

Bagworm bags as portable armour against invertebrate predators

Shinji Sugiura

Some animals have evolved the use of environmental materials as “portable armour” against natural enemies. Portable bags that bagworm larvae (Lepidoptera: Psychidae) construct using their own silk and plant parts are generally believed to play an important role as a physical barrier against natural enemies. However, no experimental studies have tested the importance of bags as portable armour against predators. To clarify the defensive function, I studied the bagworm *Eumeta minuscula* and a potential predator *Calosoma maximoviczi* (Coleoptera: Carabidae). Under laboratory conditions, all bagworm larvae were attacked by carabid adults, but successfully defended themselves against the predators’ mandibles using their own bags. The portable bags, which are composed mainly of host plant twigs, may function as a physical barrier against predator mandibles. To test this hypothesis, I removed the twig bags and replaced some with herb leaf bags; all bag-removed larvae were easily caught and predated by carabids, while all bag-replaced larvae could successfully defend themselves against carabid attacks. Therefore, various types of portable bag can protect bagworm larvae from carabid attacks. This is the first study to test the defensive function of bagworm portable bags against invertebrate predators.

Bagworm bags as portable armour against invertebrate predators

Shinji Sugiura

Graduate School of Agricultural Science, Kobe University, Kobe, Hyogo, Japan

Correspondence author

Shinji Sugiura,

sugiura.shinji@gmail.com.

Running title: Bagworm defence against predators

ABSTRACT

Some animals have evolved the use of environmental materials as “portable armour” against natural enemies. Portable bags that bagworm larvae (Lepidoptera: Psychidae) construct using their own silk and plant parts are generally believed to play an important role as a physical barrier against natural enemies. However, no experimental studies have tested the importance of bags as portable armour against predators. To clarify the defensive function, I studied the bagworm *Eumeta minuscula* and a potential predator *Calosoma maximoviczi* (Coleoptera: Carabidae). Under laboratory conditions, all bagworm larvae were attacked by carabid adults, but successfully defended themselves against the predators’ mandibles using their own bags. The portable bags, which are composed mainly of host plant twigs, may function as a physical barrier against predator mandibles. To test this hypothesis, I removed the twig bags and replaced some with herb leaf bags; all bag-removed larvae were easily caught and predated by carabids, while all bag-replaced larvae could successfully defend themselves against carabid attacks. Therefore, various types of portable bag can protect bagworm larvae from carabid attacks. This is the first study to test the defensive function of bagworm portable bags against invertebrate predators.

Subjects Animal Behaviour – Ecology – Entomology – Evolutionary Studies – Zoology

Keywords Carabidae – physical defense – portable cases – predation – Psychidae

INTRODUCTION

Animals have evolved defensive armour to protect themselves from predators; for example, armadillos and crabs have hardened their exoskeletons, hedgehogs and sticklebacks have developed spines, and snails have developed shells as defensive armour (Edmunds, 1974; Eisner, 2003; Emlen, 2014). Conversely, some animals, such as hermit crabs, have evolved the use of environmental materials (i.e., gastropod shells) as “portable armour” against predators (Edmunds, 1974).

The larvae of holometabolous insects are vulnerable to enemy attacks because of their soft bodies, and have developed various types of defensive armour (Greeney, Dyer & Smilanich, 2012). For example, the spines and hairs of caterpillars constitute physical defences against predators (Dyer, 1995, 1997; Murphy et al., 2009; Sugiura & Yamazaki, 2014). Some insect larvae construct “portable cases” using their own silk thread, excrement, or environmental materials (e.g., plant parts and stones). Such case-bearing behaviour has been found in three holometabolous insect orders (Root & Messina, 1983): Trichoptera (e.g., caddisfly larvae of the suborder Integripalpia; Holzenthal et al., 2007); Coleoptera (e.g., leaf beetle larvae of the subfamilies, Clytrinae, Cryptocephalinae, Chlamisinae, and Lamprosomatinae; Brown & Funk, 2005; Chaboo, Brown & Funk, 2008); and Lepidoptera (e.g., moth larvae of the superfamilies Incurvarioidea, Tineoidea, and Gelechioidea; Stehr, 1987). Physical defence against predators using portable cases has been tested experimentally in Trichoptera (Otto & Svensson, 1980; Ferry et al., 2013) and Coleoptera (Root & Messina, 1983; Brown & Funk, 2010), but not in Lepidoptera.

The bagworm family Psychidae (Lepidoptera: Tineoidea) includes ca. 1000 species, and all of their larvae construct portable cases (Rhainds, Davis & Price, 2009). The materials used for

constructing bags differ among bagworm species; e.g., tree/herb/grass leaves, lichens, twigs, petioles, bark fragments, wood debris, and sand particles (Sugimoto, 2009a,b). The portable bags are generally believed to play an important role as portable armour against natural enemies (Rhainds, Davis & Price, 2009). For example, bags have been reported to function as a physical barrier against parasitoid attack; the ovipositor of an ichneumonid parasitoid was too short to reach pupae of the bagworm *Thyridopteryx ephemeraeformis* (Haworth) inside the larger bags, and the parasitism rate was inversely correlated with bag size (Cronin & Gill, 1989). However, bagworm larvae and pupae inside bags are generally known to suffer heavier parasitism by more diverse parasitoids than are other external-feeding caterpillars (Hawkins, 1994), suggesting that bagworm bags may not be effective armour against parasitoids. Rather, predators such as birds and predacious arthropods may impose a selective pressure on the evolution or maintenance of bags. Although the impacts of predators have been reported in some bagworm species (Rhainds, Davis & Price, 2009; Pierre & Idris, 2013), no experimental studies have tested the importance of bags and materials used for bags as defensive armour against predators. Clarifying the defensive function of bags would contribute to further understanding of how portable armour has evolved in animals.

