

## Mate location in the deathwatch beetle, *Xestobium rufovillosum* De Geer (Anobiidae): orientation to substrate vibrations

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**Abstract.** Deathwatch beetles produce taps, by drumming the head on the substrate, which enable males to locate females. The orientation mechanism used by males was examined experimentally using a mechanical tapper to simulate female replies. When searching for a female, males moved short distances before stopping to tap, tapped only once or twice if they got a reply, and turned frequently. In the absence of replies males moved longer distances before stopping to tap, and turned less. Males did not use tropotaxis during mate location, but exhibited a weak klinokinesis. Their turn angles tended to be larger when a long way from the female, and following a movement away from the female, so that they turned back towards it. However, the mechanism is not efficient as many males studied failed to locate the female. Mechanisms for the evolution of this unusual mate-locating system are discussed in the context of the recently available artificial habitat occupied by deathwatch beetles.

Communication by sound is found in most animal groups, and has been widely studied (e.g. Lewis 1983). Communication using substrate vibrations is less well studied, perhaps because human senses are not well suited to detect them. Nevertheless, seismic communication, as this form of signalling has been termed (Narins 1990), has evolved in diverse organisms such as mole rats (Heth et al. 1987; Rado et al. 1987), kangaroos (Gregory et al. 1986), kangaroo rats (Randall 1989), frogs (Narins 1990), and amongst the arthropods in fiddler crabs (Salmon & Horch 1972), spiders (Rovner & Barth 1981; Schüch & Barth 1985), stoneflies (Plecoptera; Stewart & Maketon 1990), pondskaters and plant sucking bugs (Hemiptera; Wilcox 1972; Ota & Cokl 1991; Hunt et al. 1992), booklice (Psocoptera; Pearman 1928), caterpillars (Lepidoptera; DeVries 1990), and particularly in the social insects, bees, ants and wasps (Hymenoptera; Fuchs 1976; Ishay et al. 1974; Towne 1985) and termites (Isoptera; Howse 1964). The functions of vibrations are equally diverse, including conspecific recognition, territory maintenance, courtship, mate location, and even attraction of symbiotic ants by Lepidopteran

larvae (DeVries 1990). The feature common to all is that production of vibrations advertises the presence of the organism: it may also convey information on its location, species, sex and receptivity.

Recent studies on tapping in the deathwatch beetle have revealed some of the details of this behaviour (Birch & Keenlyside, 1991; Birch & Menendez 1991). Both male and female beetles tap by striking the head against the substrate. An entire 'tapping bout' consists of 4–11 strikes in rapid succession, at a mean frequency of about 10 Hz. Tapping is a means of sexual communication (Birch & Keenlyside 1991): males frequently tap spontaneously, while females tap only in immediate response to a tap. Tapping is a mechanism by which females advertise receptivity, and also appears to aid males in locating them. Males receive information as to the location of a female only when the latter replies to a tap. Upon locating a tapping female, males invariably attempt to copulate (Goulson et al. 1993).

We hypothesize that there are three possible mechanisms of male orientation to a female tap. First, males may compare the timing or amplitude of sounds reaching different parts of their body (tropotaxis). For example, the scorpion *Paruroctonus mesaensis* can accurately detect the direction and distance of prey from vibrations transmitted

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through the sand substrate by comparing the amplitude and timing of vibrations reaching different legs (Brownell 1977, 1984; Brownell & Farley 1979a, b). Second, comparison of replies from different positions could provide a basis for orientation. If distance can be accurately judged from amplitude, or from the time delay between signalling and receiving a reply, then males could triangulate the position of the female having received replies from three or more positions. Finally, turning rate may increase with decreasing amplitude of the female reply, so that if the male beetle is travelling away from the female it tends to turn back towards it (klinokinesis; Bell 1991).

In this paper we describe a series of experiments designed to distinguish between these mechanisms by analysing male behaviour in a range of experimental situations.

## METHODS

### Source of Insects

We collected adult beetles between March and June in 1992 from two churches in north Oxfordshire, U.K. Between experiments beetles were stored on damp tissue paper in an environmental chamber (14:10 h light:dark; 14:6°C).

