HERPETOLOGICAL JOURNAL, Vol. 3, pp. 136-139 (1993)

THE RELATIONSHIP BETWEEN DISTURBANCE, RESPIRATION RATE AND FEEDING IN COMMON LIZARDS (*LACERTA VIVIPARA*)

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(Accepted 24.3.93)

ABSTRACT

Slightly disturbing captive common lizards, *Lacerta vivipara*, by movement and noise while they are basking in laboratory arenas resulted in an increase in respiration frequency (R_f) and a decrease in the probability that a lizard would respond to the introduction of a potential prey item. Two categories of prey (crickets and mealworms) were presented at three locations defined in relation to the snout of a lizard; there were clear negative correlations between R_f and probability of feeding in all cases. Respiration frequency can thus be used as a means for determining whether a lizard in a feeding trial has been diverted by extraneous stimuli. This is important in investigations of foraging efficiency in relation to perceptual fields and movement patterns, in which it is necessary to know that experimental animals have not been diverted in this way.

INTRODUCTION

This paper is part of a programme designed to investigate pause-travel movement (Andersson, 1981) and its relation to perceptual fields in lizards (see Avery, Mueller, Jones, Smith & Bond, 1987 and Cowlishaw & Avery, 1991, for background information on pause-travel movement in Lacertidae). However, there are several factors which may potentially confound experimental hypothesis testing, especially on relationships between movement patterns and food distribution. One of the most important is the qualitative observation that lizards in both the field and the laboratory are easily diverted by extraneous stimuli, especially those caused by movements of the experimenter, reducing responsiveness to potential prey (Avery & Mynott, 1990). It is important to have some check that an animal in an experimental feeding trial is not diverted in this way. One potential method is to make use of the fact that the respiration frequency (R_f), which is readily observed from ventilatory movements of the anterior thorax (Milsom, 1984), often increases in response to external stimuli; the analysis of feeding trials can be confined to those trials in which R_f has not increased to a level above the undisturbed range. This requires an understanding of the relationship between R_f and the probability that responsiveness to prey will be reduced. The experiments described here investigate this relationship.

MATERIALS AND METHODS

LIZARDS AND FEEDING TRIALS

Fifteen adult male common lizards, *Lacerta vivipara* Jacquin (mass 3-4 g, snout-vent length (SVL) 46-49 mm), were housed individually in open-topped cages measuring 60 x 45 x 10 cm and maintained as described by Avery & Mynott (1990). The cages were floored with plywood. Each cage contained a scale ruled in cm along two edges and a protractor placed horizontally near one edge. Screens were placed in such a way that only a small part of the experimenter's face was visible to each lizard.

Feeding trials involved dropping an item of prey through a metal tube, only the lower tip of which, at a height of 30 cm, was visible to the lizard. The position at which the prey fell was recorded; the horizontal distance from the snout of the lizard was estimated using the scales at the edges of the cage, and the angle from the longitudinal axis of the lizard at the snout estimated by comparison with the protractor. Trials using a dummy lizard showed that distances could be estimated with an accuracy of ±4 mm, angle with an accuracy of ±8°. Because the lizards were not exactly the same size, distances were standardised for each lizard to SVL. Prey were presented on a schedule which was randomised for distance and angle (within the limits with which it could be placed accurately) to prevent a lizard associating any particular place with food. The reponse of each was recorded for 10 s after the presentation of an item of prey. All potential prey items were preweighed and only those whose mass relative to that of the lizard lay within the range 0.01-0.02 were used, since *L. vivipara* respond readily to prey in this size range, capturing and swallowing them rapidly (Avery & Mynott, 1990). If the prey were approached the trial was scored as a success, if not as a failure. No lizard was presented with more than two items of prey on any day. The capture probability for any kind of prey at any distance and orientation was defined as the proportion approached (it was only very rarely that a lizard approached an item of prey and then failed to capture it), summed for all lizards. The prey were either live crickets (*Acheta domestica*) or mealworms (larvae of the beetle *Tenebrio molitor*).