To test whether portable bags can protect bagworms from predator attacks, *Calosoma* adults (Coleoptera: Carabidae) were observed attacking larvae of a bagworm species under laboratory conditions. Adults of the carabid genus *Calosoma* hunt lepidopteran larvae and pupae (Forsythe, 1982; Weseloh, 1985; Bruschi, 2013), providing a good model predator for investigating the defensive behaviour of lepidopteran larvae (Sugiura & Yamazaki, 2014). In this study, I first investigated the defensive success or failure of bagworm larvae against carabid attacks. Second, I tested whether bag-removed larvae could defend themselves against carabids in order to clarify the importance of bags. Furthermore, I investigated the effects of bag replacement (with a

different type of bag) on the defensive success of bagworm larvae against carabid attacks to elucidate the importance of materials for constructing bags.

MATERIAL AND METHODS

Study species

To clarify the defensive function of portable bags, I used the bagworm species *Eumeta minuscula* Butler and the potential predator *Calosoma maximoviczi* Morawitz.

Larvae of *E. minuscula* feed on leaves of various woody species, including both angiosperms and gymnosperms, and construct portable bags using their own silk thread and leaf fragments/petioles/twigs of host plants (Fig. 1a,b; Kobayashi & Taketani, 1993; Sugimoto, 2009b). In Japan, *E. minuscula* overwinters as middle-instar larvae and pupates in early summer (Kobayashi & Taketani, 1993). Various natural enemies are known to attack *E. minuscula* larvae and pupae inside the bags (Kobayashi & Taketani, 1993), including 25 parasitoid wasp species (Nishida, 1983), three parasitoid fly species (Shima, 1999), one ant species (Nishida, 1983), and one bird species (Ikeda, 1988). For laboratory experiments, all *E. minuscula* larvae were collected from the forest edge in Shimosasori, Takarazuka, Hyogo (34°55'N, 135°18'E, 190 m above sea level) in late May 2015. Active larvae were used in laboratory experiments, although unhatched eggs of parasitoid flies (Diptera: Tachinidae) were found on some active larvae.

Before the experiments, I measured the fresh weight of each *E. minuscula* larva and its bag to the nearest 0.1 mg using an electronic balance (PA64JP, Ohaus, Tokyo, Japan). I also used slide callipers to measure the bag length, larval length, and head capsule width of *E. minuscula* to the closest 0.1 mm. Sampled larvae were determined to be 6th or 7th (last) instar based on the head

capsule width (Nishida, 1983). The bags were ca. 1.8 times the length of the larvae (Fig. 1b; mean larval body length, 17.7 ± 2.5 mm (mean \pm SD), mean bag length, 32.4 ± 4.9 mm, $n = 36$) and as heavy as larvae (mean fresh larval weight, 245.3 ± 71.1 mg, mean fresh bag weight, 245.0 ± 74.4 mg, $n = 36$). All bags were composed mainly of plant twigs (Fig. 1a,b).

Calosoma maximoviczi adults exclusively hunt lepidopteran larvae on both the ground and vegetation (Kamata & Igarashi, 1995; Sugiura & Yamazaki, 2014). This carabid species uses its mandibles to catch and injure caterpillars, and then feeds on them (Sugiura & Yamazaki, 2014). Since *C. maximoviczi* adults can attack caterpillars of various species and size under laboratory conditions, *C. maximoviczi* adults are considered appropriate for investigating the defence behaviour of lepidopteran larvae against generalist predators (Sugiura & Yamazaki, 2014). For laboratory experiments, all adults of *C. maximoviczi* were collected from a secondary forest in Nunobiki, Kobe, Hyogo ($34^{\circ}42'N$, $134^{\circ}11'E$, 60–170 m above sea level), in early May 2015. I have not observed *C. maximoviczi* adults attacking bagworms under field conditions; however, the habitat and active season partly overlap between *E. minuscula* larvae and *C. maximoviczi* adults in this sampling region, suggesting that *E. minuscula* larvae can encounter *C. maximoviczi* adults on trunks or twigs of woody plants. Active adults of *C. maximoviczi*, which attacked caterpillars under laboratory conditions, were used in the laboratory experiments. Before the experiments, I measured the fresh weight of each adult of *C. maximoviczi* to the nearest 0.1 mg using an electronic balance. I also used slide callipers to measure the body and mandible lengths of *C. maximoviczi* to the closest 0.1 mm.

Laboratory experiments

To test the defensive function of portable bags, I conducted the following experiment in a

well-lit laboratory (25°C) in late May 2015. A bagworm larva and a carabid adult were placed on bamboo material (width 7 mm, height 15 mm; Fig. 1c, 2), which modelled tree twigs and trunks, because both carabids and bagworms forage on tree twigs and trunks under field conditions. The bamboo material was looped (Fig. 2; length 700 mm, diameter 200 mm) so that bagworms could encounter carabids in all trials. The looped bamboo material was also surrounded by a plastic circular cylinder (diameter 220 mm, height 120 mm).

