

BEHAVIORAL OBSERVATIONS ON THE EARLY STAGES OF *JAMIDES CELENO* (CRAMER)
(LYCAENIDAE) AT CAT TIEN NATIONAL PARK, VIETNAM: AN OBLIGATE MYRMECOPHILE?

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ABSTRACT. The life history of *Jamides celeno* has been well documented across its range. The larvae feed on plants from six families and are attended by ants from seven genera. This paper documents a new host plant record and additional attendant ant species from observations made in Cat Tien National Park, Vietnam. We discuss ecological and behavioral traits of the early stages of *J. celeno* and their associated ants, and suggest that the categorization of *J. celeno* as a facultative myrmecophile may be incorrect.

Additional key words: Ant feeding, *Camponotus*, facultative, Formicidae, mutualism, Polyommatae.

The lycaenid butterfly, *Jamides celeno* (Cramer) is a sexually dimorphic species in the subfamily Polyommatae. It is widespread in south and east Asia distributed from Sri Lanka, India and Nepal to Taiwan and south China, and throughout the Malaysian Archipelago to New Guinea and the Solomon Islands (Corbet *et al.* 1992). In Vietnam, *J. celeno* is one of the most common species of butterflies, occurring in many habitats ranging from primary evergreen forest and forest gaps to cultivated areas (Monastyrskii & Devyatkin 2002). Larvae of *J. celeno* feed on a variety of plants in the families Fabaceae, Caesalpinaceae, Sterculiaceae, Meliaceae, Zingiberaceae and Marantaceae (Robinson *et al.* 2001), and the early stages have been recorded in association with ant species across seven genera (Corbet *et al.* 1992, Ballmer 2003, Cleary & Grill 2004). Larval association with ants, termed myrmecophily, is a well-known phenomenon in the Lycaenidae (Newcomer 1912, Hinton 1951, Pierce *et al.* 2002). Symbiotic interactions fall into two broad categories: obligate, where the survival of the butterfly species is dependent on the presence of ants; or facultative, where butterfly larvae may or may not have ants in attendance (Fiedler 1991a, Eastwood & Fraser 1999). As a rule, obligate myrmecophiles associate with a single species or a group of closely related species of ants, whereas facultative myrmecophiles typically associate with a variety of ant species, often from different genera or subfamilies (Pierce *et al.* 2002). Accordingly, recent workers have categorized *J. celeno* as a facultative myrmecophile (Fiedler 1996, Ballmer 2003). During a survey of arthropod biodiversity in Nam Cat Tien Park, Vietnam, we observed *J. celeno* adults and early stages on a regular basis. The Nam Cat Tien

section of Cat Tien National Park is located in Dong Nai Province 150 km north of Ho Chi Minh City in the monsoonal tropical region of southern Vietnam. It contains the largest remaining lowland tropical forest in southern Vietnam. A semi-evergreen regeneration forest dominated by *Lagerstroemia* spp. (Lithraceae), it has an average annual rainfall of ~2300 mm and average temperatures ranging from 15 °C to 35 °C. The local Chau Ma and S'Tieng people have practiced shifting cultivation in and around the park for generations. Our visit in July 2002 coincided with the wet season, which lasts from April/May to October/November. This paper documents new ecological and behavioral traits of *J. celeno* early stages and their associated ants, and discusses the category of myrmecophily to which *J. celeno* is usually assigned.

OBSERVATIONS

Adult *J. celeno* were often encountered in open areas adjoining tracks and roads through Cat Tien National Park, but many adults were also observed within the forest where their presence usually indicated the proximity of a breeding site. Understory plants were typically less than 3 m in height and larvae were encountered on leaf flushes about 1.8 m above ground ($1.82 \text{ m} \pm 0.63 \text{ SD}$, $n=11$). Larvae formed loose aggregations ($2.36 \pm 0.92 \text{ SD}$ individuals, $n=11$) and fed exclusively on the soft new growth flush of *Euodia meliaefolia* Benth. (Rutaceae) growing in the understory. Eggs were laid on the new leaves when there was sufficient foliage to sustain a small cohort of larvae. Leaf flush varied from pale green to pale yellow in color before changing to a darker green as the leaves hardened. Larvae were either green or yellow, but

always matched the color of the leaves on which they were resting. Mature larvae became brown before leaving the tree to pupate. Larvae rested under the foliage during the day and began feeding late in the afternoon (ca. 1600 h). Their feeding patterns followed the flush of new growth as it progressed but larvae did not appear to be food-limited. Nevertheless, the butterfly had a window of only about 2-3 weeks on each tree in which the life cycles of multiple broods could be completed before the leaves hardened. Larval duration was approximately six days from egg hatching to prepupa, and pupal duration for three individuals was seven (n=2) and eight days.

