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Evasive behaviour in the cave-cricket, *Troglophilus cavicola*

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ABSTRACT. Cave crickets of the genus *Troglophilus* occur in caves of the Alps and Dinarides generally in wintertime. Most hibernation sites in caves were inclined at more than 60° to the horizontal. The crickets show a striking escape behaviour which is strongly influenced by the inclination of the surface on which they are standing: stimulated adequately, they readily jump from horizontal surfaces, but only rarely from the side walls or roofs of caves. An arena with a tiltable floor was used to quantify this and other behavioural effects in relation to the degree of inclination of the floor, and gave the following results. (a) From 0° to 60° the rate of evasive jumping was inversely related to the steepness of the floor; above 60° jumping was almost completely inhibited. (b) Below 75° more than half the crickets showed a positive thigmotaxis to the arena walls, above 75° this thigmotaxis was much weaker. (c) The effect of blinding was to reduce these levels of thigmotaxis at inclinations lower than 60° and to increase the thigmotactic response at steeper inclinations. (d) Standing orientation was generally upwards at inclinations steeper than 60°; below 45°, the steeper the floor, the greater this upward orientation tendency. (e) If the cricket was standing orientated downwards, evasive jumping was less inhibited on slopes between 15° and 60°.

Key words. Orthoptera, Ensifera, *Troglophilus*, evasive behaviour, inclination, geotaxis, caves.

Introduction

The cave cricket, *Troglophilus cavicola* (Ensifera, Gryllacridoidea), can be found in caves of the Alps and the Dinarides, generally in winter-time (Hölzel, 1955). During the summer the crickets are mainly outside the caves under foliage, old wood, stones, etc. In the caves, hibernating crickets are distributed openly on the side walls and roof, and show either cryptic behaviour (hiding in clefts) or evasive behaviour (moving away or jumping) when disturbed by noise, tactile stimuli or light. That these escape responses are influenced by the inclination of ground on which the crickets are situated is obvious from observing them in caves. Suitably stimulated, they do not jump from cave walls, but do jump from horizontal surfaces such as the floor. This attribute is presumably a useful adaptation for cave-dwelling, preventing falling from the wall. Such inhibition of the jumping reflex is apparently much less developed in locusts and grasshoppers, whose escape behaviour is mainly determined optically.

This paper reports the first investigation of this behaviour in cave crickets. It is concerned mainly with the influence of the inclination of the ground on evasive jumping in *Troglophilus*, but its additional aim is to examine the interrelations of other behaviours also apparently influenced by gravity (Schwartz-

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kopff, 1974). A later study will analyse more precisely the sensory input involved in the inhibition of evasive jumping on steep surfaces.

Materials and Methods

Troglophilus cavicola were caught in caves near Graz, Austria. As no significant differences in the investigated behaviours were found between the sexes or between adults and larvae the results of all stages are aggregated in the analyses reported here.

Experiments were performed in the laboratory in an open-topped rectangular glass arena (45 x 25 x 30 cm) with a flat but rough wooden floor, at an ambient light intensity of about 100 lux and at 20–22°C, from November 1980 to February 1981. The arena and its floor could be inclined from 0° to 120° above the horizontal. Stimulation was provided either as a gentle air-puff blown at the cricket with constant intensity via a syringe and a membrane-pump, or as a touch on the cerci or legs with a metal rod. All such stimulations took place when the cricket was not moving.

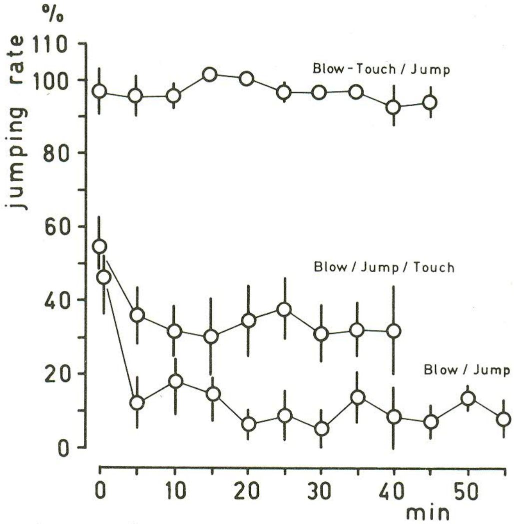

FIG. 1. Habituation in evasive jumping in the cave cricket. Three different modes of stimulation were used: 'Blow/Jump', puff of air alone used to elicit jumping; 'Blow/Jump/Touch', involved the same puff stimulus with the legs or cerci touched with a metal rod immediately after the jump response; 'Blow-Touch/Jump', puff and touch stimuli given simultaneously: 100% response level indicates that each stimulation caused one jump, if more than one jump was elicited, the rate increases to more than 100%. The floor of the arena was horizontal. Bars, standard errors; $n = 2940$ single stimuli on ten individuals.

