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Cycloalexy in an Australian Pergid Sawfly (Hymenoptera, Pergidae)

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Introduction

The ring defence strategy adopted by larval chrysomelids (Chrysomelidae: Coleoptera) has recently been formally described as cycloalexy (VASCONCELLOS-NETO and JOLIVET, 1988). The strategy is also adopted by some tenthredinid sawflies, and is described here from the Australian *Perga dorsalis* (Pergidae: Hymenoptera).

Perga dorsalis is a defoliator of *Eucalyptus* in south-eastern Australia. In the Adelaide region of South Australia, where this study was done, adult females oviposit in autumn (February-March). The gregarious larvae feed as colonies during winter. In spring (September-October), still as colonies, the mature sixth instar larvae burrow into the soil and form cocoon masses. The final (non-feeding) instar diapauses over summer, and sometimes for one, two, or even three further seasons. Pupation occurs in early autumn, with emergence of adults after some two weeks.

Gregarious Larval Behaviour

Eggs are deposited in groups of 40 to 50; they are inserted into the mesophyll of *Eucalyptus* leaves to form a pod adjacent to the midrib. After an incubation period of some 30 days, 2 to 4 first instar larvae chew their way out through the leaf epidermis. The remaining larvae follow them out through these emergence holes, and all larvae aggregate on the underside of the leaf. The first arriving larvae assume a ring formation within minutes, and are joined by the remaining larvae as they emerge, usually well within one hour (fig. 1). The larvae are nocturnal, moving to the leaf margins to feed during the night, and reassemble in their circular formation during the day (fig. 2). In the second or third instar, the larvae can no longer fit under a leaf in this formation. They now interlock in a cylindrical mass around a twig or branch (fig. 3), still crawling out to feed on the main trunk, and may be made up of several colonies from the same tree which have coalesced. I have observed some such groups to contain more than one species of sawfly in the field.

Colony cohesion is maintained by the larvae in front, by holding the ends of their abdomens over the thoracic region of those behind them. The hardened terminal abdominal sternite (uropod) is also rhythmically tapped against the substrate, and it is thought that this provides the low frequency vibration which the feeding colony uses for orientation in reassembly (CARNE, 1962).

Defensive larval behaviour

The early instars adopt a circular formation with their heads facing outwards. If the group is large, the larvae form concentric circles, with the abdomens of the outer ring interdigitating with the heads and thoraces of the inner. I have as yet not determined whether the same larvae consistently adopt the outer positions, but there is obviously no age differentiation within the group. If disturbed, the larvae rear up, raising their head and abdomen in a «U» shape (fig. 4). In this manner an oesophageal diverticulum is compressed within the thorax so as to eject a drop of its contents at the oral cavity. This drop is thus the most prominent part of the larva, and may in part smear off onto the dorsal abdomen, which is flicked repeatedly. The drop is of an oily substance smelling strongly of *Eucalyptus*. At colder temperatures, it is highly viscous, and remains adherent to the mouthparts. On hot days the substance can be very liquid and may eject some 10-15 cm if the larvae rear up violently, earning them the common name «spitfire grubs». MORROW *et al.* (1976) have shown that this oil is chromatographically identical to that contained in the *Eucalyptus* leaves on which the larvae feed, but the means by which it is sequestered in the diverticulum is not known. The oil is an effective deterrent to potential predators such as ants, birds and mice (MORROW *et al.* 1976). It follows that the larvae adopt this circular pattern, in which they regurgitate in unison, specifically for the purpose of defence. The behaviour can therefore be classified as cycloalexy, as described by VASCONCELLOS-NETO and JOLIVET (1988).

Once the disturbance has passed, the larvae actively swallow the regurgitate back down. This even includes «spilled oil», and I have observed mutual grooming where larvae clean oil off the head capsules of their siblings with their mouthparts. This is probably necessary so as to not seal over ecdysial lines with the sticky substance. In addition, the oil is required for subsequent defence and in the construction and waterproofing of the cocoon (CARNE, 1962).

Cycloalexy and parasitoids

Although demonstrably effective against polyphagous predators, cycloalexy does not protect *Perga dorsalis* larvae form parasitoids. In the Adelaide region, the sawfly is associated with a complex of 3 parasitoids. They are all larval-pupal parasitoids, attacking early (mainly second) instar larvae, and emerging from the host cocoons.

(a) *Froggatimyia* spp. (Diptera : Tachinidae), at least 3 species with superficially identical behaviour. The fly «stalks» the host larvae, approaching very slowly on foot, and stopping for several minutes should the larvae show any sign of disturbance. In this way the fly works her way close enough to oviposit on the larvae, with her abdomen curled through her front legs. The fly often walks very close to or even on top of the larvae, without ever eliciting a defence reaction.

