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(Citation)
Entomological Science,12(1):107-109

(Issue Date)
2009

(Resource Type)
journal article

(Version)
Accepted Manuscript

Entomological Science (2009) 12, 107–109
doi:10.1111/j.1479-8298.2009.00301.x

Suspending cocoons to evade ant predation in *Meteorus pulchricornis*, a braconid parasitoid of exposed- living lepidopteran larvae

Running title: Cocoon suspension against ant predation

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Abstract

We tested the hypothesis that cocoon suspension by a thread in hymenopteran parasitoids is a defense tactic against predators, by comparing predation against suspended and non-suspended cocoons of the braconid wasp *Meteorus pulchricornis* on a *Quercus phillyraeoides* hedge on which workers of the common small ant *Crematogaster matsumurai* were foraging. The lost proportion of non-suspended cocoons, which were artificially attached to leaves of *Q. phillyraeoides*, markedly decreased with cocoon age, indicating a critical phase of predation on young cocoons. No suspended cocoons at age 1-12 h at the beginning of exposure were lost within 12 h, whereas more than 75 % of same-aged non-suspended cocoons were lost in the same period. Predation against such young cocoons would be a strong force driving the evolution of cocoon suspension in parasitoids of exposed-living host insects.

Key words: cocoon age, *Crematogaster matsumurai*, defense, parasitic wasps, predators, suspension

Many unrelated hymenopteran parasitoids of exposed- living hosts suspend their cocoon (or host mummy) with a silk thread (e.g., Gauld & Bolton 1988; Maeto 1989, 1990; Eberhard 2000; Quicke et al. 2006). Such cocoon suspension has been speculated to be a defense tactic against predators (Shaw & Huddleston 1991; Zitani & Shaw 2002), though less probably against hyperparasitoids or psudohyperparasitoids (Zitani & Shaw 2002; Quicke et al. 2006). No experimental proof, however, had existed to support

this hypothesis. We tested this hypothesis by comparing ant predation on suspended and non-suspended cocoons of the braconid wasp *Meteorus pulchricornis* (Wesmael), a solitary endoparasitoid of various exposed- living lepidopteran larvae (Huddleston, 1980; Berry & Walker 2004; Chau & Maeto 2008). Fully grown *M. pulchricornis* larvae spin a suspended cocoon within 30 to 60 min after emergence from the host larva, continuing to add inner layers of silk to the fresh and delicate cocoon for more than 20 h before completion (Askari et al. 1977).

We conducted two field experiments on a *Quercus phillyraeoides* hedge, on which workers of the small ant *Crematogaster matsumurai* (2.5-3.5 mm in body length) were foraging, at Nigawa, Takarazuka City, Honshu, Japan, in August and September 2007. *Crematogaster matsumurai* is a common arboreal ant that forages on dead or small living arthropods as well as honeydew (Harada 2005). No other predatory arthropods were regularly observed on the hedge during the experiments.

In the first experiment, we placed an artificially non-suspended (i.e., the silk thread had been cut off) cocoon of *M. pulchricornis*, 0-96 h after emergence from the host larva (*Spodoptera litura*) in the laboratory, on a *Q. phillyraeoides* leaf with adhesive tape. After 12 h of exposure, we determined if the cocoons were intact or lost (including partially broken cases). Logistic regression was used to test the effects of month (August or September), time (24:00-06:00, 06:00-12:00, 12:00-18:00, 18:00-24:00), and cocoon age (0-12, 12-24, 24-48, 48-72, 72-96 h) at the beginning of exposure on the proportion of lost cocoons using SPSS for Windows (ver. 11.5; SPSS Inc., Chicago, IL). In the second experiment, we placed a pair of suspended and non-suspended

cocoons (1-12 h after emergence) on a *Q. phillyraeoides* leaf with adhesive tape (Fig. 1) and determined if they were intact or lost after 12 h. Cocoon length was 5-6 mm, and the distance of the silk thread from the leaf to the top of the suspended cocoon was 3-42 mm (mean±SD, 8.6±5.9 mm, n = 39). The proportion of suspended and non-suspended cocoon lost was examined with a McNemar test. In both experiments, we used *Q. phillyraeoides* leaves up to 150 cm above the ground, and we lured workers of *C. matumurai* with a living dipteran maggot (undetermined Calliphoridae) in advance (Fig. 1).

In the first experiment, the proportion of lost non-suspended cocoons was significantly affected by month and cocoon age at the beginning of exposure, but not by the time of exposure (Table 1). Over 50 % of cocoons younger than 12 h at the beginning of exposure were lost, but the percent decreased with cocoon age both in August and September (Fig. 2, Table 2). In the second experiment, no suspended cocoons were lost, whereas 75-84 % of non-suspended cocoons were lost within 12 h (Table 2). The proportion of lost cocoons was significantly different between suspended and non-suspended cocoons in each month (Table 2).