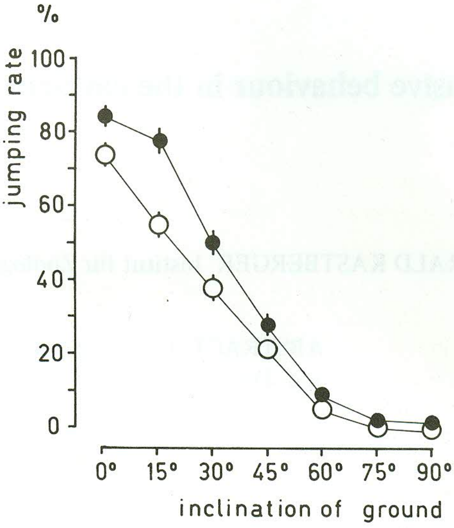

FIG. 2. Dependence of the rate of evasive jumping on the inclination of ground (arena floor). Two different stimulation modes were used: Blow/Jump/Touch (open circles), Blow-Touch/Jump (solid circles); see Fig. 1 legend. Bars, standard errors; $n = 16\,035$ single stimuli on seventy-seven individuals.

Results

Habituation in evasive jumping

Fig. 1 shows the rate of habituation of the jumping response to three stimulation modes when the floor of the arena was horizontal. When stimulation was blowing alone, the jumping rate decreased within 20 min to near zero. When the touch stimulus was given after a jump response to blowing, a lower habituation level occurred, at about a 30% response level. And when blowing and touching were delivered simultaneously, no detectable habituation occurred over an hour of testing.

Influence of floor inclination on evasive jumping

The rate of evasive jumping was markedly dependent upon the inclination of the arena floor (Fig. 2). At 0° a high jumping rate occurred with both stimulus modes used, but even at an inclination of only 15° the response was already significantly inhibited, and by 60°

it was almost totally inhibited. The relationship is approximately linear from 0° to 60°. No significant change occurred in response level over 20 days of repeatedly testing the same individuals.

Influence of floor inclination on thigmotaxis

Thigmotaxis was also studied in the arena. The cricket had a choice of two thigmotactic conditions. It could either be in the centre of the arena without touching the glass walls, even with its antennae or legs (a zero thigmotactic score), or be in contact with the walls (a positive thigmotactic score). The crickets were stimulated by air-puffs and touches, repeatedly every 1–3 min. Before they had been stimulated the crickets were free to move up or down a sloping floor, and locomotor activity was certainly much stronger when the floor was horizontal than when it was at a slope (cf. Fig. 2).

Thigmotactic behaviour was scored only after locomotion had ceased for at least 5 s (generally this was for > 15 s). Stimulation then made the animals change the thigmotactic condition they had chosen, and so prevented them staying at a certain site all the time. Evidently a 50% response level in this system is specific to this particular arena and to the chosen interval between stimulations, but it happened to be the level of response that occurred with the floor horizontal (Fig. 3, 0°), and is thus taken as a standard for comparison.

