and near the top of the wall were particularly associated with irregularities on the surface, due either to vegetation (mostly *Callaris spinosa* or small annual weeds) or to bricks which stood slightly proud of their surroundings. In order to test this association, a flat unvegetated area at a height of 3 m, and measuring 60 x 60 cm, was delineated. This was within the area of overlap of the home ranges of two identifiable juvenile lizards. The frequency of periods for which these two lizards were stationary for >5 s within nine subareas measuring 20 x 20 cm (all areas were delineated by marking bricks with a spot of paint) during the period 1000-1200 hr for four days were recorded. A piece of wood measuring 20 x 1 x 1 cm was then glued along the base of the central cell. No observations were made for 7 days to allow the lizards to adapt to the strip of wood. The observations were repeated, for a further four days.

RESULTS

August

Lizards were active over the whole wall for the entire period 1000-1600 hr every day although there was a reduction in the amount of movement observed from 1200-1500 hr. Adult males were recorded as stationary for 86.5% of a total observation period of 33 hr. The frequencies of recorded stationary periods at different heights on the wall were not equal; 56% of stationary periods (irrespective of their duration) were within 1.5 m of the base of the wall (left hand kite diagram in Fig. 1; $X^2_{(5)}=76$ calculated with frequencies at 0-0.5 and 0.5-1.5 m combined and with expected values adjusted for differences in sampling width, n=296, P<0.001). The frequency of the 'survey' posture as a fraction of all periods stationary decreased progressively with increasing height (histograms on the left hand side of Fig. 1; Z=4.5, df=294, P<0.001) and exceeded random expectation of 12.5% i.e. 100/8, since there are eight possible orientations when measured at 45° intervals, at all heights up to 2.5-3.5 m (binomial tests: P<0.001 for 0-0.5 m and 0.5-1.5 m; 0.01<P<0.05 for 2.5-3.5 m). The lizards on average spent longer periods stationary when in the 'survey' posture than at other orientations (Table 1; one-way ANOVA calculated on log-transformed data, $F_{2\ 294}$=7.4, PO.001).

Adult females were stationary for 76.5% of a total observation time of 7.5 hr. They showed significant excess of stationary periods within 1.5 m of the base of the wall (44%; middle kite diagram in Fig. 1; $X^2_{(5)}=39$, n=61, P<0.001, calculated as above). Apparent peaks near the middle and the top of the wall were not significant (binomial tests, P<.05). There was no apparent trend in the frequency of the 'survey' posture with height, although the frequency at 0-0.5 m exceeded random expectation (middle histogram in Fig. 1; binomial test, 0.01<$P<0.05$).

Juveniles were stationary for only 61.4% of a total observation time of 8.3 hr. Stationary periods were

Orientation	n	Frequency (%) observed	expected	Mean duration (s)	CV (%)
180° ('survey')	108	36.5	12.5	293.9	67.3
135° and 225°	68	23.0	25.0	175.2	76.4
other	120	40.5	62.5	137.9	54.3

TABLE 1. Orientation of adult male lizards while stationary for more than 5 s on the wall in August.

concentrated at the middle of the wall; 36.5% were within the band 2.5-3.5 m (right hand kite diagram of Fig. 1; $x^2_{(4)}$ =63, *n*=82, P<0.00l, calculated as above except that frequencies for the top two bands were combined because of small sample sizes). Frequency of' survey' postures exceeded random expectation at 0-0.5, 0.5-1.5 and 2.5-3.5 m (histograms on the right hand side of Fig. 1; binomial tests, $0.05<P<0.1$, $0.01<P<0.05$ and $P<0.1$ respectively). 'Survey' postures were significantly lower than random expectation at the remaining four heights (binomial tests, $P<0.05$ in all cases).