RESPIRATION FREQUENCY

Respiration frequency of lizards in the laboratory was determined by measuring the Doppler shift of a 25 kHz ultrasonic signal produced by movement of the body wall caused by the contractions of thoracic muscles and consequent movements of anterior ribs which power ventilation. The signal generator and receiver were placed diagonally above the basking site (Fig. 1). The technique can only be used successfully if the lizard is otherwise not moving (Avery & D'Eath, 1986; Avery & Mynott, 1990). If a lizard is disturbed, even only slightly, it becomes vigilant and tends to look upwards, and R_f usually rises; the probability that it will then respond to the presence of prey is reduced. A variable R_f was achieved by disturbing the lizard immediately prior to the presentation of prey. Slight disturbance involved slow movement of the experimenter's hands within sight of the lizard (by placing them above the screen used during food presentation), sometimes accompanied by a soft noise. A greater degree of disturbance was achieved by more rapid movements, sometimes accompanied by louder noises; occasions involving this level of disturbance were separated by at least one week. Each prey item was introduced during the period between 5 and 10 s following the disturbance, and the R_f recorded as the number of ventilatory movements from 1 s following the disturbance to the time of food presentation (i.e. a period of 4-9 s; further measurement of R_f was impossible because of the extraneous signal due to movement by the experimenter, the prey and the lizard). The R_f of control lizards which were neither disturbed nor fed but in which the experimenter's hands were moved behind the screen was measured over periods of 9 s, and of totally undisturbed lizards over periods of 3 min. The R_f of three adult male lizards in the field was also determined over 3 min periods by observing lizards which had been basking on warm mornings for more than 15 min through a telescope from distances of more than 8 m, and counting the number of thoracic movements using a stopwatch to determine the overall time.

BODY TEMPERATURES

The cages containing experimental lizards were maintained in a room at 18-21°C. A 60 W tungsten bulb, oriented diagonally above the wooden floor of the cage and shone through a metal funnel with a cardboard tube so that a pool of light and heat radiation was confined to a small patch (Fig. 1), was switched on for 2 hr each morning to enable the animals to thermoregulate. Prey were presented at times when body temperatures were in the range 30.5-33.0°C, which is within the activity temperature range of the species (Jones & Avery, 1989). This was monitored by placing an infra-red video camera immediately above the basking site, enabling body temperatures to be recorded at regular intervals (Jones & Avery, 1989). Care was taken to ensure that the image of the lizard was not obscured by the cardboard tube (Fig. 1).

RESULTS

The R_f of undisturbed experimental lizards had a mean value of 30.2 min^{-1} ($n=100$, SD=4.46, range=21.3-40.2). The mean R_f values for control lizards (quiet movement of the experimenter behind the screen and with no presentation of food) and of basking lizards in the field were similar (controls, $\bar{x}=29.1$ min^{-1}, $n=100$, SD=4.81, $t=1.69$, $P>0.5$: field, $\bar{x}=28.6$, n=30, SD=5.86, $t=1.39$, $P>0.1$). Differences between individual lizards were not significant in either experimentais, controls, undisturbed lizards or the field (one-way ANOVA, $P>0.1$ in all four cases) and so data for individuals have been pooled in all subsequent analyses. Although this procedure may have violated the assumptions of independence of observations, the results are sufficiently clear cut to support the conclusions and the statistical tests are included to give an approximation of significance levels.

Capture probabilities were recorded for both crickets and mealworms when dropped 0.5 SVL (equivalent to 2-3 cm) and 2 SVL in front of the tip of the snout, and 0.5 SVL behind the snout on an imaginary line subtending an angle of 150° to the forward extrapolation of the longitudinal axis of the body (Fig. 1). The relationships between capture probabilities for these three positions and R_f grouped in increments of 5 min^{-1} are shown in Fig. 2. Each data point represents a capture probability determined from a total of between 20 and 45 presentations. In no case was there any significant difference between capture probabilities at R_f values in increments of 5 min^{-1} within the normal range for undisturbed lizards, i.e. 20-40 min^{-1} (Kruskal-Wallis tests, $P>0.1$ in all six cases). Above $R_f=35$-40 min^{-1}, however, there was for both prey types and in all three prey positions a progressive decrease in capture probabilities with increasing R_f (Kruskal-Wallis tests treating values for $R_f=20$-40 min^{-1} as single pooled subsamples and with probabilities for $R_f>65$ min^{-1} ignored since almost all were zero; $P<0.001$ in all six cases). with very high levels of disturbance

