Animal behaviour

Not looking where you are leaping: a novel method of oriented travel in the caterpillar Calindoea trifascialis (Moore) (Lepidoptera: Thyrididae)

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The prepupation caterpillar of the Southeast Asian moth Calindoea trifascialis constructs a leaf shelter that jumps across the ground using a jumping method novel among the insects. We found that movement path direction was correlated to the direction opposite to the most intense light. Correlated random walk (CRW) analyses found net squared displacements higher than predicted by a CRW, and fractal dimension analysis indicated straighter paths at large spatial scales. Rearing experiments showed high mortality from predation on the ground, but higher mortality resulted from sun exposure. We interpret jumping path orientation as an efficient search strategy to find shade in a variable landscape, given limited perception, in the presence of overheating and desiccation risks.

1. Introduction

Jumping insects are not rare, but in the Holometabola the behaviour is more common among adults. Larvae rarely jump, possibly because muscles used in locomotion usually have to act against rigid sclerites or apodemes. Interestingly, when used as a means of displacement, the behaviour seems confined to the prepupation or ‘wandering phase’, regardless of taxon or jumping method used. Several jumping dipteran larvae have been described [1–3]. In these examples, the unconfined insect grasps its posterior end with its mouthparts, then suddenly straightens its body, springing airborne. A second, similar kind of jumping occurs within the confines of a plant seed or gall. A sudden flexion in the curvature of the larva causes the seed or gall to ‘jump’. The ‘Mexican jumping bean’ caterpillar, Cydia deshaisiana, uses this method, causing movement in the seeds of Sebastiania spp. (Euphorbiaceae) [4]. Similarly, the caterpillar Emporia melanobasis Janse jumps inside its host plant seeds [5], and white oak (Quercus lobata Née (Fagaceae)) leaf galls jump owing to flexing gall wasp (Neuroterus saltatorius (Edwards)) larvae inside [6,7].

Calindoea trifascialis uses a novel jumping method. The caterpillar makes conical leaf-feeding shelters (see [8] for details) on the upper leaf surface of host plants Dipterocarpus tuberculatus, Dipterocarpus obtusifolius or Dipterocarpus alatus. After feeding for about three weeks, a different leaf shelter—a leaf roll—is made for pupation (figure 1a). At night, this pupal shelter detaches from the leaf and jumps repeatedly on the ground. In the presence of warm sunlight, jumping continues diurnally for about three days. Jump frequency increases linearly with temperature (about 1 jump s⁻¹ at 29°C). The average jump length is about 0.75 cm.

To jump, the caterpillar anchors its anal prolegs to the substrate and lowers its head. The anterior portion suddenly moves backward, arching upward.
The dorsal surface strikes the inner top of the shelter near the centre. This force is backward and upward: the shelter moves opposite to the direction that the caterpillar faces (see the electronic supplementary material, videos). Tracings of resultant paths show elements of random 'wandering' (figure 1b), but the end result is usually a considerable displacement, suggesting a directional element to travel, rather than the random methods of the other jumpers mentioned above. Jumping in a self-made shelter and using this propulsion method make it unique among jumping larvae.

Explanations of larval jumping per se seem speculative, with protection from heat [9,10] and predators [2,3,9] suggested. In these studies though, survivorship and dispersal patterns resulting from jumping were not examined. The jumping method of Calindoea trifascialis provides a unique opportunity for such analyses.

During pupation site searches, caterpillar mortality depends on exposure to predators, parasitoids and sunlight. These risks, we suggest, influence displacement. As we frequently observed the insect moving away from bright light, we tested whether average displacement direction was correlated with light intensity. Because the caterpillar ‘pistons’ backward mostly aligned with the leaf roll, each subsequent movement direction is correlated to the previous one. Thus, we assumed a correlated random walk (CRW) as a null hypothesis. We compared observed paths to a CRW and tested whether the displacement vector distribution differed from uniformity. We hypothesized that displacement direction in sunlight and artificial light would be similar. To test survivorship, we subjected caterpillars in shelters to various combinations of location and sunlight, to change exposure to light, predators and parasitoids. We predicted high survivorship on the ground and in shade.