### Production of Artificial Taps

A mechanical tapper was used to generate artificial taps similar to beetle taps, but with controllable strike frequency and number per tap. The tapper consisted of a plastic pipette tip glued to the centre of the cone of a small loudspeaker (diameter 6 cm). This assembly was supported so that the tip of the pipette made firm contact with the substrate. The tap signal fed to the loudspeaker was generated by a model 8048 stimulator (C. F. Palmer (London) Ltd; pulse width 0.1 ms, 17.5 V), amplified by an audio amplifier, and gated by a solid state relay (National Controls Corporation, West Chicago, Model TMM-0999M-462). The frequency of the artificial tap was controlled by the stimulator output, whilst the duration (and hence the strike number) of the taps was set by the relay switch.

We recorded beetle taps and artificial taps using a gramophone stylus (piezoelectric crystal type) to pick up substrate-borne vibrations. The output

was amplified by an Isleworth Electronics A101 AC preamplifier, and displayed on a Tektronix 5223 storage oscilloscope. The substrate was a sheet of model aircraft cellulose tissue glued across the opening of a 10-cm plastic pot. The tissue was then stretched taut by painting with model aircraft dope (High-Grade, J. Perkins, London). This membrane transmits vibrations to the stylus more effectively than wood, allowing more accurate recording of signal parameters. During recording, beetles were contained within a Perspex ring 2 cm in diameter placed upon the membrane, and the stylus suspended on a gramophone stylus arm, rested next to the ring. The apparatus was insulated from background vibration by placing it on a heavy steel sheet supported by rubber blocks, and contained within an earthed wire-mesh cage to reduce electrical interference.

Characteristics of beetle taps in terms of strike number and frequency are described in Birch & Keenlyside (1991). Artificial taps were adjusted to mimic beetle taps as closely as possible. During experiments, artificial taps were generated at 10 Hz with a duration of 0.9 s (the mean for real beetle taps) and the amplification adjusted to give a signal that, within the accuracy of recording measurement, was the same as beetle taps.

### Experiments

All experiments were carried out between 19 and 22°C. The experimental surfaces used to study beetle movement were all flat, to enable analysis of movement in two dimensions rather than three. In the source colonies used for this study the beetles were found in abundance on the church floor and on the flat surfaces of wooden beams and benches, justifying this procedure.

#### *Male orientation using tropotaxis*

To test for a taxis it was necessary to evaluate the ability of a beetle to orient towards a female after receiving replies from only one position (if replies come from more than one position other means of orientation are possible). A strip of wood (oak) measuring 44 × 4 × 1.5 cm was held horizontally at one end by a metal retort stand, and the artificial tapper placed in contact with the wood at the opposite end. An active (tapping) male was placed in the centre of the strip at right angles to the long axis. Artificial taps were used to

stimulate beetles into activity after handling. Most beetles started tapping before walking: if they did not, the experiment was abandoned. For the remainder, when beetle taps commenced, artificial taps were given in reply in imitation of a female. The male beetles always tapped several times to establish a duet before walking. As they were facing the edge of the wooden strip they were forced into a turn towards or away from the artificial female. The direction of the turn was recorded. This was replicated 32 times, using each male only once, and with random allocation of the tapper to one end of the wooden strip or the other.

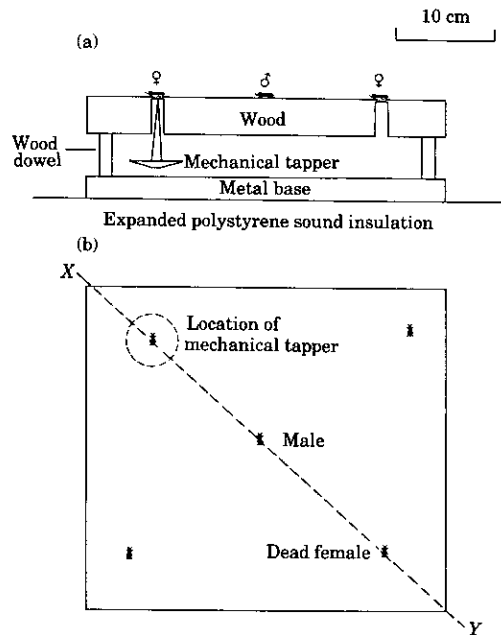
#### *Male orientation in an arena*

We recorded male searching behaviour on two flat horizontal arenas of solid hardwood, both insulated from external vibration by support on expanded polystyrene blocks.

**Circular arena (1000 mm diameter  $\times$  50 mm):** this arena was used to compare the responses of males to real taps from a female, to artificial taps and when no replies were received. The mechanical tapper and the male beetle were placed equidistant between the centre of the disc and the edge, and approximately 500 mm apart. The experiment was replicated 10 times with the same female (contained within a 2-cm Perspex ring), 10 times with the mechanical female and eight times with no female, as a control, each time using a different male.