(b) *Westwoodia* sp. (Hymenoptera : Ichneumonidae). This is a large wasp which, having located a colony, straddles the group of larvae and starts to oviposit into them. The larvae at first rear up and regurgitate their repellent *Eucalyptus* oil. This has no apparent effect on the wasp, and within seconds the larvae break formation and disperse upon the leaf (fig. 5). The ichneumonid sometimes follows individual larvae, probing after them with her ovipositor. Under these circumstances the sawfly larvae may resort to biting. This is very effective, although altruistically suicidal, should one be lucky enough to sieze and hold the parasitoid's ovipositor (fig. 6)

(c) *Taeniogonalos venatoria* (Hymenoptera : Trigonalyidae). This unique wasp oviposits on foliage, and depends on the young host larvae to consume her eggs with the foliage they eat. The eggs only hatch if ingested by a suitable host, and the first instars presumably penetrate the gut wall (CLAUSEN, 1931). The defensive ring of regurgitating larvae is thus never encountered by the parasitoid. if primitive sawflies were the ancestral hosts of trigonalyids, it is tempting to suggest that cycloalexy may have been an influencing factor in the evolution of the unique trigonalyid oviposition strategy.

Conclusion

Cycloalexy has been described here in the early instars of *Perga dorsalis*. Similar behaviour is recorded for another species of *Perga*, *P. affinis* (CARNE, 1962). In related genera, cycloalexy occurs in *Pergagrapta condei* (personal observation) and in *Pseudoperga lewisii* (LEWIS, 1837). Based on the few detailed behavioural observations which have been made on Australian sawflies, it would appear that cycloalexy is widespread if not ubiquitous in the subfamily Perginae of Australian Pergidae.

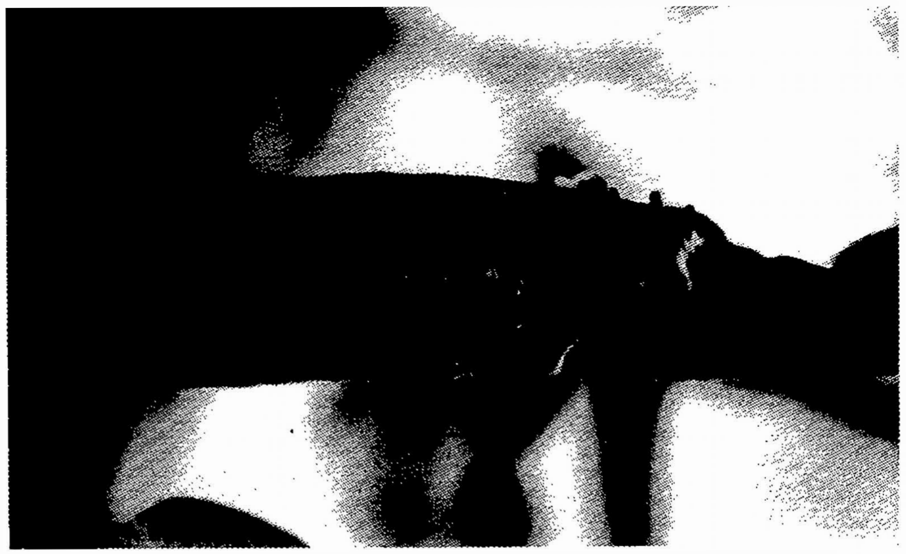

Fig. 1 - First instar larvae emerge from their eggpod and assemble in a circular formation.

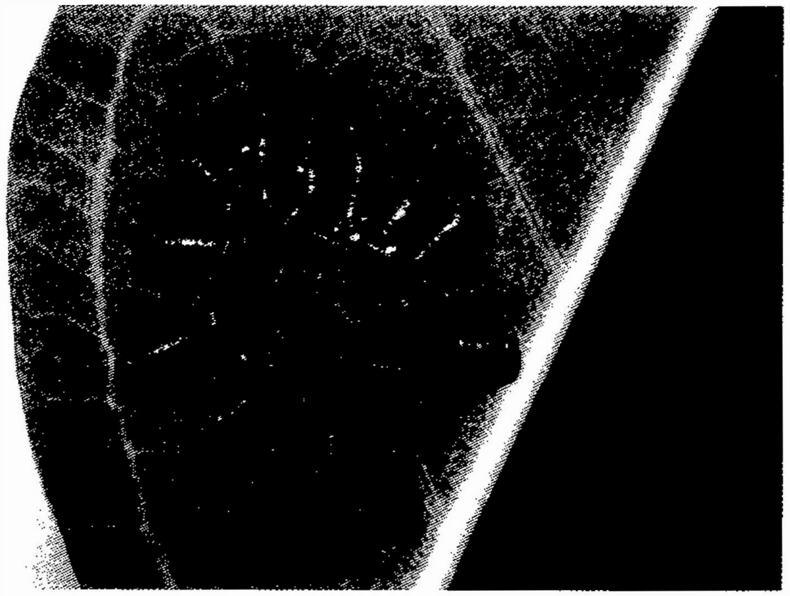

Fig. 2 - Second instar larvae demonstrating cycloalexy. White tachinid eggs can be seen on the thoracic cuticles of some larvae.