2. Material and methods

(a) Location
Research was conducted in dry dipterocarp forest in Yok Don National Park (12°54′ N, 108°42′ E), Dak Lak Province, Vietnam from 1999 to 2006.

(b) Path analysis
We filmed 16 shelters jumping for several minutes in morning or afternoon sun (so that the Sun’s east/west direction varied and the angle above the horizon was considerably less than 90°). Coordinate positions were determined at 4 s intervals and ‘turning angles’ were calculated for each position (sensu Kareiva & Shigesada [11]) and their distributions were plotted. We used their method to plot mean squared displacement against the move number, comparing it to a CRW having identical move length and turning angle distributions. We calculated $R_{diff}$ values (mean difference between net displacement² and expected CRW displacement² [12]). To determine the scale to test for orientation, we used the program Fractal V [13] to plot fractal dimension (D) against scale for the combined paths (D is a continuous measure of path tortuosity—1 represents a straight line, 2 a line so tortuous it covers a plane). We then placed 41 shelters in a 1 m² ‘arena’ outdoors (at different times of morning and afternoon) and measured the resultant displacement vector direction (when the perimeter was reached) relative to the Sun’s direction. We repeated the experiment indoors for 72 caterpillars with a 500 W lamp 3 m from the arena. Circular statistics (see [14] and [15]) were used for data analyses. For all distributions, Oriana software (Kovach Computing Services, Penrith, Wales, UK) was used to calculate mean vector ($\mu$), length of the mean vector (r) and a Rayleigh test for uniformity for indoor and outdoor distributions. The latter distributions were compared using a Watson–Williams test in R [16]; see the package ‘circular’.

(c) Rearing study
We collected and reared 658 final-instar caterpillars to produce pupal shelters. These were reared to eclosion using one of 10 rearing treatments, of varying location and time. Shelters were wired to leaves of host trees, fixed to the ground under host trees and/or reared in the laboratory (laboratory treatments were in containers that excluded predators and parasitoids). See table 1 for details. We tabulated numbers of pupae preyed upon, parasitized, successfully enclosed or died in the shelter. $\chi^2$ and Fisher’s exact tests were used to compare treatments, using Bonferroni corrections for multiple comparisons [17,18].

3. Results

(a) Path analysis
For 504 turning angles, we found a symmetric distribution with mean vector ($\mu \pm$ s.e.) = $-1.57^\circ \pm 2.53^\circ$, 95% CIs $\pm 3.04^\circ$ and mean vector length, r, of 0.66 (figure 2a). Figure 2b shows net squared displacement observed for 15 paths; this exceeded the CRW prediction. In all cases where individual runs were significantly different from a CRW, they exceeded the CRW prediction. The $R_{diff}$ for all paths when combined as one long path was significantly larger than a CRW prediction ($R_{diff} = 7.3162, p < 0.0001$).

Figure 1. Pupal shelters. (a) Shelter about to detach from leaf; (b) example of a shelter’s path over ground (see the electronic supplementary materials, video S2). (Online version in colour.)
(a) Observed distribution for 504 turning angles; (b) observed net squared displacement for 15 paths and CRW prediction; (c) combined mean fractal dimension (D) from all trials versus scale; and (d) circular histogram for 72 caterpillars, indoor experiment.

Figure 2. Pupal shelter movement analyses. (a) Observed distribution for 504 turning angles; (b) observed net squared displacement for 15 paths and CRW prediction; (c) combined mean fractal dimension (D) from all trials versus scale; and (d) circular histogram for 72 caterpillars, indoor experiment.