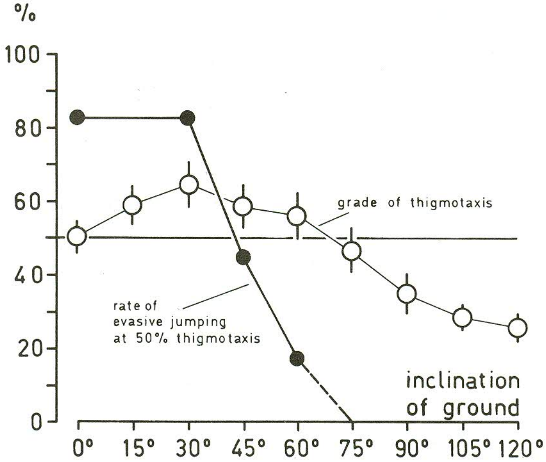

FIG. 3. Influence of the inclination of ground on intensity of thigmotaxis (open circles); see text for criteria. The values for 30°, 90°, 105° and 120° differ significantly ($P < 0.05$) from the value for 0°. Bars, standard errors; $n = 5556$ single stimuli on eleven individuals. Solid symbols, relation between thigmotaxis and evasive jumping, the points representing the rate of evasive jumping at 50% thigmotaxis ($n = 5351$ single stimuli on ten individuals; 15° regression not significant). Ordinate shows per cent positive thigmotaxis or % jumping at 50% positive thigmotaxis.

There was a strong influence of the inclination of the floor on the thigmotactic response. Fig. 3 shows an increase in strength of thigmotaxis between horizontal and 30°, followed by a decline from 30° to about 90°, to a low response level elicited at all steeper slopes. The strength of thigmotaxis was markedly higher than the reference (horizontal) at inclinations up to about 60°, and *lower* at inclinations greater than about 60°.

In addition, at slopes of less than 75°, on which rather high jumping rates occurred, the thigmotactic behaviour correlated positively with the jumping behaviour of the same individuals: the greater the tendency to jump, the stronger the thigmotactic response. If the thigmotactic response levels are standardized at the 50% level in these regressions, a distribution of jumping responsiveness similar to that in Fig. 2 is then revealed (solid circles in Fig. 3).

Influence of floor inclination on geotactic orientation

Geotactic behaviour was also investigated

TABLE 1. Geotaxis (choice of facing direction) in relation to slope of ground in cave-crickets tested in the arena (see also Fig. 4).

Slope of floor	% Orienting (± SE)			*n*
	Down	Side	Up	
15°	25.4 ± 1.8	32.6 ± 2.9	42.1 ± 1.6	12
30°	21.1 ± 2 4	30.4 ± 1.8	48.6 ± 2.5	12
45°	18.4 ± 2.1	25.7 ± 2.9	56.0 ± 4.1	12
60°	18.8 ± 1.7	20.8 ± 2.6	60.5 ± 3.7	10
75°	8.9 ± 3.2	25.1 ± 3.5	66.0 ± 5.6	10
90°	7.2 ± 3.6	24.6 ± 5.0	68.2 ± 5.0	10

n = no. of individuals tested; total number of stimuli = 6096. ‘Up’ refers to animals standing facing between 180° and 120° to a line drawn vertically down sloping floor; ‘Side’, animals facing (L or R) at 120–60° to this line; ‘Down’, animals facing 60–0° to this line.

