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Territoriality and Resource Defence in Wall Lizards *(Podarcis muralis)*

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INTRODUCTION

For territoriality to occur it is generally agreed that the territory must contain some limited and defensible resource which gives the owner a benefit that exceeds the cost of defence. Examples of such resources are food, shelter, oviposition sites, sleeping places and burrows to hide in. In the family Lacertidae, territorial behaviour is comparatively rare /Stamps, 1977/ but it has been reported for Podarcis muralis /Weber, 1957; Boag, 1973/. This study focuses on possible limiting resources within the territory and on the effect of territoriality on male reproductive success in wall lizards.

MATERIAL AND METHODS

During the month of May, 1983 a population of wall lizards /P. muralis/ was studied. They inhabited a south facing stonewall /80 x 4 meters/ 8 km north of Florence, Italy. Lizards were captured with a noose, sexed, weighed and snout-to-vent length /SV/ was measured to the nearest mm. Pieces of coloured tape were attached around the tail-base for individual recognition and photographs of the colour pattern were taken for permanent identification. A grid system was superimposed on the wall, making it possible to determine positions of lizards to an accuracy of 0.5 meters. The positions and behaviour of individual lizards were recorded while slowly walking alongside the wall. Focal individuals were also followed by direct observations lasting 45-150 minutes. All activities, their duration and interactions with other lizards were noted.

Temperature readings were taken, in the sun, on the wall using a thermometer that, when tested in the laboratory, had heating and cooling rates similar to a 5 gram male wall lizard.

The insect distribution along the wall was sampled. Plastic cylinders with an area of 50 cm^2 were coated with a nondrying sticky glue. They were placed at the foot of the wall, at 2.5 meters intervals, in contact with the ground so that both ground dwelling and flying insects would be caught. The traps were collected after 3 days and checked for number, size and genus of caught insects.

RESULTS

The resident population of lizards consisted of 40 individuals: 22 males, 13 females

and 5 juveniles. Some males defended more or less non-overlapping exclusive territories /Fig. 1/. These males were longer /64 ± 4 versus 54 ± 4 mm/ and heavier /7.3 ± 1.6 versus 4.3 ± 1.7 grams/ than the other males which did not defend territories. Territory size was positively correlated with male weight /Fig. 2/. Females were regarded as being reproductive if their size was larger than or equal to 51 mm, since that was the smallest sized female that was seen copulating and laying eggs. Reproductive females also showed site-specific behaviour, and each occupied a restricted area on the wall throughout the study. The number of reproductive females observed on male territories increased with territory size /Fig. 3/. Both territorial and non-territorial males courted females, but of the 40 mating attempts observed, all 18 successful copulations were achieved by territorial males. Females were seen to reject mating attempts from other males by displaying, biting the male or pulling away from him.

Food captured by the insect traps was estimated in terms of mg dry weight using the relationship:

$$\text{Dry weight} = 0.0305 \times \text{Length}^{2.62},$$

where length refers to the total length of each insect measured in mm /Rogers et al., 1976/. Average food supply was then estimated on the different territories. The food distribution on the wall showed no relationship to territory size. Highest daily food consumption is known for P. muralis /Avery, 1978; formula 5/. Calculating the food demand of the biggest lizard /9 grams/, an area of less than 1 m^2, even on the territory with the lowest food supply, would satisfy its food requirements. Territory sizes on the wall ranged from 14 to 68 m^2, suggesting that there is a superabundance of food on all territories.

Lizards spent most of their time during the day on the wall. Basking behaviour had high priority /Fig. 4/. When temperature on the wall was close to their preferred body temperature /PBT ≙ 34° C, Avery, 1978; Licht et al., 1969/, lizards spent up to 95% of their time basking. Some spots were used more often than others for basking and interactions and displacements of one lizard by another were seen frequently at these places.

DISCUSSION

The two resources most often proposed as objectives of defence within a territory are food and mates /Stamps, 1977/. For P. muralis, food supply was plentiful, and therefore probably not a limited resource defended within a territory /see also Avery, 1978/. But, by defending a territory a male gets exclusive access to females, since females never copulate with non-territorial males. Whatever resources territorial males might offer to females, food may be unimportant since it is superabundant on the wall.

The effect of body temperature on the physiology and behaviour of reptiles is well known. Examples range from its influence on growth rate and egg production, to effects on movement speed and predation success /Huey, 1982/. We also know that basking has high priority in this species; individual wall lizards prefer certain basking places and interact around them intensively.