**Square arena (330  $\times$  330  $\times$  30 mm):** this arena was a refinement of the one used previously as it removed possible sources of bias on male orientation. The mechanical tapper was removed from view, by placing it beneath the arena. The end of the pipette tip was inserted in one of four holes drilled in the underside of the wood to within 2 mm of the upper surface (Fig. 1). Each hole was 6 cm from a corner of the arena. A real female beetle (recently killed by freezing) was placed on the arena directly above each hole, so that short range visual orientation could operate normally. The male was placed in the centre of the arena and the position of the mechanical tapper moved randomly between experiments. This was replicated 10 times with different males.

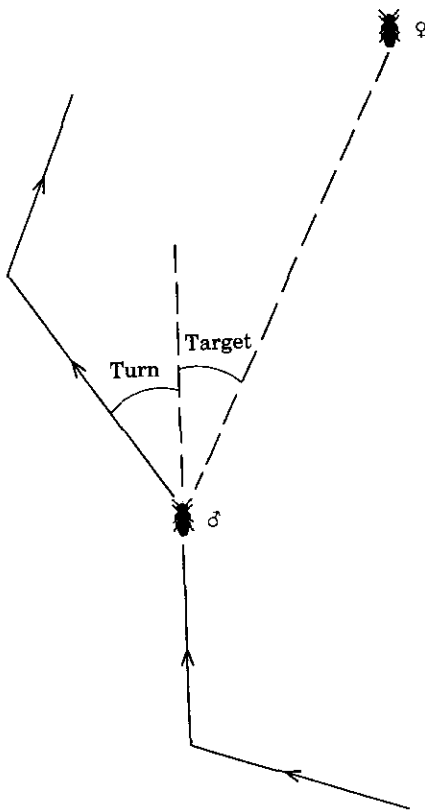
On both arenas taps were given in reply to all taps by males, and the experiment continued until the male came within 5 mm of the tapper, or



**Figure 1.** The square arena (a) side view ( $X$ - $Y$ ) and (b) top view, showing the position of the mechanical tapper, freshly killed females and starting point of the male. All responses were given with the mechanical tapper.

reached the edge of the arena. In the square arena, experiments were also terminated if males located a dead female.

Movements were recorded using a video camera. Beetle tracks were marked onto acetate sheets overlaid onto a monitor. Tracks consisted of a sequence of more or less linear movements punctuated by pauses to tap. Turns were executed at the tapping position following the tap. Tracks were converted into a series of  $X$ - $Y$  coordinates joined by straight lines, using graph paper. Each pair of coordinates represented a point at which the male beetle had stopped and tapped, and received a reply. These are considered to be the important points in the track as they represent the points at which the male received new information on the female's location.  $X$ - $Y$  coordinates were then used to calculate the distance moved between points, the distance from the female at each point, the bearing to the female (target angle) and the angle of the turn made at each point (Fig. 2). Turn angles of greater than  $180^\circ$  were converted into effective turn angles between  $0^\circ$  and  $180^\circ$ .



**Figure 2.** Angles measured to analyse orientation mechanisms. Male movements consist of points at which the beetle pauses, taps and turns, joined by approximately straight walks. Turn angle is the actual angle turned by the beetle at each tapping position. Target angle is the angle the beetle should turn to be facing directly towards the female.

Although resulting in loss of data (a clockwise turn of  $350^\circ$  is different from an anticlockwise turn of  $10^\circ$ , although the outcome is the same), the rarity of turns of greater than  $180^\circ$ , and the greater simplicity of analysis of linear ( $0\text{--}180^\circ$ ) rather than circular ( $0\text{--}360^\circ$ ) statistics (Batschelet 1981), were judged to justify this procedure.

Relationships between male turn angles and other aspects of their behaviour (number of taps given, target angle to the female, distance to the female) were examined using GLIM (generalized linear interactive modelling system). This enables linear relationships between variables to be assessed while partitioning out variation between individual males, and also tests for differences

between males in the slope of relationships. Residuals were inspected to confirm approximation to normality.