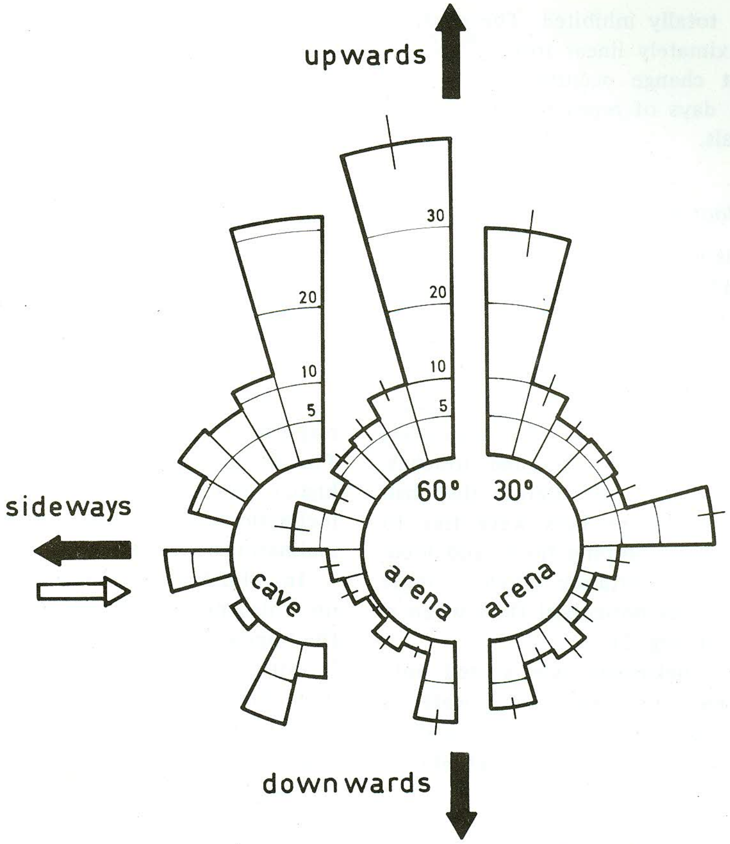

FIG. 4. Detailed distribution of geotactic orientations in the arena at 30° and 60° inclination of the floor (see Table 1) and in caves (see Table 2). Whether the crickets were facing left or right is ignored. Numbers in the columns give the per cent of all observations for that particular radial histogram. Bars, standard errors.

in the arena. Before they were stimulated, the crickets' direction of body axis was observed and classified as facing upwards, sideways or downwards. A clear relation of geotactic orientation to the slope of the floor was revealed (Table 1). At inclinations of 75° and greater, two-thirds of the individuals faced upwards; at 45–60° the majority still faced upwards; but below 30° there was no apparent bias in orientation direction.

Again, the length of interval between the stimuli (at least 15 s) must have influenced the results. However, the distribution of orientations measured in the arena are comparable to those observed on floors and walls of caves at up to 120° inclinations (Table 2).

In the arena, thigmotaxis to the walls influenced the geotactic distribution. This can be seen in Fig. 4 by the pronounced sideways orientation at the 30° floor inclination. If the floor was steeper (e.g. 60°), however, this thigmotactic influence was reduced. Fig. 4 also shows the distribution of geotactic orientations by the crickets observed in caves,

TABLE 2. Geotactic stance in relation to slope of substrate observed in wild crickets in four caves (May 1981).

Slope of ground	n	Overall distribution (%)	% Orienting		
			Down	Side	Up
0–60°	5	6	20	~~30~~ 40	~~50~~ 40
60–120°	56	74	1~~3~~4	1~~4~~3	73
120–180°	15	20	3~~5~~3	2~~5~~7	40

Detailed overall distribution shown in Fig. 4. Observations on seventy-six crickets. Other details as in Table 1.

TABLE 3. The influence of the geotactic orientation of crickets (whether they were standing facing upwards or downwards) on their evasive jumping tendency at different inclinations of the ground, expressed as the percentage difference from the mean overall per cent jumping at each inclination as shown in Fig. 2 (blow-touch/jump).

Crickets' orientation	Slope of floor				
	0°	15°	30°	45°	60°
Downwards		+1.9	+8.3	+5.9	+7.0
Upwards		−2.7	−3.7	−4.0	−3.6
P		< 0.100	< 0.005	< 0.025	< 0.001

P refers to difference between downwards and upwards tendencies. $n = 5409$ observations on twelve crickets.

where the majority (74%) were found on wall sites inclined at 60–120°, on which they were mostly (73%) orientated upwards (see also Table 2).

Influence of geotactic orientation on evasive jumping

Geotactic orientation significantly influenced the rate of evasive jumping (Table 3). When the crickets stood facing upwards on slopes between 15° and 60°, their rate of jumping was about 3–4% less than their average rate on that slope; when facing downwards, it was about 6–8% greater than the average rate (except on 15° slopes). Evidently, if the cricket is orientated downwards, evasive jumping is less inhibited.

Influence of vision at different inclinations

Individuals were first tested under light conditions and then blinded by having their compound eyes and ocelli covered in opaque black enamel. The influence of vision on the thigmotactic behaviour, though slight, is significantly correlated with the inclination of the ground (Fig. 5). Blinding reduced the thigmotactic response on slopes of less than 30°, but increased it on slopes steeper than about 60°.

Jumping in blinded crickets was generally lowered for slopes of less than 60°, and at 0–30° was significantly reduced, to about 15% ($P < 0.005$).

