- Congdon, J. D. and J. W. Gibbons (1983). Relationships of reproductive characteristics to body size in *Pseudemys scripte*. Herpetologica **39(2)**, 147-151.
- Congdon, J. D. and J. W. Gibbons (1985). Egg components reproductive characteristics of turtles: relationships to body size. Herpetologica **41(2)**, 194-205.
- Ehrenfeld, D. W. (1979). Behaviour associated with nesting. In: Turtles perspectives and research, 417-434. Harless, M. and H. Morlock (eds.). Willey-Interscience.
- Flower, S. S. (1933). Note on the recent reptiles and amphibians of Egypt. Proc. Zool. Soc. Lond. 745-749.
- Geffen, E. (1985). On the biology of the Egyptian tortoise (*Testudo kleinmanni*) in Holot Agur, Israel. M.Sc. thesis, Tel Aviv Univ. (in Hebrew with English summary).
- Geffen, E. and H. Mendelssohn (1988). Home range use and seasonal movements in the Egyptian tortoise (*Testudo kleinmanni*) in the northwestern Negev, Israel. Herpetologica **44(5)**, 354-359.
- Geffen, E. and H. Mendelssohn (1989). Activity patterns and thermoregulatory behaviour of the Egyptian tortoise *Testudo kleinmanni* in Israel. J. Herpetol. 23(4), 404-409.
- Gibbons, J. W. and J. L. Green (1979). X-ray photography: a technique to determine reproductive patterns of freshwater turtles. Herpetologica **35**, 86-89.
- Hailey, A. and N. S. Loumbourdis (1988). Eggsize and shape, clutch dynamics, and reproductive effort in European tortoises. *Can. J. Zool.* 66(8), 1527-1536.
- Iverson, J. B. (1986). A check list with distribution maps of the turtles of the world. Indiana: Paust Printing.

- Landers, I., J., J. A. Garner and W. A. McRae (1980). Reproduction of the Gopher tortoise (*Gopherus polyphemus*), in southwestern Georgia. Herpetologica 36, 353-361.
- Lortet, L. (1987). Observations sur les tortues et paludines du bassin de la Meditérranée. Archiv. Mus. Natur. Lyon. 4, 1-26.
- Loveridge, A. and E. E. Williams (1957). Revision on the African tortoises and turtles of the suborder Cryptodira. *Bull. Mus. Comp. Zool.* **115**, 276-283.
- Mendelssohn, H. (1982). Egyptian tortoise. In: The IUCN Amphihibia-Reptilia red data book, 1, 133-136. Groombridge, B. (ed.), Switzerland, Gland: IUCN.
- Moll, E. O. (1979). Reproductive cycles and adaptations. In: Turtles perspectives and research. 305-331. Harless, M. and H. Morlock (eds.), Willey-Interscience.
- Patterson, R. (1971). The role of urination in egg predator defense in the desert tortoise (*Gopherus agassizii*). Herpetologica 27, 197-199.
- Schleich, H. H. (1989). Merkwalsausbildungen an Landschildkröten in Nordost-Libyen. Herpetozoa 1, 97-108.
- Swingland, I. R. and D. Stubbs (1985). The ecology of the Mediterranean tortoise (*Testudo hermanni*): reproduction. J. Zool. 205, 595-610.
- Turner, F. B., P. A. Medica and C. L. Lyons (1984). Reproduction and survival of the desert tortoise (*Scaptochyles* agassizii) in Ivanpah valley, California. Copeia 4, 811-820.
- Waisel, Y., G. Pollak and Y. Cohen (1982). The ecology of vegetation of Israel. Tel Aviv Univ. Tel Aviv: Sifriat Poalim L.T.D. Publ. House (in Hebrew).

HERPETOLOGICAL JOURNAL, Vol. 1, pp. 577-579 (1991)

SHORT NOTE: VISUAL STIMULI AND SPONTANEOUS LOCOMOTOR PATTERNS OF COMMON LIZARDS, *LACERTA VIVIPARA*

¹G. COWLISHAW AND ²R. A. AVERY

Department of Zoology, The University, Bristol BS8 1UG.

¹Present Address: Anthropology Department, University College, University of London, London WCIE 6BT. ²Author for correspondence.

(Accepted 22.3.90)

ABSTRACT

The movement pattern of adult male *Lacerta vivipara* travelling spontaneously along a wooden-walled channel was similar to the previously measured pattern of animals moving across an open space, comprising an alternation of short (~ 1 s) bursts of locomotion with even shorter (~ 0.1 s) pauses. Changing the structure and appearance of the walls of the channel altered the locomotor pattern. Grass turf separated from the lizards by glass had the greatest effect, causing a decrease in mean burst speed and an increase in mean pause duration. This persisted for 25 trials, suggesting that the response to the visual stimulus presented by turf was investigatory and not merely due to its novelty, whereas the smaller effect seen when the walls were of white card waned with time and so may have been primarily a response to change.