Figure 2c shows combined mean fractal dimension (D) from all trials against scale. Tortuosity was low at small scales, increased to a maximum at around 18 cm, then decreased to low levels at greater than 0.5 m. This determined the arena size we used to test for orientation, because distances this large would reveal orientation extant at larger scales. Using 41 shelters outdoors, 41 resultant angles were calculated. We found $\mu \pm s.e. = -2.36^\circ \pm 4.56^\circ$ (95% CI $6.56^\circ$, $r = 0.8779$). The Rayleigh test for uniformity gave $p < 0.0001$. Using 72 shelters indoors, we found $\mu \pm s.e. = 5.67^\circ \pm 3.20^\circ$ (95% CI $5.97^\circ$, $r = 0.8919$). The Rayleigh test for uniformity gave $p < 0.0001$. Both distributions were significantly different from uniformity. The 95% CIs for the mean included the point opposite to the most intense light for both distributions. A null hypothesis that the indoor and outdoor distributions were not significantly different cannot be rejected (Watson–Williams test, $F_{obs} = 2.1559 < F_{1,111} = 3.9266$, $p = 0.1449$). Figure 2d shows the circular histogram for the indoor experiment.

(b) Rearing study

Table 1 shows counts for successful emergences, predation, parasitoidy and other mortality factors. A table-wide null hypothesis of no difference between the treatments can be rejected ($\chi^2_{0.05,44} = 27 = 455.109$, $p < 0.001$). The following paired comparisons were significantly different: A-B, A-D, B-C, C-D, C-I, D-I, E-F, G-H, D-F, F-H, I-J (bold—see discussion). These comparisons were not significantly different: C-E, E-G, D-H. These conclusions remain valid with Bonferroni corrections.

4. Discussion

Jumping Calindoea trifascialis caterpillars have a marked tendency to move opposite to the most intense light. Path tortuosity reaches a maximum at a scale of about 18 cm, but this diminishes thereafter and displacement exceeds a CRW prediction. Higher tortuosity at smaller scales may be a way to assess relative light intensities through all angles.

Predation (mostly from Pheidole ants) was higher on the ground (the ground treatments C, E and G had high predation counts compared with leaf analogues D, F and H). J was a leaf treatment (but near the ground to ensure full shade) and also had high predation. Despite such mortality, detaching from the leaf followed by ground pupation seems to confer an advantage though, as we found significant effects on mortality owing to sun exposure (compare, for example, numbers not emerged in I (full sun) with D (partial sun)). Even with higher predation on the ground, there were more successful ground eclosions (compare C (shaded ground) with I (full sun on leaves)).

The open dipterocarp forest provides no guarantee that, following leaf detachment, the caterpillar will end up in shade. Jumping may be a way to find shade. Sealed in its shelter, the insect may be able to perceive the direction to the Sun and move opposite that direction. But it clearly has no perception that it is heading in the direction of shade or the Sun. In these circumstances, why use an oriented search strategy? Put another way: why know your direction if you do not know where you are going?
Table 1. Results of rearing 658 caterpillars in pupal shelters, using 10 different treatment regimes. The numbers in the treatment column indicate the number of days exposed to the treatment; ‘+’ indicates the number of additional days necessary to rear to eclosion (in laboratory). (Note: in all treatments, the insect was in the laboratory after 11 days, because the minimum time from completion of the pupal shelter to moth eclosion was observed to be 12 days.)

<table>
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<th>moth</th>
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The use of a specific search strategy implies that costs exist. Without costs, even inefficient searches will be successful [19]. The strongest candidate for a cost in our study appears to be sun exposure (overheating and desiccation). Computer simulation has shown that the straightness of CRWs is positively correlated with landscape uniformity, increasing mortality risk and decreasing perceptual range while dispersing [20]. We found paths less tortuous than CRWs at a large scale, though the efficiency of such oriented paths compared with nearly straight CRWs is uncertain [21]. As noted earlier, the ‘piston in a cylinder’ arrangement might naturally lead to a nearly straight CRWs is unclear [21]. As noted earlier, the ‘piston in a cylinder’ arrangement might naturally lead to a nearly straight CRWs is unclear [21]. As noted earlier, the ‘piston in a cylinder’ arrangement might naturally lead to a nearly straight CRWs is unclear [21]. As noted earlier, the ‘piston in a cylinder’ arrangement might naturally lead to a nearly straight CRWs is unclear [21]. As noted earlier, the ‘piston in a cylinder’ arrangement might naturally lead to a

References