I deemed that a bagworm larva could not defend itself against a carabid adult when the carabid was observed to catch and injure the larva. When an adult carabid gave up attacking a bagworm without injuring it, I deemed that the bagworm successfully defended itself against the carabid. I removed each bagworm from the bamboo material just after the successful or unsuccessful defence. I used 15 adults (4 females and 11 males) of *C. maximoviczi* (mean body weight, 447.1 ± 104.7 mg (mean \pm SD), mean body length, 25.1 ± 2.0 mm, mean mandible length, 1.9 ± 0.1 mm, $n = 15$) to conduct three types of experiments (Table 1); body weight and length significantly differed among three types of experiments (one-way analyses of variance; body weight, $F = 4.3$, $P = 0.04$; body length, $F = 4.1$, $P = 0.04$), while mandible length did not differ ($F = 0.9$, $P = 0.44$).

Experiment 1: Normal *E. minuscula* larvae (bag treatment, control) were provided as the first prey to five adult *C. maximoviczi* (Table 1). To clarify the importance of bags as a defensive barrier against predators, I provided bag-removed *E. minuscula* larvae (bag treatment, removed) as the second prey to the same five carabid individuals just after the attack on the first prey (Table 1). I used a pair of scissors to remove the bags from *E. minuscula* larvae; first prey that successfully defended itself against carabid attacks was also used as the second prey. When the first prey was predated, I used a different larva of *E. minuscula* as the second prey.

Experiment 2: Bag-removed *E. minuscula* larvae were provided as the first prey to five adult

C. maximoviczi (Table 1). I provided control *E. minuscula* larvae as the second prey to the same five carabids just after the attack on the first prey (Table 1). Different *E. minuscula* larvae were used as the second prey. I conducted this experiment to avoid any potential systematic effects of the first prey on responses to the second prey by carabids.

Experiment 3: Bag-replaced *E. minuscula* larvae (bag treatment, replaced) were provided as the first prey to five adult *C. maximoviczi* (Table 1). To clarify the importance of materials for constructing bags, I replaced the normal (tight) bags with soft bags. I used a pair of scissors to remove the bags from ten *E. minuscula* larvae. The larvae were placed individually in plastic Petri dishes (90 mm diameter, 30 mm high) with minced leaves of the herb species *Artemisia indica* var. *maximowiczii* (Asteraceae). I used a pair of scissors to mince the leaves (mean fragment length, 4.4 ± 1.7 mm, $n = 27$). Five of ten *E. minuscula* larvae constructed sufficiently large bags (bag length > 25 mm) using their own silk thread and the leaf fragments (Fig. 3) one day after placement. The replaced bags were ca. 1.5 times the length of the larvae (mean larval body length, 18.6 ± 2.7 mm, mean bag length, 27.9 ± 1.2 mm, $n = 5$) and half as heavy as larvae (mean fresh larval weight, 266.9 ± 75.1 mg, mean fresh bag weight, 135.3 ± 35.8 mg, $n = 5$). Such replacement with a different type of bag has been conducted in another bagworm species (Kaufmann, 1968). Five larvae constructing new bags were used as the first prey in this experiment. Just after observing the attack on the first prey (i.e., bag-replaced larvae), I provided bag-removed *E. minuscula* larvae as the second prey to the same five carabids (Table 1). First prey that had successfully defended itself against carabid attacks was also used as second prey. When the first prey was predated, I used a different *E. minuscula* larva as the second prey.

All adult carabids attacked each bagworm within the 10-min period. Even when bagworms did not actively walk, carabids were observed to attack and bite motionless bags. Larval weight, bag weight, total (larval + bag) weight, bag length, and larval length of the *E. minuscula* used in

this study did not differ among the three experiments (one-way ANOVA; $F = 0.2\text{--}1.1$, $P = 0.38\text{--}0.84$).

Data analysis

In the previous section, one-way analysis of variance (ANOVA) models were used to compare the weight and length of the bagworm *E. minuscula* and the predator *C. maximoviczi* among different experimental treatments. Values are reported as the mean \pm SD.

I observed attack–defence behaviour in 30 pairs of the predator *C. maximoviczi* and the prey *E. minuscula* (Table 1). To examine the effects of bag treatments on bagworm defence, I tentatively used a generalised linear mixed model (GLMM) with a binomial error distribution and a logit link. The binary response variable was defensive success or failure (1/0) by bagworms, fixed factors were bag treatments (control, removed, and replaced) and the random effect was carabid individuals. When all bagworms successfully defended themselves in at least one treatment group, parameters were extended to infinity in these cases when all values in a category were 0 or 1 (c.f., Sugiura & Yamazaki, 2014); therefore, the GLMM could not be conducted in this case. Alternatively, I used Fisher’s exact test to compare the success rate of defence by bagworms between control, bag-removed, and bag-replaced treatments. Considering the independence of the data, I excluded the data for the second prey from the analysis.

All analyses were performed using R ver. 2.15.1 (R Development Core Team, 2012).

RESULTS

Experiment 1: all control *E. minuscula* larvae ($n = 5$) were attacked by *C. maximoviczi* adults, but successfully defended themselves against the predator attacks (Table 1; Fig. 1c,d). When

bagworm larvae were attacked by carabids, the larvae quickly retracted their heads and thoraxes into their bags to escape from the attacks (Fig. 1d; Supplemental Information Movie S1). Carabids frequently bit the bags, but could not injure the larvae due to the bag protection (Fig. 1d). Finally, all of the carabids gave up attacking the larvae. However, all of the bag-removed larvae were easily caught and injured by the same individual carabids (Fig. 1e; Table 1; Movie S1). The dorsal, lateral, or ventral abdomens of larvae were the locations injured by carabid mandibles.