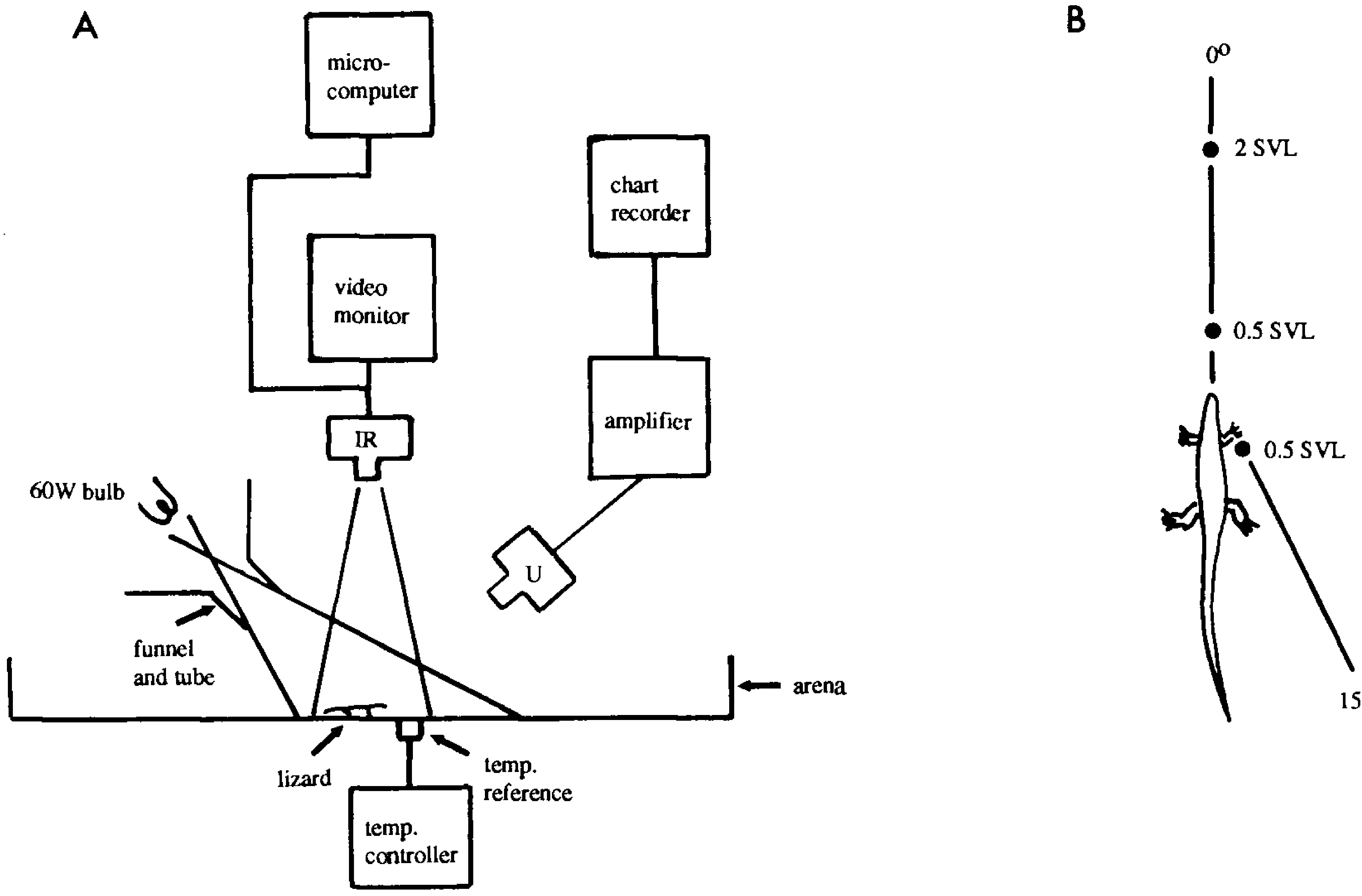

Fig. 1. A. Diagram of experimental apparatus. IR = infra-red camera, U = ultrasound generator and receiver. B. Positions at which food was presented in relation to the snout of an experimental animal.

