The Structure of the Trap and Trap-building Behaviour in *Callistoleon manselli* New (Neuroptera : Myrmeleontidae)

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Abstract

Larvae of the antlion *Callistoleon manselli* New build pitfall traps that have attached radiating furrows. In order to evaluate this unique trap-building behaviour from an evolutionary viewpoint, we analysed the shape of traps in the field, then examined the process of trap construction and the efficiency of the pitfalls in prey capture. Larvae of *C. manselli* construct the radiating furrows after building the central pit. Larvae provided with food *ad libitum* tend not to construct furrows at all. Capture efficiency for the pits with furrows was greater than for pits without furrows. The pitfall traps constructed by *C. manselli* evidently represent a more advanced development than the simple pits of other species.

Introduction

Many predacious arthropods have evolved techniques for assisting their capture of prey: the webs of spiders, the nets of caddisfly larvae and the sticky threads of Australasian ‘glowworms’ (Diptera : Mycetophilidae). The conical pits constructed by the larvae of antlions (Myrmeleontidae) represent a further example that has attracted much attention in the recent literature (e.g. Griffiths 1980, 1986; Lucas 1982; Matsura 1986, 1987, 1989a; Jenkins and Kitching 1987).

The majority of the Myrmeleontidae do not construct pitfalls (New 1986) but act as sit-and-wait predators beneath the surface of fine sand or in bark crevices (Wheeler 1930). The pit-building habit is restricted to the tribe Myrmeleontini (New 1986). Other closely related families within the Neuroptera, the Nymphidae and Ascalaphidae, also contain no members that build pits. Accordingly, it has been assumed, probably correctly, that the pit-building habit is a derived character (Withycombe 1925). Nevertheless, as Mansell (1988) has pointed out, it remains an adaptation of considerable antiquity given the near cosmopolitan range of the genus *Myrmeleon*—a pit-building genus.

Although Wheeler (1930) discussed the evolution of pit-building behaviour he remained silent on how pit-building antlions may have evolved from non-pit-building antecedents. One possibility is that the furrows in the substrate surface made by all sand- and dust-dwelling antlions (including simple pit-building species) as they move backwards from place to place represent the precursors of the pit-building habit. Heinrich and Heinrich (1984) found that such furrows work, on occasion, as a trap, resulting in the capture of small ants. The recent discovery by Mansell (1988) of a unique Australian antlion larva<sup>1</sup> which constructs a pitfall trap with associated radiating furrows accordingly is of considerable interest. Mansell (1988) concluded that this peculiar trap-building behaviour was a newly derived habit.

<sup>1</sup>Mansell (1988) referred to the species he observed as *Callistoleon illustris* (Gerstaecker). New and Matsura (1993) confirm that it is in fact a new species, which they name *Callistoleon manselli*. 

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We suggest that there are two alternative explanations for the pits constructed by *C. manselli*. The combination of pit and furrows may represent a primitive state in which the furrows are 'relics' of a behaviour that preceded pit-building or, as Mansell suggested, the furrows are additions to an ancestral pit-building habit and the pit-structure of *C. manselli* is a recent development. We set out to examine these alternatives by analysing the trap structure of *C. manselli* in the field, observing the trap-building process in the laboratory, and evaluating the capture efficiency of the trap, again in the laboratory.

**Material and Methods**

Field observations of pitfalls and collection of antlion larvae were made at Carnarvon Gorge, Queensland (25°8'N, 148°7'E) in mid-November 1990. The larvae occurred in very fine white sand eroded from the many undercuts and shallow caves along the course of Carnarvon Creek. Shapes and locations of pitfalls were recorded by placing transparent plastic sheets over patches where pitfalls occurred in high density and then tracing the outlines of the pitfalls onto the sheets using felt-tipped pens. Subsequently, the larvae themselves were collected from within the pitfalls so that instar determinations could be made.

Pit-building behaviour by larvae of *C. manselli* was observed in the laboratory by releasing eight larvae (four Instar II and four Instar III) into a 55×70×10-cm container filled with white sand collected at the field site. A National NV-8050 time-lapse video recorder was used to record events over the period 15 November 1990 to 1 December 1990. Further observations were made over a period of a week in a similar manner on a further 18 antlion larvae kept in separate 17.5×12×9-cm containers.