Experiment 2: all bag-removed larvae ($n = 5$) were easily caught and predated by carabids (Table 1). All control larvae ($n = 5$) were attacked by the same individual carabids, but successfully defended themselves against the attacks due to bag protection (Table 1).

Experiment 3: all bag-replaced larvae ($n = 5$) were attacked by carabids, but successfully defended themselves against the attacks (Fig. 1f; Table 1). Carabids frequently bit the soft bags, but could not injure the larvae due to the bag protection (Movie S1). However, all the bag-removed larvae were easily predated by the same individual carabids (Table 1).

The success rate of bagworm defence differed significantly among bag treatments (Fig. 3); the defensive success rate of control, bag-removed, and bag-replaced larvae was 100%, 0%, and 100%, respectively (Table 1; Fisher's exact test; control vs. bag-removal, $P = 0.0008$, control vs. bag-replacement, $P = 1.0$, bag-removal vs. bag-replacement, $P = 0.0008$).

DISCUSSION

Portable cases of bagworms are generally believed to play an important role as a physical defence against natural enemies (Rhainds, Davis & Price, 2009); however, no studies have tested their effectiveness experimentally. This study demonstrated that bags could protect *E. minuscula*

larvae from *C. maximoviczi* attacks (Table 1; Fig. 3). This is the first study to test the defensive function of portable cases against invertebrate predators in Lepidoptera. Although the bag defence of a single bagworm species was shown in this study, my experiment showed that bags made from two different materials (i.e., twig and herb leaf bags) could effectively defend bagworms against the predator (Table 1; Fig. 3). Accordingly, bags made of other materials may also function as defensive armour against invertebrate predators, although further studies are needed. Studies have clarified the defensive function of portable cases in the two holometabolous insect orders Trichoptera (Otto & Svensson, 1980; Ferry et al., 2013) and Coleoptera (Root & Messina, 1983; Brown & Funk, 2010). This study clarified the defensive function in the order Lepidoptera, strengthening the hypothesis that case-bearing behaviour has repeatedly evolved for anti-predator defence in insects.

Although the large bags of bagworms can prevent parasitoid oviposition (Cronin & Gill, 1989), more diverse parasitoid species and higher parasitism rates have been reported for case-bearing caterpillars than bare caterpillars (Hawkins, 1994). This may be related to the “refugia” hypothesis; i.e., caterpillars that are unlikely to be eaten by predators can provide enemy-free space for parasitoids (Gentry & Dyer, 2002; Stireman & Singer, 2003). In fact, more parasitoid species are known to parasitise *Eumeta* bagworms (Nishida, 1983). Studies have used predators from various groups, including ants, bugs, and wasps, to test the effectiveness of caterpillar defences against natural enemies (Dyer, 1995, 1997; Murphy et al., 2009); however, I used a single predator species in this study. Many interaction factors such as attack size, strategy, and natural history of the predators may cause the variation in defensive effectiveness in caterpillars. Consequently, bagworm defences against predators other than carabid beetles should be tested to clarify the selective agents leading to the evolution of portable bags.

Bagworm bags may have other functions (Rhainds, Davis & Price, 2009). For example, bags

can provide microclimate conditions that protect immature bagworm from desiccation or that accelerate development (Barbosa, Waldvogel & Breisch, 1983; Smith & Barrows, 1991; Rivers, Antonelli & Yoder, 2002; Rhainds, Davis & Price, 2009). In addition, constructing bags can magnify their relative size to arthropod predators; e.g., bags were ca. 1.8 times the length of larvae in *E. minuscula* (Fig. 1b). The size magnification by bag construction can provide protection through increased effectiveness of physical or behavioural defences against arthropod predators because predation by arthropods is generally negatively size-dependent (Rommel, Davison & Tammaru, 2011; Greeney, Dyer & Smilanich, 2012). However, one study indicated that *C. maximoviczi* adults could attack and predate various sizes of lepidopteran larvae (body weight, 33.3–566.7 mg, body length, 12.6–34.6 mm; Sugiura & Yamazaki, 2014). Therefore, the different predation rate by *C. maximoviczi* adults between control and bag-removed larvae (Table 1; Fig. 3) was not caused by the size difference between control and bag-removed larvae, but by the presence/absence of bags. Furthermore, the cryptic appearance can also serve as camouflage (Rhainds, Davis & Price, 2009), and although this study did not test the importance of cryptic appearance for bagworms, *C. maximoviczi* adults were frequently observed to attack and bite motionless bags of *E. minuscula* larvae. This suggests that carabids can use scent as well as appearance to locate prey. Therefore, the cryptic appearance of bagworms was unlikely to influence my results. Taken together, bagworm bags may have various types of functions that are not mutually exclusive. Portable cases that have more than one function may be selected more frequently and evolve more rapidly than those with a single function.

ADDITIONAL INFORMATION AND DECLARATIONS

Competing Interests

The author declares there are no competing interests.

Author Contributions

Shinji Sugiura conceived and designed the experiments, performed the experiments, analysed the data, contributed materials/analysis tools, wrote the paper, prepared figures and tables, and reviewed drafts of the paper.

Animal Ethics

The insects used in this study were not endangered or protected species in the sampling region. The experiments were undertaken according to the Kobe University Animal Experimentation Regulations. The experiments also comply with the current laws of Japan.