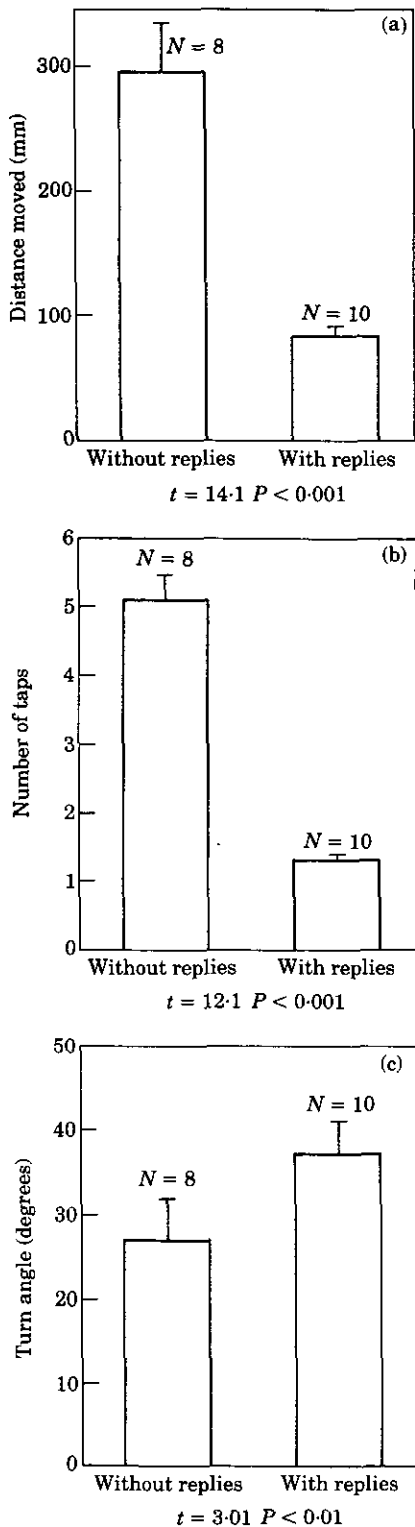
For each aspect of male behaviour recorded (number of taps at each position, turn angle, distance moved) a mean was calculated for each male used, and *t*-tests assuming heteroscedasticity carried out on the means for comparison of behaviour in the absence of replies, with replies from a female, and with replies from the mechanical tapper. The success of males in locating females was compared with that which would be expected by random movement.

#### *Male behaviour at cessation of replies*

Analysis of male movement in the arenas suggested that males tended to turn more when further from the female, perhaps as a response to the decreased perceived strength of the female reply. To test this male beetles were placed in the centre of the square arena, and a duet established between the beetle and the artificial tapper. Once a sequence of 10 taps and replies had taken place replies were stopped. The male always tapped repeatedly at this point, presumably in an attempt to elicit a response. Eventually the beetle continued moving. The turn angle and number of taps at this point were recorded. This was replicated 30 times with different beetles. *t*-tests were used to compare male behaviour after cessation of replies with male behaviour in the circular arena with and without female replies.

## RESULTS

To validate artificial taps as accurate mimics of real taps we compared male mate location behaviour in the circular arena with real taps and artificial taps. There were no significant differences in the number of taps produced at each position ( $t=1.65$ ,  $df=15$ , NS), distance moved between taps ( $t=1.09$ ,  $df=14$ , NS), and turning angle at each position ( $t=0.78$ ,  $df=15$ , NS). One male out of 10 successfully located the real female, while two males out of 10 located the artificial one. Patterns of movement in the presence of artificial or real taps differed quite markedly from those observed in control experiments where there were no replies to taps (see below).



### Characterization of Male Behaviour

In the circular arena male behaviour can be characterized into two types, according to whether or not the male received replies to its taps. In the presence of a response males tapped repeatedly from their starting position to establish a duet with a female. Once a duet was established, the males began moving. The movement patterns were characterized by short straight walks ( $\bar{X} \pm \text{SD} = 84.5 \pm 22.1$  mm,  $N=10$ ) at the end of which the male tapped, usually once, occasionally twice ( $1.31 \pm 0.29$ ,  $N=10$ ). The males then executed a turn ( $37.2 \pm 11.1^\circ$ ,  $N=10$ ) before repeating the cycle.

In the absence of a response males were either inactive, or travelled significantly longer distances between stopping to tap ( $297 \pm 125$  mm,  $N=8$ ), tapped more from each position ( $5.10 \pm 1.20$ ,  $N=8$ ), and turned less at each position ( $27.0 \pm 15.5^\circ$ ,  $N=8$ ; Fig. 3). Figure 4 shows sample tracks of males with and without replies to their taps.