Of the eleven larval aggregations observed, five ant species in two subfamilies were in attendance: *Camponotus* (*Tanaemyrmex*) sp. (n=3); *Camponotus* (*Myrmosaulos*) *singularis* (F. Smith) (n=2); *Polyrhachis* (*Myrmhopla*) *rufipes* F. Smith (n=1); *Anoplolepis gracilipes* (F. Smith) (n=2) (all Formicinae); and *Crematogaster* sp. (n=2) (Myrmicinae). Ant and butterfly voucher specimens are lodged at the Museum of Comparative Zoology, Harvard University (RE-02-A057, 58, 61, 73, 87, 88, 90, 91, 94, 105, 106, 107, 108, 160). Two larvae were found untended on different plants but the following day one (presumably the same larva) was tended by six *C. singularis* and the other mature larva could not be found on the plant or in the leaf litter. Six to ten ants typically tended larval aggregations, thus providing a significant deterrent to potential enemies of the larva. On one occasion a single *Crematogaster* was found tending a larva together with several *Camponotus singularis*. When the *Crematogaster* came into contact with one of the *Camponotus*, however, it leapt off the leaf. On another occasion several *Crematogaster* were observed tending three *J. celeno* larvae but later the same day the larvae were tended by *Camponotus singularis*. Ants were observed antennating the entire dorsal surface of the larvae and at times the ant's tongue could be seen extending to touch the larval cuticle as well as the dorsal nectary organ (see Bell 1918 for a very detailed description of the morphology of *J. celeno* early stages).

J. celeno larvae pupated at the base of the host-plant or in the leaf litter surrounding the base of the tree. Larvae tended by *Camponotus* (*Tanaemyrmex*) sp. pupated in a protective chamber or byre constructed by the ants from soil and leaf debris at the base of the tree where ants remained in attendance. Other ant species, including *C. singularis*, which did not construct a byre, were not found tending pupae. *A. gracilipes* were found in proximity to, but not tending, three prepupal larvae in the leaf litter.

Individuals of both species of *Camponotus*, but

especially *C. singularis*, were observed chewing on leaf edges where *J. celeno* larvae had been feeding. *C. singularis* remained on the leaves and continued chewing the leaf edges, after the lycaenid larvae had left to pupate, eventually leaving a rough sawtooth pattern along the leaf margin. Evidence of ant chewing was also seen on the edges of leaves adjoining those where lycaenid larvae had been feeding. A few small stingless bees were attracted to the lycaenid feeding sites.

DISCUSSION

The presence of ants at leaf margins in proximity to feeding lepidopteran larvae has been recorded previously (Ford 1945, Owen 1971, Fiedler 1991a); the ants apparently taking phloem exuding from leaves damaged by butterfly larval feeding. It is known that adult leafcutter ants in South America derive most of their nutrition from leaf phloem as they cut or chew the leaves before feeding the pulp to their fungal symbionts (Hölldobler & Wilson 1990). We could find no other records of ant chewing on leaves damaged by herbivores or around the leaf edges, and it is not known if ants behave in this manner in the absence of butterfly larvae.

The construction of a byre or gallery to house phytophagous lycaenid larvae, or to 'farm' honeydew-producing insects generally, is a well-known phenomenon among nectar-gathering ants (Hölldobler & Wilson 1990; Anderson & McShea 2001). Several lycaenid species in the Australian genus *Ogyris*, namely *O. genoveva* (Hewitson), *O. zosine* (Hewitson), *O. idmo* (Hewitson), and *O. otales* (C. Felder & R. Felder), have an obligate relationship with *Camponotus* ants (Eastwood & Fraser 1999). In these associations, butterfly larvae feed nocturnally on mistletoe high up in the trees but hide during the day in galleries constructed by the ants at the base of the trees (Eastwood 1997). Accordingly, it was surprising to find that *Camponotus* ants in Vietnam constructed a similar structure for *J. celeno*, suggesting that the behavior is a plesiomorphic trait in *Camponotus* that evolved before the evolution of mutualistic associations with *Ogyris* or *Jamides*. A similar behavior has been recorded with Mexican *C. (abdominalis) atriceps* F. Smith, tending the riodinid *Anatole rossi* Clench (Ross 1966), and South American *Camponotus* tending Polyommata lycaenids (Benyamini 1995). It seems that the butterfly larvae on all three continents are independently exploiting a trait in *Camponotus* ants, which are pre-adapted to construct byres around free-living insect mutualists. It is also interesting that *J. celeno* larvae behaved differently in choosing pupation sites when attended by different ant species. The *Camponotus* (*Tanaemyrmex*) sp. may have shepherded penultimate lycaenid instars into the byre.