Funding

This research was partly supported by a Grant-in-Aid for Scientific Research (no. 25292034).

Supplemental Information

Movie S1 A movie showing the carabid *Calosoma maximoviczi* attacking normal, bag-removed, and bag-replaced larvae of *Eumeta minuscula* under laboratory conditions. Normal and bag-replaced larvae could successfully defend themselves against carabid mandibles due to bag protection, while bag-removed larvae were easily predated by carabids.

REFERENCES

- 298 **Barbosa P, Waldvogel MG, Breisch NL. 1983.** Temperature modification by bags of the
299 bagworm *Thyridopteryx ephemeraeformis* (Lepidoptera: Psychidae). *Canadian*
300 *Entomologist* **115**:855–858.
- 301 **Brown CG, Funk DJ. 2005.** Aspects of the natural history of *Neochlamisus* (Coleoptera:
302 Chrysomelidae): fecal case-associated life history and behavior, with a method for studying
303 insect constructions. *Annals of the Entomological Society of America* **98**:711-725. DOI
304 [10.1603/0013-8746\(2005\)098\[0711:AOTNHO\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2005)098[0711:AOTNHO]2.0.CO;2).
- 305 **Brown CG, Funk DJ. 2010.** Antipredatory properties of an animal architecture: how complex
306 faecal cases thwart arthropod attack. *Animal Behaviour* **79**:127–136 DOI
307 [10.1016/j.anbehav.2009.10.010](https://doi.org/10.1016/j.anbehav.2009.10.010).
- 308 **Bruschi S. 2013.** *Calosoma of the world*. Bologna: Natura Edizioni Scientifiche.
- 309 **Chaboo CS, Brown CG, Funk DJ. 2008.** Faecal case architecture in the gibbosus species group
310 of *Neochlamisus* Karren, 1972 (Coleoptera: Chrysomelidae: Cryptocephalinae: Chlamisini).
311 *Zoological Journal of the Linnean Society* **152**:315–351 DOI [10.1111/j.1096-](https://doi.org/10.1111/j.1096-3642.2007.00343.x)
312 [3642.2007.00343.x](https://doi.org/10.1111/j.1096-3642.2007.00343.x).
- 313 **Cronin JT, Gill DE. 1989.** The influence of host distribution, sex, and size on the level of
314 parasitism by *Itoplectis conquisitor* (Hymenoptera: Ichneumonidae). *Ecological*
315 *Entomology* **14**:163–173 DOI [10.1111/j.1365-2311.1989.tb00766.x](https://doi.org/10.1111/j.1365-2311.1989.tb00766.x).
- 316 **Dyer LA. 1995.** Tasty generalists and nasty specialists? Antipredator mechanisms in tropical
317 lepidopteran larvae. *Ecology* **76**:1483–1496 DOI [10.2307/1938150](https://doi.org/10.2307/1938150).
- 318 **Dyer LA. 1997.** Effectiveness of caterpillar defense against three species of invertebrate
319 predators. *Journal of Research on the Lepidoptera* **34**:48–68.
- 320 **Edmunds M. 1974.** *Defense in animals*. Harlow: Longman.
- 321 **Eisner T. 2003.** *For love of insects*. Cambridge: The Belknap Press of the Harvard University

Press.

Emlen DJ. 2014. *Animal weapons: the evolution of battle*. New York: Holt.

Ferry EE, Hopkins GR, Stokes AN, Mohammadi S, Brodie ED, Gall BG. 2013. Do all portable cases constructed by caddisfly larvae function in defense? *Journal of Insect Science* **13**:5 DOI [10.1673/031.013.0501](https://doi.org/10.1673/031.013.0501).

Forsythe TG. 1982. Feeding mechanisms of certain ground beetles (Coleoptera: Carabidae). *The Coleopterists' Bulletin* **36**:26–73.

Gentry GL, Dyer LA. 2002. On the conditional nature of neotropical caterpillar defenses against their natural enemies. *Ecology* **83**:3108–3119 DOI [10.1890/0012-9658\(2002\)083\[3108:OTCNON\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[3108:OTCNON]2.0.CO;2).

Greeney HF, Dyer LA, Smilanich AM. 2012. Feeding by lepidopteran larvae is dangerous: a review of caterpillars' chemical, physiological, morphological, and behavioral defenses against natural enemies. *Invertebrate Survival Journal* **9**:7–34.

Hawkins BA. 1994. *Pattern and process in host-parasitoid interactions*. Cambridge: Cambridge University Press.

Holzenthal RW, Blahnik RJ, Prather AL, Kjer KM. 2007. Order Trichoptera Kirby, 1813 (Insecta), Caddisflies. *Zootaxa* **1668**:639–698.

Ikeda K. 1988. Predation on the bagworms *Eumeta minuscula* and *Eumeta japonica* by the Japanese White-eye *Zosterops japonicus* in winter. *Forest Pest* **37**:28–31. (In Japanese)

Kamata N, Igarashi Y. 1995. An example of numerical response of the carabid beetle, *Calosoma maximowiczii* Morawitz (Col., Carabidae), to the beech caterpillar, *Quadricalcarifera punctatella* (Motschulsky) (Lep., Notodontidae). *Journal of Applied Entomology* **119**:139–142 DOI [10.1111/j.1439-0418.1995.tb01259.x](https://doi.org/10.1111/j.1439-0418.1995.tb01259.x).