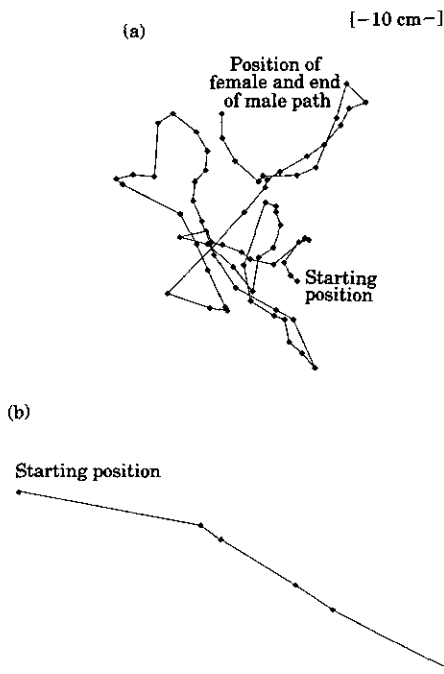
### Test for Tropotaxis

Of 32 males, 17 made an initial turn away from the mechanical female, 15 towards, suggesting that males are unable to use tropotaxis, at least under these experimental conditions. There was no significant bias of turns towards one end of the wooden strip (14 versus 18 turns).

### Test for Klinokinesis

In the square arena, the turn angle of males increased with increasing distance from the female ( $F_{1,264} = 4.65$ ,  $P < 0.05$ ), and when the target angle was large ( $F_{1,255} = 6.60$ ,  $P < 0.05$ ). The turn angle was also greater at positions where the number of taps produced was large ( $F_{1,251} = 8.30$ ,  $P < 0.01$ ; Fig. 5). The slopes of these three relationships did not differ significantly between individuals ( $F_{9,255} = 1.64$ ,  $F_{9,255} = 0.67$ ,  $F_{11,251} = 0.79$ , respectively).

**Figure 3.** Comparison of male behaviour with and without a mechanical reply to the taps ( $\bar{X} \pm \text{SD}$ ; measured in the circular arena). (a) Distance moved by the male between two stops to tap. (b) Number of taps made by males at each stop. (c) Angle turned by males when setting off after a stop.



**Figure 4.** Tracks of representative male deathwatch beetles. Points represent places where the male stopped to tap. (a) With replies to taps, and female successfully located. (b) Without replies to taps.

#### Male Success in Locating Females

In the square arena males located the female (mechanical tapper) on three occasions out of 10. The mean distance travelled by males was  $506 \pm 162$  mm ( $\bar{X} \pm \text{SD}$ ,  $N=10$ ). As males were judged to have found the female if they came within 5 mm, this equates to a combined swept search area of  $50\,620$  mm<sup>2</sup>. The arena area was  $108\,900$  mm<sup>2</sup>, giving a probability of finding a female of  $1/108\,900$  per mm<sup>2</sup> searched. The probability of obtaining three or more successes assuming random movement of males is 0.012 (calculated from a binomial distribution). Even assuming perfect systematic searching the probability of three or more successes due to chance is 0.013. Hence males were significantly more successful than could be achieved in the absence of an orientation mechanism. The males were 150 mm from the female at the start of the experiments, and travelled a mean distance of 394 mm to reach the female, demonstrating that the track taken is generally tortuous.