This makes it plausible to suggest an important resource which is defended by the lizards: good basking places or "hot spots" /see also Magnuson et al., 1979/. A good basking place can be a stone that is either darker, sticking out or situated at such an angle that it is exposed to sunlight earlier in the morning or later in the afternoon.

Thus, it will also accumulate more heat during the day. By controlling such a good basking site, a male lizard can reach the body temperature at which he functions most efficiently in a shorter time, and therefore can be active for a longer period of the day. This is crucial, especially early in spring, when time is required for territorial defence and courtship. Furthermore, ambient temperature is lower at this time of the year, and in the absence of a good basking site, it may be difficult for a lizard to achieve and maintain PBT.

By choosing to stay with a territorial male a female lizard also obtains the benefit of a good basking place. Thus a male's ability to defend a big territory, containing many "hot spots", will have a direct impact on his reproductive success.

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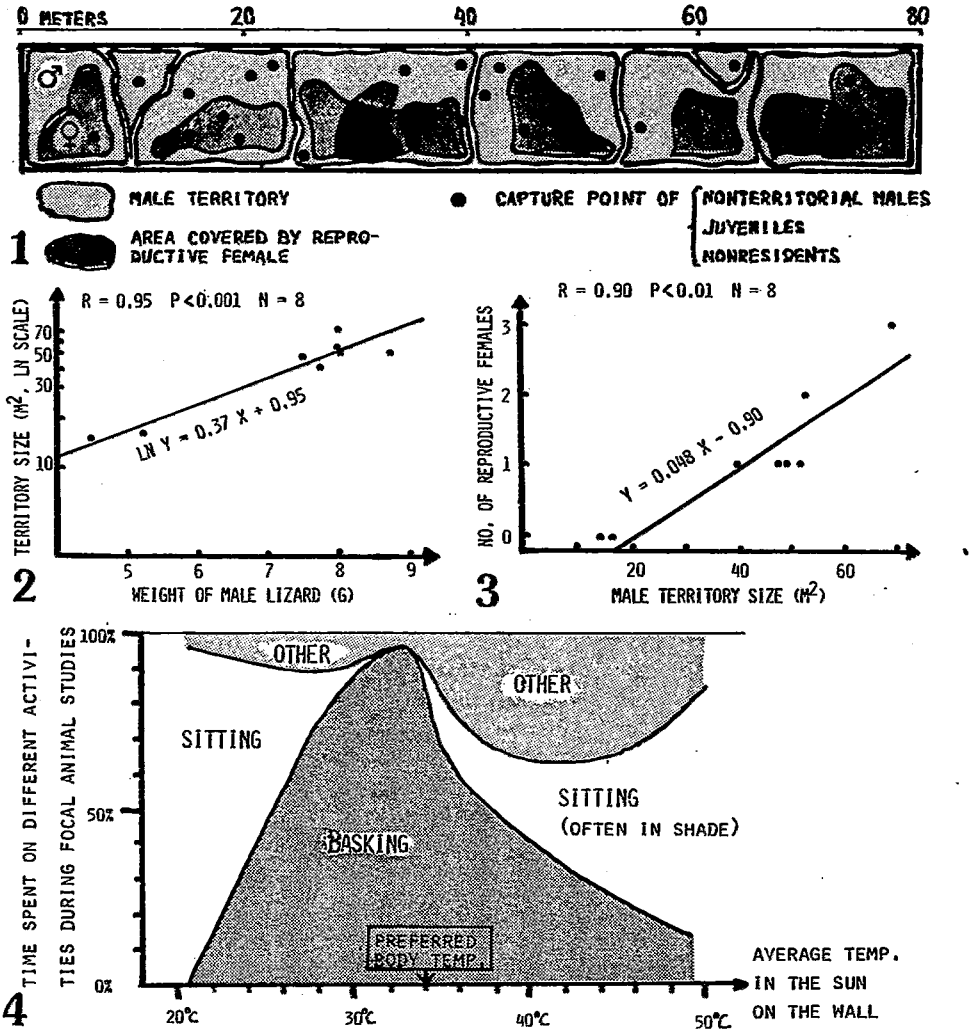

Fig. 1: Spatial relationships amongst the lizards on the wall. Fig. 2: The relationship between weight and territory size in male wall lizards. Fig. 3: The relationship between male territory size and number of reproductive females within his territory. Fig. 4 Time spent on different activities, during focal animal studies, at different temperatures on the wall. Based on 21 focal animal observations.