Kaufmann T. 1968. Observations on the biology and behavior of the evergreen bagworm moth,

Thyridopteryx ephemeraeformis (Lepidoptera: Psychidae). *Annals of the Entomological Society of America* **61**:38–44 DOI [10.1093/aesa/61.1.38](https://doi.org/10.1093/aesa/61.1.38).

Kobayashi F, Taketani A. eds. 1993. *Forest insects*. Tokyo: Yokendo. (In Japanese)

Murphy SM, Leahy SM, Williams LS, Lill JT. 2009. Stinging spines protect slug caterpillars (Limacodidae) from multiple generalist predators. *Behavioral Ecology* **21**:253–160 DOI [10.1093/beheco/arp166](https://doi.org/10.1093/beheco/arp166).

Nishida E. 1983. Biologies and parasite complexes of two bagworms, *Eumeta japonica* and *Eumeta minuscula* (Lepidoptera, Psychidae), in Japan. *Kontyû* **51**:394–411.

Otto C, Svensson BS. 1980. The significance of case material selection for the survival of caddis larvae. *Journal of Animal Ecology* **49**:855–865.

Pierre EM, Idris AH. 2013. Studies on the predatory activities of *Oecophylla smaragdina* (Hymenoptera: Formicidae) on *Pteroma pendula* (Lepidoptera: Psychidae) in oil palm plantations in Teluk Intan, Perak (Malaysia). *Asian Myrmecology* **5**:163–176.

R Development Core Team. 2012. R, a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Rommel T, Davison J, Tammaru T. 2011. Quantifying predation on folivorous insect larvae: the perspective of life-history evolution. *Biological Journal of the Linnean Society* **104**:1–18 DOI [10.1111/j.1095-8312.2011.01721.x](https://doi.org/10.1111/j.1095-8312.2011.01721.x).

Rhainds M, Davis DR, Price PW. 2009. Bionomics of bagworms (Lepidoptera: Psychidae). *Annual Review of Entomology* **54**:209–226 DOI [10.1146/annurev.ento.54.110807.090448](https://doi.org/10.1146/annurev.ento.54.110807.090448).

Rivers DB, Antonelli AL, Yoder JA. 2002. Bags of the bagworm *Thyridopteryx ephemeraeformis* (Lepidoptera: Psychidae) protect diapausing eggs from water loss and chilling injury. *Annals of the Entomological Society of America* **95**:481–486 DOI [10.1603/0013-8746\(2002\)095\[0481:BOTBTE\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2002)095[0481:BOTBTE]2.0.CO;2).

- 370 **Root RB, Messina FJ. 1983.** Defensive apdaptation and natural enemies of a case-bearing
371 beetle *Exema canadensis* (Coleoptera: Chrysomelidae). *Psyche* **90**:67–80 DOI
372 [10.1155/1983/47471](https://doi.org/10.1155/1983/47471).
- 373 **Shima H. 1999.** Host-parasite catalog of Japanese Tachinidae (Diptera). *Makunagi: Acta*
374 *Dipterologica* Suppl. **1**:1–108.
- 375 **Smith MP, Barrows EM. 1991.** Effects of larval case size and host plant species on case
376 internal temperature in the bagworm, *Thyridopteryx ephemeraeformis*
377 (Haworth)(Lepidoptera: Psychidae). *Proceedings of the Entomological Society of*
378 *Washington* **93**: 834–838.
- 379 **Stehr FW. 1987.** *Immature insects, vol. 1*. Dubuque: Kendall/Hunt.
- 380 **Stireman JO III, Singer MS. 2003.** Determinants of parasitoid-host associations: insights from
381 a natural tachinid-lepidopteran community. *Ecology* **84**:296–310 DOI [10.1890/0012-](https://doi.org/10.1890/0012-9658(2003)084[0296:DOPHAI]2.0.CO;2)
382 [9658\(2003\)084\[0296:DOPHAI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0296:DOPHAI]2.0.CO;2)
- 383 **Sugimoto M. 2009a.** A comparative study of larval cases of Japanese Psychidae (Lepidoptera)
384 (1). *Japanese Journal of Entomology (New Series)* **12**:1–15.
- 385 **Sugimoto M. 2009b.** A comparative study of larval cases of Japanese Psychidae (Lepidoptera)
386 (2). *Japanese Journal of Entomology (New Series)* **12**:17–29.
- 387 **Sugiura S, Yamazaki K. 2014.** Caterpillar hair as a physical barrier against invertebrate
388 predators. *Behavioral Ecology* **25**:975–983 DOI [10.1093/beheco/aru080](https://doi.org/10.1093/beheco/aru080)
- 389 **Weseloh RM. 1985.** Predation by *Calosoma sycophanta* L. (Coleoptera: Carabidae): evidence
390 for a large impact on gypsy moth, *Lymantria dispar* L. (Lepidoptera: Lymantriidae), pupae.
391 *Canadian Entomologist* **117**:1117–1126.

394 The English in this document has been checked by at least two professional editors, both native
 395 speakers of English. For a certificate, please see:

396

397 <http://www.textcheck.com/certificate/xHnZj6>

398

Figure legends

Figure 1 The bagworm *Eumeta minuscula* and its potential predator *Calosoma maximoviczi*. (a) *Eumeta minuscula* bags on shrubs. (b) An *E. minuscula* larva and the inside of its bag. (c) A bagworm and a carabid on bamboo material under laboratory conditions. (d) A bag protecting the larva from a carabid attack. (e) A bag-removed larva eaten by a carabid. (f) A replaced bag protecting the larva from a carabid attack.