#### Male Behaviour after Cessation of Replies

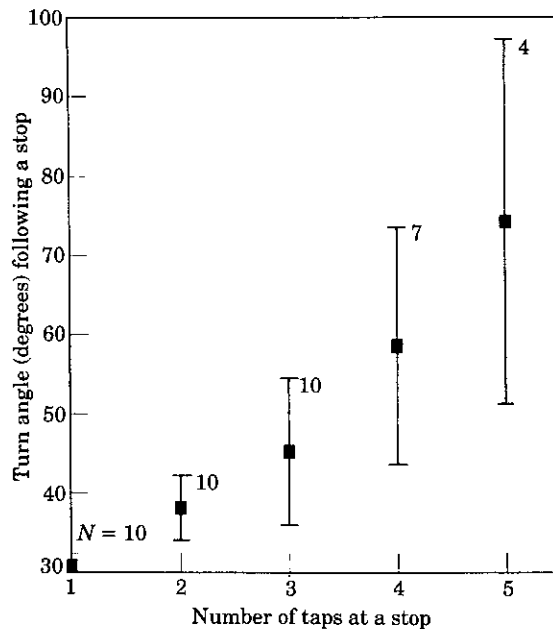
When female replies ceased following a duet between a male and the mechanical female, males tapped repeatedly from the same position, presumably in an attempt to elicit a response. The number of taps ( $\bar{X} \pm \text{SD} = 8.43 \pm 5.18$ ,  $N=30$ ) was greater than that given by males that received a consistent reply from a female ( $1.31 \pm 0.29$ ,  $N=10$ ) or no reply to all taps ( $5.10 \pm 1.20$ ,  $N=8$ ;  $t=6.98$ ,  $P<0.001$  and  $t=2.40$ ,  $P<0.05$ , respectively). The males eventually executed a turn before moving. The turn angle ( $\bar{X} \pm \text{SD} = 98.0 \pm 50.1^\circ$ ,  $N=30$ ) was also greater than that found in males that received a consistent reply ( $37.2 \pm 11.1^\circ$ ,  $N=10$ ) or no reply to all taps ( $27.0 \pm 15.5^\circ$ ,  $N=8$ ;  $t=5.21$ ,  $P<0.001$  and  $t=7.10$ ,  $P<0.001$ , respectively).

#### DISCUSSION

Males exhibited a simple switch between types of behaviour according to whether a responsive female could be detected. If no female was perceived, males often remained inactive. If they did become active, walks were long between stops, and they tapped many times at each stop. Presumably having established, by repeated tapping, that a female was not present in one area, there is little to be gained by stopping to tap again until the beetle has moved away from the barren area. This is analogous to the 'call-fly' behaviour of male tick-tock cicadas, *Cicadetta quadricincta*, described by Gwynne (1987) and, for a leaf-hopper, *Graminella nigrifrons*, by Hunt & Nault (1991).

Alternatively, if a female was detected by her response to taps, males began mate location behaviour. This was characterized by continual activity which consisted of alternating short walks, tapping until a reply was received, and turns. The result was that the beetle tended to remain in the vicinity of the female. Clearly the increased activity of males in the presence of females served in itself to increase the chances of finding a mate.

The second mate location mechanism consisted of a means of orienting to the female tap. It was a type of klinokinesis in which turning rate increased following a movement away from the female, and when the distance to the female was



**Figure 5.** The relationship between turn angles of male beetles when setting off and the number of taps made by the male at that stop ( $\bar{X} \pm \text{SD}$ ).

great: after walking away from the female, males tended to tap more and then to make a larger turn. The males' response to artificial cessation of mechanical replies suggests that the movement away from the female was detected by a decrease in amplitude of the female response, since large turning angles could be induced regardless of movement relative to the female if replies ceased. Presumably this situation simulates movement of the male beyond the range of the female reply, as would occur if the male moved too far from the female or crossed a small air gap in the substrate (the vibrations are not transmitted in air, Birch & Keenlyside 1991). When this occurred the male tapped repeatedly in an attempt to elicit a response, and when none was forthcoming turned sharply: this served to bring him back towards the female. Moths exhibit similar behaviour on leaving a pheromone plume: although the precise mechanism is not known, the rate of turning changes upon leaving the plume so as to tend to bring the moth back into it (Kennedy 1986). An analysis of turn angles following reduction in amplitude of replies from the mechanical tapper may shed more light on this response.

The mechanism described did not allow males to locate the female quickly, as demonstrated by the tortuous routes taken by males to locate females (Fig. 4), by the weak relationship between target angle and turn angle, and by the number of males that failed to find the female before leaving the arena. Tropotaxis would be more efficient, but is perhaps not possible for an insect of this size (legspan approximately 3 mm). Rayleigh waves, the form of vibration detected by other arthropods (Brownell 1984), travel at approximately 3800 m/s in wood (Gogala 1985), and attenuate more slowly than other vibrational waves (Narins 1990). The time delay between waves arriving at different legs, allowing a generous legspan estimate of 3 mm, is 0.8  $\mu\text{s}$ , which is too short for detection (Bailey 1991).

The inefficiency of tapping as a means of mate location poses the question as to why tapping evolved instead of, or probably in place of, alternatives such as pheromones? Tapping has far lower energetic costs than production of airborne sounds (Leighton 1987), but its cost relative to pheromone production has not been quantified. Answers as to why tapping evolved may be

suggested by studies of deathwatch beetles in their natural environment, where very little is known of their behaviour, rather than in their adopted artificial habitat which has, in evolutionary terms, been available for a very short period.

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