Most cases of lost cocoons were probably due to predation by *C. matumurai* because no other apparent predators were observed during the experiments. Cocoon suspension is likely a successful tactic to evade predation by ants and other small arthropods, as proposed by Shaw & Huddleston (1991) and Zitani & Shaw (2002). Our results also indicate that this defense is required and especially effective in the early critical phase of cocoons. Cocoon hardness increases gradually, eventually providing enough protection against small predators such as *C. matsumurai* workers, whereas

fresh and delicate cocoons under construction can be easily broken by them. Predation on such young cocoons may be a strong force driving the evolution of cocoon suspension in parasitic Hymenoptera of exposed- living hosts.

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Table 1 Logistic regression analysis of the proportion of non-suspended cocoons that were lost within 12 h

Factor	Parameter	*n*	Wald statistic	d.f.	*P*	Odds ratio exp (*B*)
Month	August	73	–	–	–	1.000
	September	72	10.580	1	0.001	0.202
Time at the beginning of exposure	24:00–06:00	40	–	–	–	1.000
	06:00–12:00	28	0.224	1	0.636	0.707
	12:00–18:00	20	1.209	1	0.272	2.833
	18:00–24:00	57	0.312	1	0.576	0.728
Age at the beginning of Exposure (h)	0–12	39	–	–	–	1.000
	12–24	15	4.819	1	0.028	0.197
	24–48	30	10.797	1	0.001	0.117
	48–72	31	21.278	1	< 0.001	0.024
	72–96	30	14.871	1	< 0.001	0.066
	Constant		10.365	1	0.001	8.194

−2 log-likelihood = 133.05.

August (Month), 24:00–06:00 (Time), and 0–12 h (Age) were selected as reference categories.

Table 2 Number of intact and lost cocoons (1- to 12-h-old at the beginning of exposure) attached to *Q. phillyraeoides* leaves in suspended and non-suspended cocoon pairs after 12 h

Month	Non-suspended cocoons	Suspended cocoons		McNemar test exact *P*-value
		+	−	
August	+	5	0	< 0.001
	−	15	0	
September	+	3	0	< 0.001
	−	16	0	

+, intact; −, lost or broken

Figure 1 Suspended (below) and non-suspended (middle) *Meteorus pulchricornis* cocoons attached to a *Quercus phillyraeoides* leaf, with a dipteran maggot (upper left) to lure *Crematogaster matsumurai* workers.

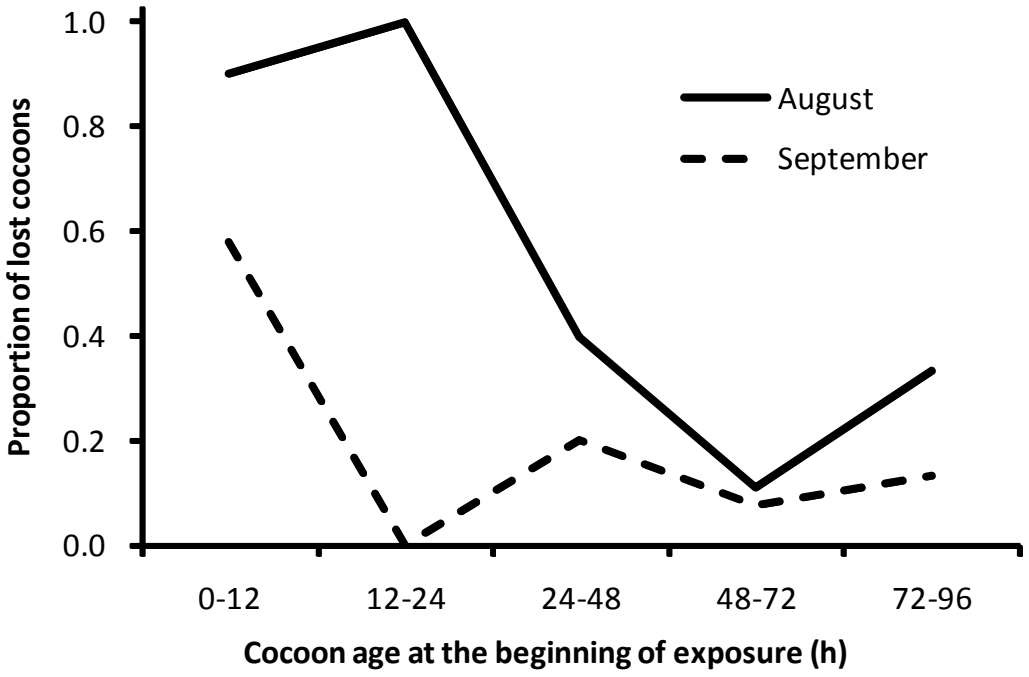

Figure 2 The proportion of non-suspended cocoons lost relative to cocoon age.