Figure 2 The arena used in the experiments. A *Eumeta minuscula* larva and a *Calosoma maximoviczi* adult were placed on bamboo material.

Figure 3 Predation success of the carabid *Calosoma maximoviczi* and defensive success of the bagworm *Eumeta minuscula* for different bag treatments (control, bag-removal, and bag-replacement).

Table 1 (on next page)

Defensive success or failure of the bagworm

Table 1. Defensive success or failure of the bagworm *Eumeta minuscula* against the potential predator *Calosoma maximoviczi* under laboratory conditions.

1 Table 1. Defensive success or failure of the bagworm *Eumeta minuscula* against the potential predator *Calosoma maximoviczi* under
2 laboratory conditions.

Predator (<i>C. maximoviczi</i>)			First prey (<i>E. minuscula</i>)				Second prey (<i>E. minuscula</i>) ¹⁾			
No. ²⁾	Sex	Weight (mg)	No. ²⁾	Bag treatment ³⁾	Weight (mg) ⁴⁾	Defence ⁵⁾	No. ²⁾	Bag treatment ³⁾	Weight (mg) ⁴⁾	Defence ⁵⁾
Experiment 1										
C1	Male	384.4	E1	Control	711.3	Success	E1	Removed	263.5	Failure
C2	Male	426.3	E2	Control	436.6	Success	E2	Removed	226.5	Failure
C3	Male	343.3	E3	Control	485.3	Success	E3	Removed	254.1	Failure
C4	Female	530.4	E4	Control	285.8	Success	E4	Removed	138.1	Failure
C5	Male	604.2	E5	Control	699.2	Success	E5	Removed	326.7	Failure
Experiment 2										
C6	Female	420.9	E6	Removed	338.2	Failure	E11	Control	236.8	Success
C7	Male	572.1	E7	Removed	218.5	Failure	E12	Control	505.7	Success
C8	Male	600.4	E8	Removed	238.4	Failure	E13	Control	330.5	Success
C9	Male	446.3	E9	Removed	118.3	Failure	E14	Control	618.0	Success
C10	Female	566.6	E10	Removed	164.7	Failure	E15	Control	377.1	Success
Experiment 3										
C11	Male	369.0	E16	Replaced	427.3	Success	E16	Removed	230.4	Failure
C12	Male	418.4	E17	Replaced	479.4	Success	E17	Removed	359.0	Failure
C13	Female	372.9	E18	Replaced	340.9	Success	E18	Removed	205.4	Failure
C14	Male	399.0	E19	Replaced	449.6	Success	E19	Removed	336.8	Failure

C15	Male	252.7	E20	Replaced	313.5	Success	E20	Removed	202.8	Failure
-----	------	-------	-----	----------	-------	---------	-----	---------	-------	---------

¹⁾ The second prey was provided to each predator just after my observation of the predator behaviour in response to the first prey.

²⁾ Different code numbers showed that different individuals were used.

³⁾ Bag treatment: control, normal bags; removed, bags were removed experimentally; replaced, normal (twig) bags were replaced with soft (herb leaf) bags (see text).

⁴⁾ Total fresh weight (including bags) was shown for control and bag-replaced larvae, while fresh body weight (except bags) was measured for bag-removed larvae.

⁵⁾ Defence success and failure of *E. minuscula* indicated predation failure and success by *C. maximoviczi*, respectively.

1

Photos of the bagworm species and its potential predator

Figure 1 The bagworm *Eumeta minuscula* and its potential predator *Calosoma maximoviczi*. (a) *Eumeta minuscula* bags on shrubs. (b) An *E. minuscula* larva and the inside of its bag. (c) A bagworm and a carabid on bamboo material under laboratory conditions. (d) A bag protecting the larva from a carabid attack. (e) A bag-removed larva eaten by a carabid. (f) A replaced bag protecting the larva from a carabid attack.



2

The arena used in the experiments.

Figure 2 The arena used in the experiments. A *Eumeta minuscula* larva and a *Calosoma maximoviczi* adult were placed on bamboo material.