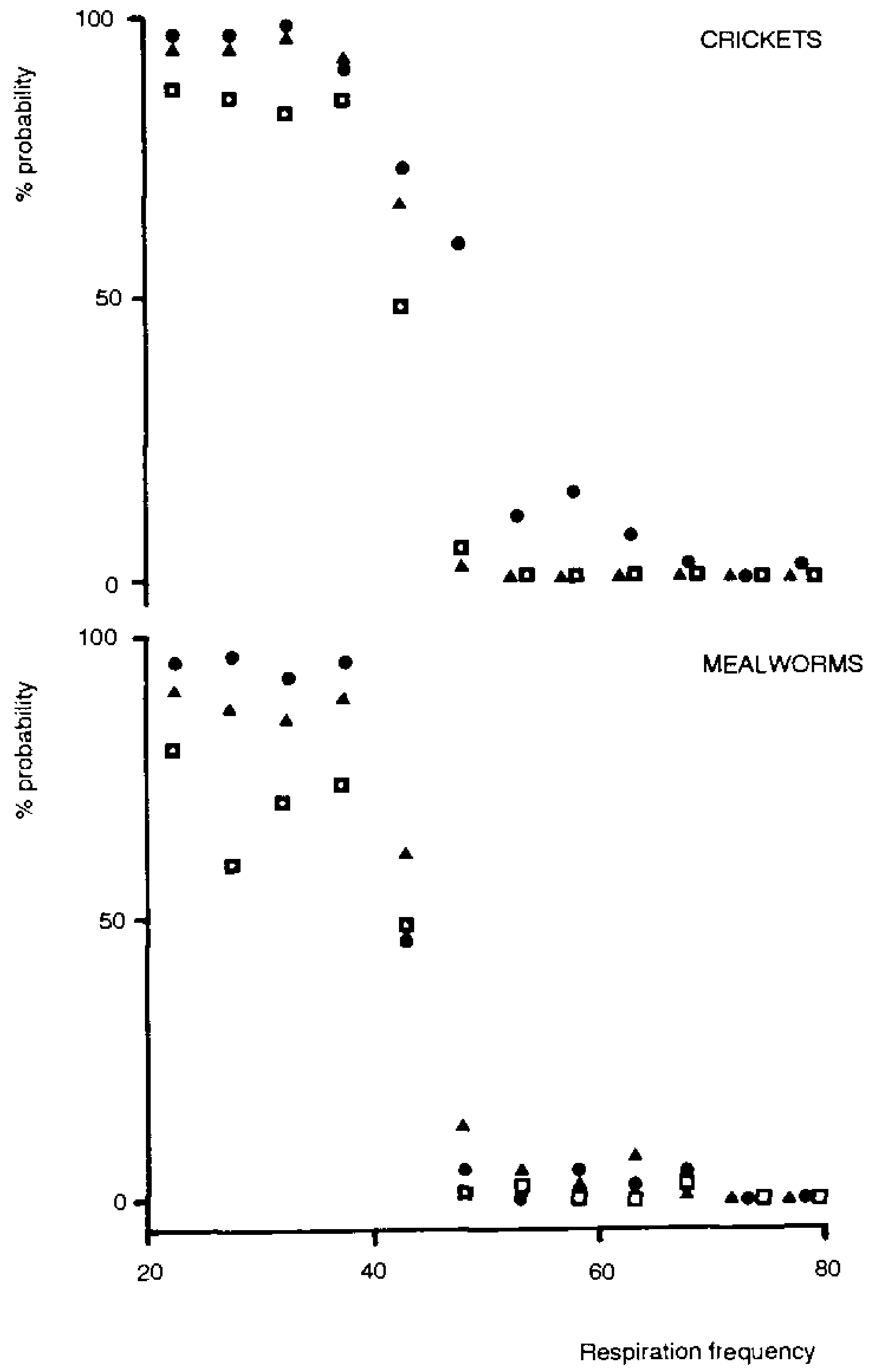

Fig. 2. Capture probabilities for crickets (upper graph) and mealworms (lower graph) presented 0.5 SVL in front of lizards (circles), 2 SVL in front of lizards (triangles) and 0.5 SVL along a line subtending an angle of 150° to the forward extrapolation of the longitudinal axis of the body (squares).

there was a change in the nature of respiratory movements, the pattern switching to rapid (R_f> 100 min^{-1}) shallow breaths; the lizards never fed when breathing in this way.