To determine the effect of hunger level on pit-building behaviour we carried out a separate experiment using 15 third-instar larvae maintained in separate containers as before. Nine larvae constructed pits (without furrows) in this situation without being fed. We fed four of these nine larvae one Slater (*Isopoda*: Oniscoidea; length c. 10 mm) each every second day. The other five antlion larvae remained unfed.

The pit diameter and number of attached furrows was recorded for each individual each day over a 12-day period.

Lastly, to obtain a measure of capture efficiency by furrowed pitfalls we measured the time interval from release of a prey item to its falling into the central pit (pre-capture time). This experiment was carried out using both slaters and ants (*Camponotus* sp.) as prey items. These were released into containers in which antlions had constructed pitfalls. Some of these pitfalls were left with undisturbed furrows whereas in others the furrows had been filled with sand.

**Results**

*Structure and Spatial Distribution of the Pitfall Traps in the Field*

An example of a pitfall trap constructed by *C. manselli* in the laboratory is shown in Fig. 1. In general the trap comprises a conical pit with furrows radiating from it. Upon completion of the pit and furrows the larvae rotate their bodies firmly at the base of the pit producing a cylindrical downward extension of the pit. This was possible only because the nature of the sand was such that vertical walls were a stable configuration. The depth of the radiating furrows increased with the number of journeys by the antlions during construction. The maximum depth we recorded for a furrow was 16 mm.

Counts of the number of furrows present in pitfalls in the field are summarised in Table 1. In all, 84.8% of the pitfalls had fewer than five furrows and the number of furrows did not differ significantly with larval instar ($F = 1.616$, $P > 0.1$). There were significant differences in the average length of furrows across instars ($t$-tests: Instar I vs. Instar II, $P < 0.001$; Instar II vs. Instar III, $P < 0.02$), with older larvae constructing longer furrows, as might be expected.

For analysis of the spatial distribution of pitfalls at field sites we calculated Clark and Evans' (1954) Index, $R$, based on the nearest neighbour distances between individual pits, viz.

\[ R = \frac{r_{A}}{r_{E}} \]

where $r_{A}$ is the mean actual nearest neighbour distance and $r_{E}$ is the expected mean nearest neighbour distance.

**Table 1. Mean Number of Furrows (per Pit) for Different Instars**

<table>
<thead>
<tr>
<th>Instar</th>
<th>Number of Furrows</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>2.5</td>
</tr>
<tr>
<td>II</td>
<td>4.0</td>
</tr>
<tr>
<td>III</td>
<td>5.0</td>
</tr>
</tbody>
</table>

**Table 2. Actual $r_{A}$ and Expected $r_{E}$ Nearest Neighbour Distances**

<table>
<thead>
<tr>
<th>Site</th>
<th>$r_{A}$</th>
<th>$r_{E}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>2.5</td>
<td>3.0</td>
</tr>
<tr>
<td>B</td>
<td>3.0</td>
<td>3.5</td>
</tr>
<tr>
<td>C</td>
<td>3.5</td>
<td>4.0</td>
</tr>
</tbody>
</table>
Construction of Pitfall Traps by Callistoleon manselli

Table 1. Measurements of the pitfall traps by each larval instar in Callistoleon manselli

<table>
<thead>
<tr>
<th>Instar</th>
<th>Number of furrows</th>
<th>Length of furrows (mm)</th>
<th>n, No. of replicates</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± s.e.</td>
<td>Range</td>
<td>Mean ± s.e.</td>
</tr>
<tr>
<td>I</td>
<td>3.6 ± 0.6</td>
<td>1-5</td>
<td>38.4 ± 3.9</td>
</tr>
<tr>
<td>II</td>
<td>3.6 ± 0.7</td>
<td>1-8</td>
<td>62.4 ± 3.7</td>
</tr>
<tr>
<td>III</td>
<td>4.9 ± 0.7</td>
<td>3-9</td>
<td>76.2 ± 4.3</td>
</tr>
</tbody>
</table>

where $\bar{r}_A$ is the mean of the nearest neighbour distances observed and $\bar{r}_E$ is the mean nearest neighbour distances expected for randomly spaced individuals. For a random population $R = 1$, under conditions of maximum agglomeration $R = 0$, and under conditions of maximum uniform spacing $R = 2.1491$. Results summarised in Table 2 suggest that pits were distributed in a fashion not statistically different from random at each of the three sites so analysed.