Discussion

Troglophilus cavicola migrates to warm caves to hibernate in October/November. In the caves the crickets are found in the warmest (12–16°C, even in winter) and most humid areas (in condensation zones) farthest from the entry. There they stay openly on the

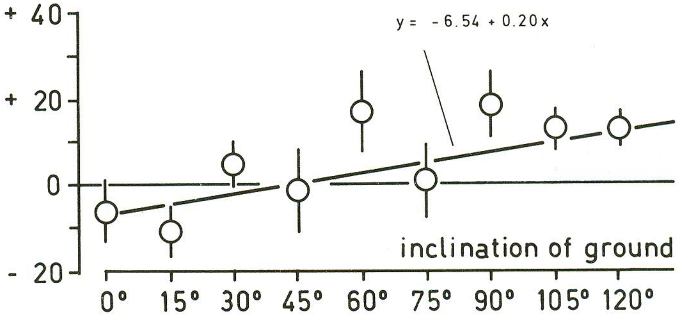

FIG. 5. Influence of vision on thigmotactic behaviour at different floor inclinations. Regression is significantly different from zero ($P < 0.005$, $n = 5550$ single stimuli on eight individuals). Ordinate gives the differences in individual per cent of thigmotaxis between crickets with unenamelled eyes and the same crickets blinded with enamel. The thigmotactic behaviour under enamelled conditions is represented by the zero horizontal line. Bars, standard errors.

walls and roof rather than creep into clefts. They can be found there in hundreds from October to May, even showing courtship and copulatory behaviour.

As already indicated, stimulated gently by touches or air-puffs they move away rather slowly if on the cave wall or roof, but jump evasively when on the flatish cave floor. Evidently, this is an example of stimuli unlocking certain reflexes which are otherwise depressed (Miller, 1974). Similar examples include the steering movements of locusts which appear only in flight (Camhi, 1970), the kicking responses of male crickets which are suppressed during courtship (Huber, 1974), the flight-inhibition reflex which is triggered by tarsal contact in most insects (Fraenkel, 1932; Kraemer & Markl, 1978), and the swimming reflex of water bugs triggered on loss of substrate contact (Dingle, 1961).

Evasive jumping in *Troglophilus* is one reaction in a hierarchy of escape responses elicited by mechanical stimulation of the cerci or legs (but not of the antennae). This hierarchy is similar to the evasive reactions of Tettigoniodea and Grylloidea (Huber, 1974): pre-evasive antennal movements, jerking, defensive kicking, running away, drawing backwards and jumping, as well as hiding in crevices (positive thigmotaxis). Most of these different escape responses of *Troglophilus* fully habituate within 10–20 min if stimulated by air-puffs only. Touches presented after an air-puff result in a much lower level of habituation, and touches presented together with air-puffs totally prevent it (Fig. 1). Touches thus seem to be stimuli causing behavioural arousal (Rowell, 1970; Godden, 1974; Hughes & Mill, 1974; Miller, 1974).

Jumping in locusts, grasshoppers and crickets may not be effected by a stereotyped fixed action pattern, but by labile neural control which is continually adjusted by sensory input (Heitler, 1974; Hoyle, 1975). This conclusion is indicated particularly by the finding that a chordotonal organ located distally in the femur appears to be essential for triggering jumping (Bassler, 1967; Burns, 1974). In the case of *Troglophilus* these findings can be seen in a special light. It is evident that its evasive jumping is multimodally triggered. Besides temperature, humidity and vibration, photo- and thigmotactic factors must be important, but the predominant influence is from the inclination of the ground (geotactic).

Surprisingly, the geotactic orientation of the crickets does not influence the inhibition of their evasive jumping on steeply inclined ground. At more moderate slopes, however, downwards facing crickets – which have to excite the flexors and relax the extensors of their metathoric legs to stabilize the body – jump rather more (*c.* 10% more) than do upwards facing crickets (Table 3).

This finding conflicts with that of Godden (1969) that relaxation of the flexor tibiae is essential for a strong jump. It may be, however, that tarsal receptors are dominantly involved in inhibiting evasive jumping on inclined grounds. As considered by Kraemer & Markl (1978), for jumping to be inhibited it may be sufficient if the body is held stabilized on inclined substrates with any single leg. This point should become clearer when the input relations of gravity reception (see Schwartzkopff, 1974) are investigated in *Troglophilus*; this work is planned for the next paper.

Finally, it can be stated that the complexity of the control of evasive jumping in *Troglophilus* may be interpreted only in the context of all the other behavioural acts which are also influenced by the inclination of ground. For example, it can be said that thigmotaxis and evasive jumping are obviously closely interrelated. Both are strongly influenced by gravity perception as can be seen by two facts. First, jumping rate and thigmotactic behaviour are both dependent on the inclination of ground. Second, the individual deviations in both are strongly correlated at inclinations of less than 75°.

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