INTRODUCTION AND METHODS

Many species of lizards move in a characteristically discontinuous way, alternating short periods of locomotor activity with short pauses when their limbs are immobile. It was shown by Avery, Mueller, Smith and Bond (1987) that in adult Lacerta vivipara at their active body temperature travelling spontaneously across an open space between two tungsten bulbs used for thermoregulation, the bursts of locomotion had a mean duration of 0.30 s and a mean speed of 14.6cm s⁻¹ (equivalent to 2.9 snout-vent lengths (SVL) s⁻¹), and that the intervening pauses had a mean duration of 0.12 s. These values were consistent in any set of experimental conditions - the coefficients of variation for mean burst speed and mean pause duration, for example, were 52 per cent and 77 per cent respectively.

The functions of the pauses which give the locomotor pattern its appearance of jerkiness are not known. It has been suggested that they might result from physiological constraints, or that they might be an adaptation to increase the probability of perception of potential prey or predators. The experiment reported in this paper investigates the suggestion by Avery *et al.* (1987) that prey detection is important by investigating the effects of a number of novel visual stimuli, some of which are indirectly related to food and others not, on locomotor variables.

The experimental animals were three adult male L. vivipara with intact tails weighing 2.5-3.0g and with snout-vent lengths of approximately 50mm. They were housed under conditions described by Avery et al. (1987) in an arena measuring 180 x 55cm with a 60W tungsten bulb beneath which they could bask at each end. The space between the bulbs at the centre of the arena contained a trackway, 45cm long and 10cm high, initially constructed of wooden blocks. Although the lizards could climb over the wooden blocks and so escape sideways out of the trackway, they rarely did so. In the first experiment the trackway was 20cm in width, in subsequent experiments 10cm in width. The lizards were video filmed whilst running along the trackway, and the tapes analysed, by the methods described in Avery et al. (1987).

Subsequently the wooden blocks were removed and replaced with glass. Grass turf was placed behind the glass and encased in further glass so that the lizards had no access to it; this also ensured that the stimulus was visual and not olfactory. As a control experiment the glass was retained, but the grass turf replaced by wooden blocks. In a further experiment the wooden blocks were replaced by plain white cardboard, providing minimal visual stimulus, in an attempt to separate the effects of stimulus complexity and novelty. Twenty-five sequences of movement were analysed in each of these five sets of conditions: the variables recorded were (a) distance moved during locomotor bursts (b) duration of locomotor bursts and (c) duration of pauses. From these the derived variables burst speed (a/b), overall speed ($\Sigma a / \Sigma b + \Sigma c$)) and pause frequency could be calculated. All speeds are expressed in units SVL s⁻¹.

RESULTS AND DISCUSSION

Locomotor variables for lizards under the two standardising sets of conditions, i.e. when moving along wooden-walled channels 20cm or 10cm in width, are shown in the first two lines of Table 1. None of the variables differed significantly between the two widths: mean burst speed and mean pause duration did not differ significantly from those observed in adult lizards of the same species moving spontaneously across an open space in the laboratory (Avery *et al.*, 1987; *t*-tests, P>0.1 in all cases), although the mean duration of bursts was higher (t = 2.41, P<0.05). This was probably because the wooden walls constrained the movement of the animals so that they had less opportunity to change direction, and so travelled in straighter lines, than when crossing an open space.

Replacing the wooden walls with turf (separated from the lizards by panes of glass) resulted in a marked change in the locomotor pattern (third line of Table 1). Mean pause duration and pause frequency increased, mean burst speed and mean duration of bursts decreased (all except mean pause duration significant at P = 0.05, one-way ANOVA with Student-Neuman-Keuls (SNK) tests).

Values for locomotor variables in lizards moving between walls of glass-fronted wood or plain white card were intermediate between the 'standardising' and the 'turf' conditions (lines 4 and 5 of Table 1). Mean burst speeds were higher, but not significantly different from, the 'turf' condition; mean burst durations and pause frequencies were not significantly

Wood, 20cm width	Mean burst speed (SVL s ⁻¹)		Overall speed (SVL s ⁻¹)		Mean burst duration (s)		Mean pause duration (s)		Mean pause frequency (s ⁻¹)		Pause duration as a percentage of total time
	2.90	41	2.62	48	0.96	73	0.13	115	0.70	93	10.6
Wood, 10cm width	2.78	29	2.53	34	1.14	57	0.15	133	0.63	95	10.2
Turf with glass	1.49 A	45	1.14 B	101	0.64 C	61	0.22	71	1.10 E	68	24.3
Wood with glass	1.83 A	19	1.61 B	31	0.97	52	0.35 D	143	0.71	87	20.2
White card with glass	1.79 A	37	1.76 B	45	0.99	70	0.14	45	0.82	51	14.0

TABLE 1: Variables relating to locomotion of *Lacerta vivipara* under defined experimental conditions. Figures in each column show means followed by their coefficients of variation. Means marked A-E differ significantly from those in the 'wood' condition (one-way ANOVA with SNK tests, P<0.05).

different from those under 'standardising' conditions (one-way ANOVA with SNK tests). Mean pause duration with walls of glass-fronted wood was higher than under any of the other four conditions, however (SNK test, P < 0.05), with a very high coefficient of variation (Table 1). This was probably because lizards were able to see their own reflection in the glass from some angles, and paused for longer to observe it ! (Reflected images were clearer when the glass was backed by wood than by turf or white card).