Table 2. Analysis of the spatial distribution of pitfall traps by the method of Clark and Evans (1954)

<table>
<thead>
<tr>
<th>Site</th>
<th>Instar</th>
<th>No. of individuals</th>
<th>Density (m$^2$)</th>
<th>$\bar{r}_A$ (cm)</th>
<th>$\bar{r}_E$ (cm)</th>
<th>R ($=\bar{r}_A/\bar{r}_E$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>I</td>
<td>6</td>
<td>16.57</td>
<td>12.9</td>
<td>1.05</td>
<td></td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>9</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>I</td>
<td>1</td>
<td>7.8</td>
<td>18.1</td>
<td>1.01</td>
<td></td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>I</td>
<td>1</td>
<td>7.8</td>
<td>20.4</td>
<td>1.14</td>
<td></td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>4</td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>
Although between 8 and 20 pitfalls occurred per square metre we never observed furrows to intersect.

There was a tendency for the direction of orientation of furrows to reflect the slope of the ground on which the pitfalls were constructed. On perfectly flat ground furrows radiated without bias. On sloping ground, however, few furrows that sloped downhill were constructed (Fig. 2).

![Fig. 2. Some examples of the pitfall traps found in the field. Those on the left of the figure were located on flat ground; those on the right, on slopes. Arrow indicates downhill direction of slope.](image)

**Pit Construction**

The pit-building process was followed in 12 individual larvae which built a total of 42 furrows. Although the experimental arena was continually lit for video purposes furrows were constructed only during the hours corresponding to night (Fig. 3), and 49% of furrows were made between 2200 and 2400 hours. On 16 occasions we were able to measure the round-trip time along a furrow by larvae from the time of departure from the perimeter of the pit to the time of returning to it. The average (± 1 s.e.) round-trip time was 5.1 ± 0.58 minutes.

The time course of construction of the furrows associated with one pit is shown in Fig. 4. In pitfall construction the larvae of *C. manselli* always constructed the conical pit first, followed by construction of the first furrow. The interval between pit building and the beginning of construction of the first furrow varied among individuals. Some larvae did not begin furrow construction for several days after pit completion; others (as in Fig. 4) began within one day. The interval between construction of successive furrows was also variable.

![Fig. 4. The process of construction of a single pit by a larva of *C. manselli*. Arrows show hatched furrows.](image)

However, position and length of new furrow origination varied among existing furrows. The larvae in the laboratory had finished construction.

**Influence of Human Activity**

The structure of the furrows, the central pit, the conical pit, and the furrows. We used...
However, positioning of new furrows was carried out in a predictable manner. Each new furrow originated within the largest undisturbed arc of the pit perimeter remaining among existing furrows. Accordingly, completed pits in the level situation presented in the laboratory had furrows arranged spoke-like all around them.

**Influence of Hunger on Pitfall Structure**

The structure of the pitfall traps of *C. manselli* may be characterised by the diameter of the central pit, the number of radiating furrows, and the directions and lengths of these furrows. We used the first two of these to test for the effects of hunger on pitfall construction. The diameter of the pit was unaffected by the hunger level of the antlion larvae.
(Fig. 5a) whereas the number of furrows per pit increased dramatically with hunger (Fig. 5b). This difference became apparent after five days of food deprivation. However, it should not be assumed that hunger is the sole cause of furrow construction: even well-fed larvae built a small number of furrows around their pits during the course of this experiment (Fig. 5b).

![Graph showing influence of hunger on pit size and number of furrows]

**Fig. 5.** The influence of hunger on the size of the pit of larvae of *Callistoleon manselli*. (a) mean diameter (± 2 s.e.); (b) numbers of furrows (mean ± s.e.). Asterisks show the level of significant differences, as indicated by a t-test, at each point in time. *P* < 0.05; **P** < 0.01.