The capture probabilities for prey presented directly in front of lizards were in almost all cases lower at 2 SVL than at 0.5 SVL for both crickets and mealworms (Wilcoxon signed-rank tests, with the same conditions as for the Kruskal-Wallis tests above, $P<0.01$ in both cases). There were no significant differences in capture probabilities for either kind of prey, however, between prey at 0.5 SVL directly in front of lizards and prey at 0.5 SVL at 150° (Wilcoxon signed-rank tests, with the same conditions as above, $P>0.1$ in both cases).

DISCUSSION

The data show that disturbance by the experimenter which results in an increase in R_f decreases the probability that a *L. vivipara* will successfully capture a cricket or mealworm which has been placed at a distance and orientation at which it would normally be eaten. The mechanism for this effect is not known. It is likely, however, that the lizard is diverted from feeding by additional sensory input. For example, a hierarchy of tectal filters for different movement stimuli have been described for toads (Saton & Shiraishi, 1991), and a similar system may operate in lizards.

Respiration frequency can be used as a means for identifying occasions when an individual lizard has been diverted in this way; as noted in the Introduction, this can be of practical importance in feeding trials. Such trials are used extensively in experiments on the relationships between the location of prey and the probability of feeding, which are important in analysing the significance of pauses in lizard locomotion (Avery, in preparation). An alternative solution to the problem of "diversion" would be to automate the food presentation. This would be feasible if the food were non-living, but *L. vivipara*, like many other lower vertebrates, will normally only respond to moving (which effectively means living) prey because the central neural mechanisms involved in feeding include movement receptors (Ewert, 1985; Saton & Shiraishi, 1991; data relating to toads). Presentation of living prey is difficult to automate.

Does the diverting effect wane with time, i.e. does a lizard habituate to the stimulus and the rise in R_f decrease with repeated exposure? It is a major criticism of this study that the possibility could not be investigated rigorously, because the disturbance could not be accurately quantified. Plotting the sequential R_f values for each individual lizard for stimuli that were judged subjectively to be equivalent, revealed no trend for the values to decrease with time. It is assumed, therefore, that habituation did not occur over the timescale of these experiments.

The experiments are artificial in the sense that they were carried out in the laboratory, but the observations of lizards in the field showed that values for resting R_f were the same in both. There is no reason to suppose that "diversion" does not also occur in the field. It is a common observation that the response of a wild *L. vivipara* to an approaching human is to watch him intently and to flee if the stimulus encroaches within the species-specific 'escape distance' (Bauwens & Thoen, 1981).

There are no previous studies with which the present data can be directly compared. The use of R_f to monitor any kind of stress in reptiles is novel, and the technique may also have other applications. The resting R_f levels recorded here are almost identical to those reported previously for *L. vivipara* at the activity temperature range (Avery & Mynott, 1990). This is the range of body temperatures within which the lizards usually feed in the field (Avery, 1971); feeding will take place at lower temperatures in the laboratory (Avery & Mynott, 1990; Van Damme, Bauwens & Verheyen, 1991), but this is facilitated by the relative ease of prey capture under captive conditions. It would have been possible to determine the effects of body temperature on the relationships reported in this paper; the primary reason that such studies were not carried out is that R_f falls rapidly with decreasing temperature and becomes so low and erratic that it is difficult to measure accurately over the short timespan between the disturbance and the presentation of food. It was necessary for this to be kept short (maximum 9 s in these experiments) because there is a gradual reduction in R_f towards resting levels after the rise induced by disturbance.

ACKNOWLEDGEMENTS

I am grateful to the Royal Society for a grant which part-funded the purchase of the infra-red camera, and to Dirk Bauwens for the benefit of his usual perceptive comments on a draft of this manuscript. Bill Cooper provided valuable advice on statistical analysis and inferences.

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