Short pauses in lizard locomotion might have a physiological explanation, for example they might be due to rapid depletion of the high energy molecule phosphagen or arginine phosphate (AP, see Prestwich, 1988); or they might be functional, relating to the ability of the animal to more successfully perceive prey when it is immobile (as in many birds, see for example Tye, 1989). The relative likelihoods of these different kinds of explanations were discussed by Avery et al. (1987): circumstantial evidence favoured the second class of hypotheses, because mean pause duration increased in the presence of crickets (Acheta domestica), on which the lizards feed avidly. The results shown in Table 1 provide further circumstantial support for such an explanation; they show that a relatively simple visual stimulus (turf) alone can elicit a change in locomotor pattern. It is suggested that this stimulus is associated with potential prey because the invertebrates on which L. vivipara feed (see Avery, 1966) tend to be more abundant in dense vegetation than in open spaces; it therefore elicits an investigatory response, resulting in slower speeds and longer pauses.

It might be argued that the responses shown in Table 1 were due to the novelty of the stimuli. This was tested by comparing mean burst speeds and mean pause durations during the first eight trials and the last eight trials within each condition. The only significant difference was in mean pause duration in trials with white card $(0.19 \pm 0.02, 0.09 \pm 0.02 \text{ s}; t = 3.06, P < 0.01)$. This suggests that the lizards initially responded to the white card because of its novelty, but habituated to it and hence reduced mean pause frequency; whereas in all other conditions they were responding to visual complexity as well as novelty, and the response remained. It is perhaps significant in this context that the mean pause duration in the last eight trials in the 'white card' condition was the lowest recorded in any of the present experiments (c.f. Table 1) - white card provides minimal visual stimulus.

Experiments examining the responses of *L. vivipara* to a potential predator (the snake *Vipera berus*) have

shown that olfactory stimuli can also alter locomotor behaviour. Changes in the proportion of the behaviour category 'no move' occurred in response to both the physical presence of the snake (primarily a visual stimulus) and to a cage in which the snake had recently been housed (an olfactory stimulus). Some of the pauses were of extremely long duration, however, and were interpreted as attempts to avoid detection (Vanderstighelen, 1987).

The experiment reported here does not investigate the possibility of individual differences in behaviour the data from the three lizards have been pooled in compiling Table I. A more detailed investigation should consider the possibility of such variation, however, since it is known to occur in both locomotor patterns (e.g. Garland, 1985; Huey and Dunham, 1987) and foraging behaviour (e.g. Ehlinger, 1989) of many kinds of animals.

REFERENCES

- Avery, R. A. (1966). Food and feeding habits of the common lizard (*Lacerta vivipara*) in the west of England. J. Zool., Lond. 149, 115-121.
- Avery, R. A., Mueller, C. F., Smith, J. A. and Bond, D. J. (1987). The movement patterns of lacertid lizards: speed, gait and pauses in *Lacerta vivipara*. J. Zool., Lond. 211, 47-63.
- Ehlinger, T. J. (1989). Learning and individual variation in bluegill foraging: habitat-specific techniques. *Anim. Behav.* **38**, 643-658.
- Garland, T. J. (1985). Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis. J. Zool., Lond.* 207, 425-439.
- Huey, R. B. and Dunham, A. E. (1987). Repeatability of locomotor performance in natural populations of the lizard *Sceloporus merriami*. *Evolution* **41**, 1116-1120.
- Prestwich, K. N. (1988). The constraints on maximal activity in spiders. II. Limitations imposed by phosphagen depletion and anaerobic metabolism. J. Comp. Physiol. B 158, 449-456.
- Tye, A. (1989). A model of search behaviour for the northern wheatear *Oenanthe oenanthe* (Aves, Turdidae) and other pause-travel predators. *Ethology* **83**, 1-18.
- Vanderstighelen, D. (1987). Responses of the common lizard (Lacerta vivipara) to visual and chemical stimuli of the viper (Vipera berus). In Proceedings of the 4th Ordinary General Meeting, Societas Europaea Herpetologica, 425-428. Van Gelder, J. J., Bergers, P. J. M. and Strijbosch, H. (Eds.). University of Nijmegen: Faculty of Science.