Fig. 3 - A cylindrical cluster of late instar larvae on an *Eucalyptus* twig.

Fig. 4 - Regurgitation of sequestered *Eucalyptus* oil by an artifically disturbed larva. Under natural conditions, the larvae react in unison.

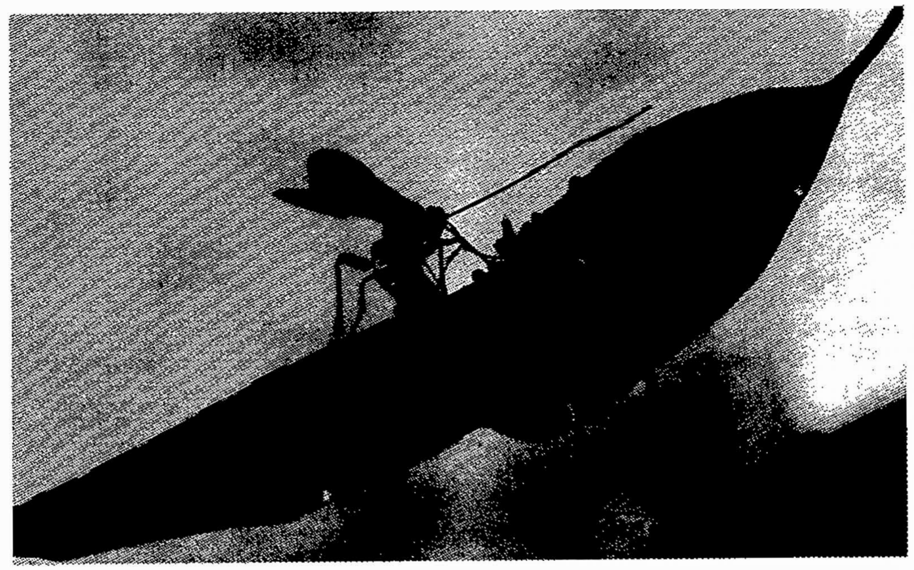

Fig. 5 - Larvae leaving their unsuccessful defensive ring in response to an ovipositing ichneumonid.

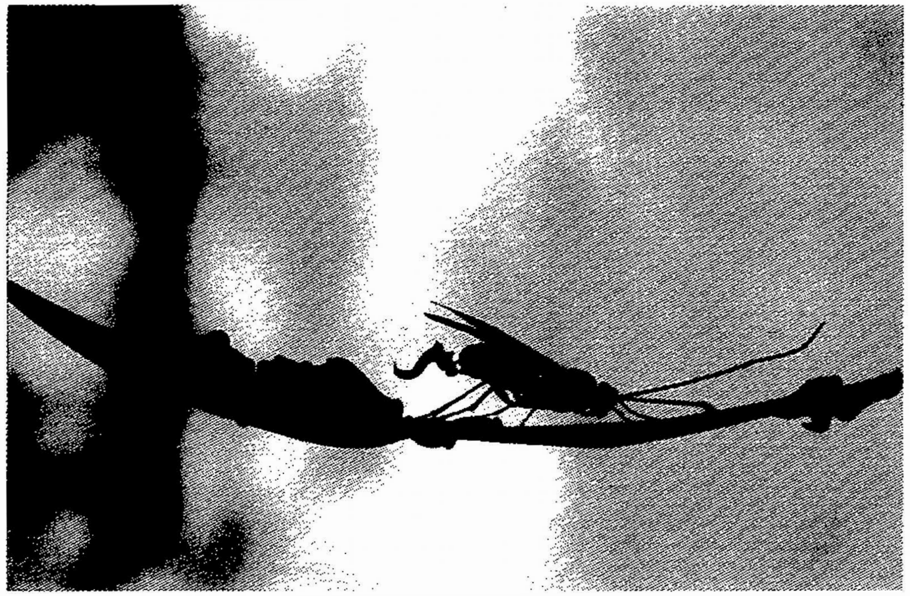

Fig. 6 - Larva gripping an ichneumonid's ovipositor with its mandibles, rendering the parasitoid incapable of further attack.

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