April

The activity patterns of lizards during April were very different from those in August, since the amount of movement depended on weather conditions. The entire height of the wall was utilised during long periods of continuous sunshine, as in August. Activity ceased when the sun was obscured by thick cloud. When overcast periods occurred after earlier sunshine, many lizards retreated into the vegetation at the base of the wall, re-emerging to bask if the sun reappeared. The kite diagram in Fig. 2 shows the distribution of lizards recorded as stationary when they were first observed at periods from 2-5, 7-10 and 20-30 min after the sun had begun to shine following a cloudy period between 1100-1200 nr. Individual frequency distributions for adult males, adult females or juveniles within any of the three sampling periods did not differ significantly (x^2 tests) and so the data for all lizards were pooled. There were significant concentrations of lizards in the lowest 1.5 m of the wall 2-5 and 7-10 min after the sun had begun shining (left hand and middle kite diagrams in Fig 2; $x^2_{(5)}$ =123 and 95, *n*=345 and 298, P<0.001, calculated as in the previous section), but this had disappeared by the 20-30 min period, when distribution with height was homogeneous (right hand kite diagram in Fig. 2; $x^2_{(5)}$=8.3, *n*=406, P>0.1). 'Survey' postures exceeded random expectation of 12.5% at 0-0.5 and 0.5-1.5 m in the first two sampling periods (left hand and middle histograms in Fig. 2; binomial tests, *P<0.05)* but did not differ significantly from random expectation at other heights (binomial tests, *P>0.5)* None of the frequencies of 'survey' postures in the third sampling period differed significantly from random expectation (right hand histogram in Fig. 2; binomial tests, P>0.05).

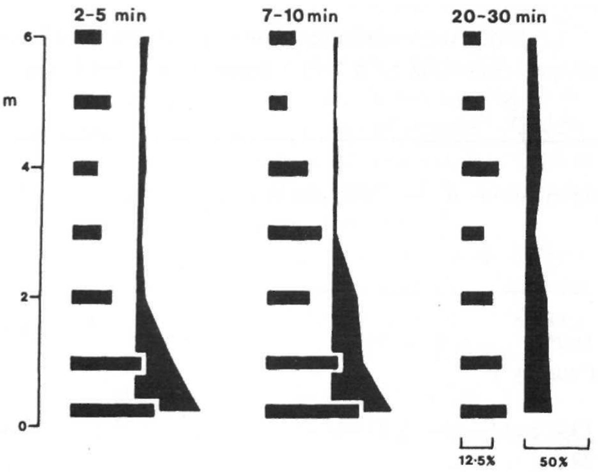

FIG. 2. Kite diagrams showing relative frequencies of periods stationary for more than 5 s at different heights on the wall by all lizards in April, 2-5 min (left hand kite), 7-10 min (middle kite) and 20-30 min (right hand kite) after the end of a cloudy interval. Horizontal histograms to the left of each kite as in Fig. 1.

The Relationship of 'Survey' postures to Surface irregularities: A Simple Experiment

The distribution of stationary periods by two juvenile lizards within nine equal sub-areas ('cells') of the study space was homogeneous (left hand box in Fig. 3, bold numbers; $x^2_{(8)}$=5.5, *n*=181, *P>0.1).* None of the frequencies of 'survey' orientations differed from random expectation of 12.5% (left hand box in Fig. 3, small numbers; binomial tests, *P>0.05* in all cases). The durations of periods stationary did not vary between cells (overall mean= 104.3 s; one-way ANOVA calculated on log-transformed data, $F_{8,103}$=1.22, *P>0.*1). Placing a wooden strip along the lower edge of the central cell, however, resulted in a significant excess in the number of periods stationary within this cell compared with the remainder (right hand box in Fig. 3, bold numbers; $x^2_{(8)}$=25.9, *n*=180, P<0.01). Frequencies of orientations did not differ from random expectation (right hand box in Fig. 3, small numbers; binomial tests, *P>0.05)* except in the cell immediately above the wooden strip (31.6%; binomial test, 0.01<P<0.05). The mean duration of stationary periods was significantly greater in the central cell (142.5 s; one-way ANOVA calculated on log-transformed data and S-N-K test, P<0.05); values in the remaining cells were homogeneous ($F_{7,135}$=1.03, *P>0.1)* and did not differ

10 **20**	8 **25**	18 **17**
17 **25**	11 **23**	4 **18**
19 **16**	21 **15**	16 **22**

17 **21**	16 **24**	18 **24**
6 **14**	32 **38**	20 **17**
8 **14**	17 **12**	6 **16**

FIG. 3. Large numbers: stationary periods observed over four days between 1000-1200 hr by two juvenile lizards in nine equal cells measuring 20 x 20 cm. Smaller numbers: frequency (%) of 'survey' postures in each cell. The two boxes show data obtained before (left) and after (right) a strip of wood was glued to the wall along the base of the central cell.

significantly from those recorded when the wooden strip was not present (Mann Witney *U*-test, P>0.1).