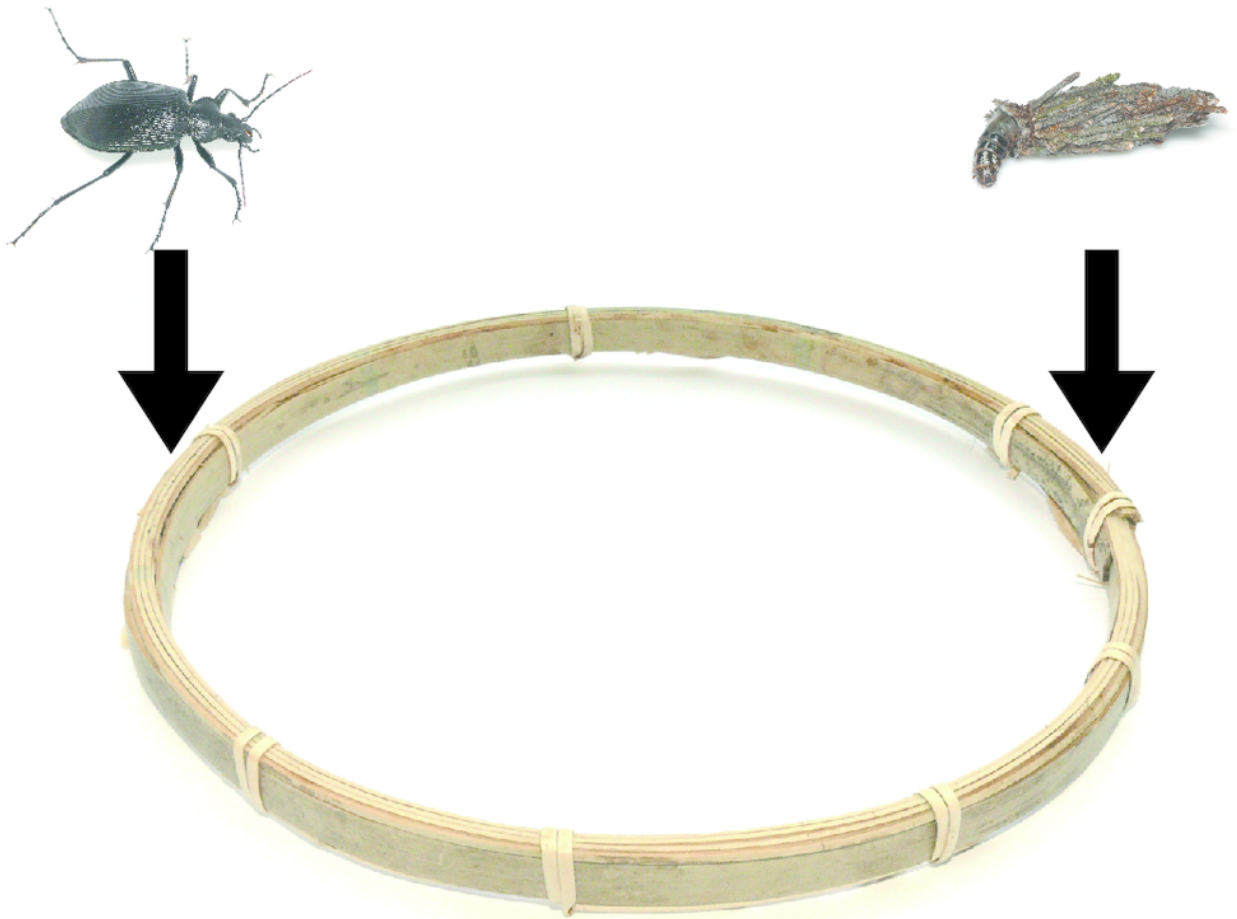


Figure 2

3

Defensive success rates of the bagworm

Figure 3 Predation success of the carabid *Calosoma maximowiczii* and defensive success of the bagworm *Eumeta minuscula* for different bag treatments (control, bag-removal, and bag-replacement).

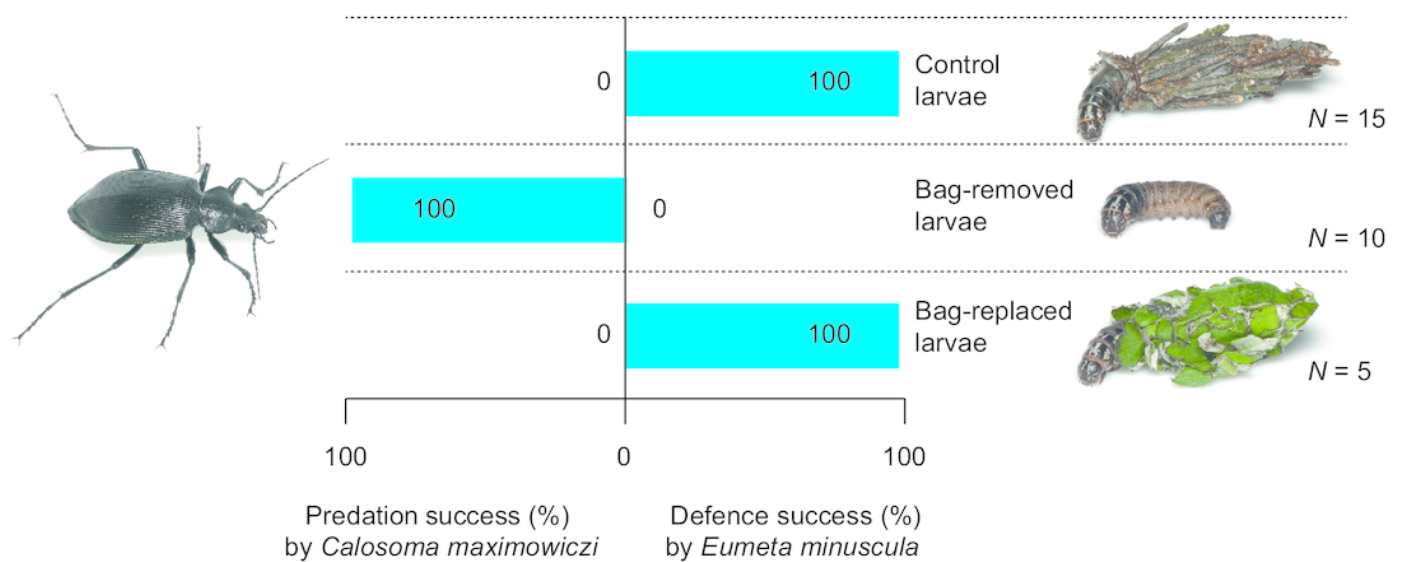


Figure 3