**Capture Efficiency of Pitfall Traps**

Precapture times in the pitfalls with furrows were 0.37 times those for pitfalls without furrows when slaters were used as prey, and 0.5 times when ants were used as prey (Table 3) although these differences were not significant. Ants were caught earlier than slaters because of their smaller size, although both were caught, in the ant stage by dropping into a furrow they were frequently parallel to the wall of the pit. Slaters and ants were sometimes caught in the larval stage when they dropped into the pit.

**Table 3.** Comparison of precapture times (in seconds) for different prey and different types of pits

<table>
<thead>
<tr>
<th></th>
<th>Prey item</th>
<th>Slaters</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ants</td>
<td>Slaters</td>
</tr>
<tr>
<td></td>
<td>Mean ± s.e.</td>
<td>Mean ± s.e.</td>
</tr>
</tbody>
</table>
| Pits with furrows| 9.6 ± 3.0 (6)     | 17.3 ± 2.6 (5)| 9.6 ± 2.0
| Pits without furrows| 19.1 ± 5.1 (6)   | 46.6 ± 21.4 (5)| 9.5 ± 12.8
| t-test for difference between means |
|                  | t₀ = 1.626       | t₀ = 1.357    |
|                  | *P* > 0.1        | *P* > 0.2     |

**Discussion**

If the hypothesis that furrow-building specialists are pit builders in the simple pit stage, and that the integrated pit stage is a more advanced stage of furrow construction does not hold true, then one can hypothesize that some species do not form furrows at all.

The frequency of multiple furrows in the field indicates that furrow construction is an efficient strategy for capturing prey. This efficiency is further illustrated by the fact that slaters are often found in the wall of a cliff or on the rim of a pit of larger size.

From considering the efficiency of the furrow-building strategy in *C. manselli* represents a more advanced stage of furrow construction.

Larvae of *C. manselli* that build only one pit are not able to obtain the necessary food substrates, and it is likely that the larvae of this species that have not yet constructed an outcrop will be eaten by the ants of the species. Ants are restricted to the pit, but slaters are not, and they are likely to be caught more frequently by ants that occur during the early stages of furrow construction.

As observed in the field, *C. illestris* were often found in sandstone caves and are able to build more complex structures, perhaps suggesting a more advanced stage of furrow construction.

Sandstone caves are also habitats for many other species of ants and slaters. The relative abundance of each species, such as the typical number of pitfall traps per species, may vary depending on the habitat and season.
slaters because of their more rapid movements on the sand surface. Slaters tended to be caught, in the arena situation, as they walked around the perimeter of the container, dropping into a furrow where that furrow intersected the edge of the container (a situation frequently paralleled in the field where furrows often abut cliff faces). Once in furrows both slaters and ants walked along them unhesitatingly and were attacked by the antlion once they dropped into the central pit.

**Discussion**

If the hypothesis that pit-building behaviour has evolved in antlions from a simple furrow-building stage, through a *C. manselli*-like integrated pit-and-furrow stage, to the simple pit stage, is true then we might expect that in constructing an integrated trap the central pit would be built after construction of at least one furrow. Although the shape of the integrated pits built by *C. manselli* conform to this notion, the process of construction does not: the central pit is constructed first, followed by the furrows. We observed, further, that some larvae that fed to satiation in the laboratory constructed no furrows at all.

The frequency of encounter with prey items increases dramatically in the presence of furrows because the length of the trapping edge similarly increases greatly (Mansell 1988). This efficiency is further increased when the furrows join an environmental ‘edge’ such as the wall of a cliff or cave. Even within a small container the increase in trapping efficiency of pits with furrows over those without was in the order of two to three times.

From consideration of these two points, the trap-construction sequence and the greater efficiency of the furrowed trap, we concur with Mansell (1988) that the pitfalls of *C. manselli* represent a highly adapted, derived structure rather than one reflecting an earlier stage in the evolution of antlion pits in general.

Larvae of *C. manselli* may invest more energy in building their pitfalls than do larvae that build only conical pits. Further, such complex structures can only be built and maintained on substrates of very stable, even adherent, fine sand protected by caves and overhangs from wind and rain. The sandstone floors of the Carnarvon Gorge caves and outcrops satisfy these requirements fully. *C. manselli* is a highly specialised species of antlion living in a highly unusual environment.