DISCUSSION

One of the major problems which arises in a study of this kind is semantic. Any functional label assigned to a specific behaviour may at best be misleading, at worst subsequently shown to be incorrect. This problem has been of long-standing concern in ethology (e.g. Tinbergen, 1951; see DeCourcy & Jenssen (1994) for a recent discussion in relation to lizard social interactions). 'Survey posture' is a case in point: it has been used as a label here because of the obvious analogy with the well-known similar behaviour of *Anolis.* In many instances, the function of the behaviour in *P. muralis* may be at least as much concerned with thermoregulation as with detection of prey, predators or conspecifics. Operationally, these individual functions would be very difficult to separate

All the circumstantial evidence points to the 'survey' posture in *P. muralis* as being partly a means to scan horizontal surfaces for potential prey, as in *Anolis* (Stamps, 1977). There is not an equivalent posture in which the lizards look upwards; no increase in either the frequency or duration of 0° orientations was seen in lizards beneath the experimental wooden strip (Fig. 3). Nor were such postures seen beneath the ledge at the top of the wall (although wall lizards tended to avoid this because many geckos, *Tarentola mauritanica,* spent the day there). The 'survey' posture is clearly equivalent to the 'scan' posture which *P. muralis* adopt at the edges of horizontal surfaces (Avery, Basker & Corti, 1993), but is less frequent. Individuals in many populations do not appear to adopt 'survey' postures at all, for example those living in scrub environments in the vicinity of Lucca (unpublished observations) or on the walls of Mont Orgueil Castle in Jersey (unpublished observations), which is near the northern limit of the distribution of the species (Perkins & Avery, 1989) and so may have comparatively low densitites of potential invertebrate prey.

The 'survey' posture as described here was not a major component of the behaviour of *P. muralis* on the wall at Lucca. Even in the situation in which it was recorded most frequently - in adult males in August - a simple calculation from the data shown at the left hand side of Fig. 1 and in Table 1 shows that it accounted for only 4% of the total time between 1000 and 1600 hr during which observations were made. In this respect it contrasts with 'survey' behaviour in *Anolis* and other Iguanidae, which may occupy a high fraction of an individual's time. *Anolis conspersus,* for example, spent 70% of the period for which they were observed in the 'survey' posture (Avery, 1988).

The methods by which the data have been recorded and analysed probably slightly underestimate the total time in the 'survey' posture, because only orientations between about 155 and 205° were included within the category. Lizards with other head-down orientations, or even with the axis of the body horizontal, can turn their heads and look directly downwards. The incidence of these orientations was not recorded because their interpretation would depend on a more detailed knowledge of the visual field and require methods for measuring and recording the orientation of the head relative to the body.

There are a number of questions raised by these data which remain unanswered. One of the most important is the significance of the differences in vertical distribution of adult males, adult females and juveniles in summer (Fig. 1). It can be hypothesized that the base of the wall represents the most favourable environment, because it provides opportunities for finding food, both on the wall and in the vegetation at its base, and that males are most abundant there because they are dominant. This hypothesis has yet to be tested.

ACKNOWLEDGEMENTS

Part of this work was carried out while I held a Small Project Grant from the Society for the Study of Animal Behaviour. I was based at the Amino Field Station of the Dipartimento di Scienze del Comportamento Animale e dell'Uomo, Universita di Pisa, thanks to the hospitality of Professor F. Papi. I also thank Professor Augusto Foa for discussion and many practical kindnesses.

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Accepted: 7.3.94