However, relationships between lycaenid larvae and ants are known to differ depending on the attendant ant species (Axén 2000; Fraser *et al.* 2001).

As is the case with other *Jamides* species (Fiedler 1996), *J. celeno* did not display preference for a particular ant species, but the regularity with which we found larvae and ants together suggests that ant attendance is important for the survival of this species in the study area. Furthermore, in Thailand, Ballmer (2003) recorded 48 *J. celeno* larvae feeding within *Pueraria phaseoloides* (Roxb.) Benth. (Fabaceae) flowers and all were tended by ants, although the ants were from six genera. Cleary and Grill (2004) recorded 1079 *J. celeno* larvae in Borneo predominantly attended by *A. gracilipes*, and found there were significantly more caterpillars on plants with ants present than on plants without ants. This present study recorded five ant species from four genera, and additional attendant-ant species are noted in the literature. Although many attendant-ant species are recorded, the regularity of attendant-ant records and the high proportion of attendance levels suggest that tending ants may play a significant role in the survival of *J. celeno* overall. *J. celeno* larvae have also been found without ants (Parsons 1999, Cleary & Grill 2004); however, many other obligate lycaenid species have likewise been found untended (e.g. Eastwood & Fraser 1999). Furthermore, a recent survey of the obligate myrmecophile *Jalmenus evagoras* (Donovan), which was thought to associate preferentially with a single species of ant, showed this butterfly associated with seven species (from the same genus) across its range (RE unpublished data). Accordingly, it is plausible that for some obligate myrmecophiles, attendant-ant species specificity may be less important.

The categorization of lycaenid-ant relationships was based historically on ant attendance in non-tropical Lepidoptera (e.g. Malicky 1969, 1970; Henning 1983; Fiedler 1991a,b). Lycaenids are regarded as facultative if they associate with a variety of ant species, and obligate if they consistently associate with only one or a few closely related ant species. Ants that attend obligate myrmecophiles are typically aggressive, are spatially or temporally dominant and form long-lived colonies (Atsatt 1981; Pierce 1987; Fiedler 1991a, 2001; Eastwood & Fraser 1999). Thus, they are a predictable resource that provides optimal protection for lycaenid larvae. In the rainforest, however, an extremely diverse and heterogeneous ant fauna could necessitate association with many ant species if lycaenid larvae are to survive attacks from predators and parasites. In particular, the protection conferred by mutualistic ants could be an important and effective defence against

predacious ants, which are ubiquitous and known to attack lepidopterous larvae in south east Asian lowland rainforests (Floren *et al.* 2002). While lycaenid survival rates may be variable, depending on the species of tending ant (Eastwood 1997; Fraser *et al.* 2001), ant association should significantly improve the survival rate overall. In particular, it seems likely that pupae tended by *Camponotus (Tanaemyrmex)* sp., would have a higher survival rate since the ants protect them in an underground chamber. So, although the relationship that *J. celeno* has with ants is less specific than generally observed for obligate myrmecophiles, lack of specificity in tending ants may be a function of the heterogeneity of the ant community and not necessarily because *J. celeno* has a facultative relationship with ants. In fact, we suggest that the dependence that *J. celeno* has on attendant ants falls somewhere in the upper bounds of the continuum between facultative and obligate. Thus, the categorization of lycaenid-ant relationships, in this instance, into obligate or facultative myrmecophiles based on the number of ant partner species may be overly simplistic or misleading (e.g. Fiedler 1991a, 1996, 2001, Eastwood & Fraser 1999, Ballmer 2003).

J. celeno was recorded feeding on a single host plant at Cat Tien Park, but the record is most likely a temporal phenological preference or local host plant preference since many host plants have been recorded for this butterfly, and local preferences, especially on new growth, are recorded elsewhere (Cleary & Grill 2004). Multiple host plant use, often across several families of plants, is a characteristic of lycaenids having obligate relationships with ants (Pierce & Elgar 1985). The larvae of *J. celeno* are also difficult to detect because of their ability to adopt the color of their substrate and their tendency to hide under foliage during the day; so, in addition to the protection afforded by ants, *J. celeno* employs multiple strategies for survival. These observations highlight how much we still do not know about the intimacy of lycaenid-ant relationships and how much we can still learn about their joint survival strategies and the evolutionary forces shaping their relationships.

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