Most furrows constructed on slopes were directed upward (Fig. 2), which suggests that antlions can detect the angle of slope and respond to it. Directing furrows upward will generally mean that they will approach cave and cliff walls and so enhance predation efficiency given the tendency of many prey items to hug such faces when foraging. The mandibles of *C. manselli* are long and slender in comparison with those of many other species of myrmecoleontid (see, for example, the species illustrated by Matsuura 1989b). In the laboratory prey often escaped the grasp of the mandibles. In the field this may mean that they are restricted to smaller softer-bodied prey. We never observed predation in the field, possibly because, as in *Myrmeleon obscurus* (Youthed and Moran 1969), this does not occur during the day. The activity rhythms observed by captive antlions in our observations of furrow construction provide circumstantial evidence of this contention.

As observed earlier, Mansell (1988) regarded *C. manselli* as *C. illustris*. Larvae of *C. illustris* were, indeed, found by one of us (Matsuura, unpublished observations) in sandstone caves in north-western New South Wales. Like most other antlion larvae, they construct simple conical pits even though congeneric with the furrow-building species, perhaps suggesting that even within the genus *Callistoleon*, *C. manselli* is to be regarded as ‘advanced’.

Sandstone caves, outcrops and overhangs are not uncommon in eastern Australia, and other species of *Callistoleon* may await discovery. Comparisons of pit-building behaviour among such species would aid our understanding of the evolution of the pit-and-furrow model of pitfall made by *C. manselli*.  

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**Table:**

<table>
<thead>
<tr>
<th>Slaters</th>
<th>± s.e.</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-6 (5)</td>
<td>9-6-26-0</td>
<td>21-4 (5)</td>
</tr>
<tr>
<td>357</td>
<td></td>
<td>0-2</td>
</tr>
</tbody>
</table>
Acknowledgments

We thank Dr Tim New of LaTrobe University, Melbourne, for identifying ant lions for us and for discussions on the evolution of ant lions, and Dr Kazuo Ogata of Kyusyu University for ant identification. We are grateful to Bill Upjohn of the University of New England for very able technical assistance in field and laboratory. The Queensland National Parks and Wildlife Service issued us with a permit to work in Carnarvon National Park, for which we thank them. The research was funded by the post-doctoral exchange programme of the Japan Society for the Promotion of Science and the Australian Academy of Science. RLK's participation was funded under the aegis of a U.N.E. Research Grant.

References


Morphology in New Guin

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Abstract

The digestive tracts of phalangerid possums (body mass 2400 g) of the genus Phalanger (Phalanger) suggest a new approach to forage selection. The black-footed tree phalanger, Phalanger bicolor (Acanthotheria bicolor), has been investigated by several workers. The Australian black-footed tree phalanger, Phalanger bicolor, is the most abundant species of its family in the region and is a major component of the diet of Dendrolagus maculatus (Phalangeridae). It is an omnivorous species that feeds on a variety of plant material, including leaves, fruits, and flowers. The digestive tract of P. bicolor is well adapted for efficient digestion of plant material, with a long digestive tract and specialized enzymes for the breakdown of fiber. The study of the digestive tract of P. bicolor provides insights into the feeding ecology and nutritional requirements of this species and sheds light on the adaptive strategies of phalangerids in general.

Introduction

The marsupials of the Northern Territory of Australia and New Guinea have a unique morphology that is often adapted for life in the region. The Australian black-footed tree phalanger, Phalanger bicolor, is one such species, belonging to the family Phalangeridae. This species is known for its distinctive black and white coloration and is often seen in the foliage of eucalyptus trees, where it feeds on leaves and other plant material. The digestive tract of P. bicolor is well adapted for efficient digestion of plant material, with a long digestive tract and specialized enzymes for the breakdown of fiber. The study of the digestive tract of P. bicolor provides insights into the feeding ecology and nutritional requirements of this species and sheds light on the adaptive strategies of phalangerids in general.

On the basis of 18 May 1992; accepted 12 January 1993