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Context-dependent fitness effects of behavioral manipulation by a parasitoid

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Many true parasites and parasitoids modify the behavior of their host, and most of these changes are thought to benefit the parasites. However, field tests of this hypothesis are scarce. We previously showed that braconid parasitoids (*Glyptapanteles* sp.) induce their caterpillar host (*Thyriniteina leucocerae*) to behave as a bodyguard of the parasitoid's pupae; they stand bent over the pupae and violently lash out at predators approaching them, resulting in reduced predation of parasitoid pupae on guava trees in the field. In contrast, we show here that this behavioral manipulation does not result in increased parasitoid survival on eucalyptus trees, an introduced host plant species. Hence, the effects of behavioral manipulation of the host depend on the ecological context. We hypothesize that this is due to a different species composition of the community of predators and hyperparasitoids on the 2 host plant species. Our results show that fitness effects of behavioral manipulation should be evaluated in a setting that includes all relevant components of the natural food web. *Key words*: defensive behavior, *Glyptapanteles*, host manipulation, parasitoid, *Thyriniteina leucocerae*, usurpation. [*Behav Ecol* 21:33–36 (2010)]

There are many spectacular examples of behavioral manipulation of hosts by parasitoids and parasites (Hohorst 1962; Brodeur and McNeil 1989; Poulin 1995; Eberhard 2000; Elliot et al. 2002; Moore 2002; Thomas et al. 2002, 2005; Cezilly and Thomas 2005; Hauber et al. 2006; Ponton et al. 2006; Hauber and Moskát 2008). Although most of this behavioral modification is thought to increase survival of parasitoids or transmission of parasites, there are only few examples showing that the behavioral manipulation, indeed, increases the parasite's fitness and not that of the host (Poulin 1995; Thomas et al. 2005; Lefèvre et al. 2008). Moreover, it is often not clear whether the observed behavior is a consequence and not a cause of parasitism, for example, because parasites more readily infect hosts that behave differently to conspecifics (Poulin 1995; Poulin and Thomas 1999).

We recently reported a case of behavioral manipulation where the behavior benefits the parasitoid and not the host (Grosman et al. 2008). The caterpillar host, the larva of the geometrid moth *Thyriniteina leucocerae* Rindge (Lepidoptera: Geometridae), is attacked by a parasitoid *Glyptapanteles* sp. (Hymenoptera: Braconidae). Adult female parasitoids oviposit in larvae of the moth, that is, first- and second-instar caterpillars that feed on foliage of various trees of the Myrtaceae family, such as guava and eucalyptus in Brazil. Parasitized caterpillars continue to develop and feed until the fourth or fifth instar, when up to approximately 80 full-grown parasitoid larvae egress from the host to pupate (Grosman AH and Janssen A, personal observations).

As in other host–parasitoid systems (Miles and Booker 2000; Tanaka and Ohsaki 2006, 2009; Harvey, Bezemer, et al. 2008),

hosts stop walking and feeding after parasitoid egression and remain near the cluster of parasitoid pupae. In addition, they defend the parasitoid pupae against approaching predators with violent head swings. Such head swings are rarely observed in unparasitized hosts, which do not defend the parasitoid pupae (see Supporting Information of Grosman et al. 2008 at the PLoS ONE Web site for movies of the behavior). Such guarding behavior has also been observed in other parasitoid species (Brodeur and Vet 1994; Harvey, Bezemer, et al. 2008; Harvey, Kos, et al. 2008). The guarding caterpillar always dies shortly after the adult parasitoids emerge from their pupae. Thus, the caterpillar never develops into a mature moth, showing that the behavioral change does not increase host fitness. A field experiment in guava trees showed that batches of parasitoid pupae suffered a 2-fold increase in predation when their guarding host was removed (Grosman et al. 2008). Thus, the parasitoid benefited from the behavioral modification.

The field experiment showed that host defense of parasitoid pupae was not effective against hyperparasitoids (i.e., parasitoids of the parasitoids). This makes sense because hyperparasitoids are specialized and may have experienced strong selection to cope with the defending host (Grosman et al. 2008; Harvey, Kos, et al. 2008; but see Tanaka and Ohsaki 2006, 2009). However, mortality caused by hyperparasitoids was low on guava trees (ca. 3%, Grosman et al. 2008). Hence, the fitness effects of host manipulation may result in small or negligible fitness increases of the parasitoid in habitats where the natural enemy community of the parasitoid is dominated by hyperparasitoids. It is also conceivable that a conspicuous, guarding host might actually attract the attention of some potential predators. Moreover, larger predators may be less impressed by the defense of the host. Lastly, the host plant species may also affect the interaction between the host and the parasitoid (Campbell and Duffey 1979).

Thus, we hypothesize that the effects of host manipulation on parasitoid (and parasite) fitness are likely to depend on the

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ecological context. We tested this by measuring the survival of parasitoid pupae with or without guarding hosts on eucalyptus, a host tree that was introduced to Brazil a century ago. It has a different associated food web from the native guava (Grosman AH, personal observations). In particular, we found more ants, spiders, and predatory wasps and bugs on guava but more parasitoids on eucalyptus (Grosman AH, personal observations).

MATERIALS AND METHODS

Thyrinteina leucocerae and *Glyptapanteles* sp. were collected from guava (*Psidium guajava*, L.) and *Eucalyptus grandis* Hill ex Maiden trees on the campus of the Federal University of Viçosa (Minas Gerais, Brazil) (20°45'S, 42°51'W). Rearing methods were as in Grosman et al. (2008). The caterpillars were reared either in groups on small eucalyptus trees (30–90 cm high) in cages (70 × 70 cm, 100 cm high) outside the laboratory or individually in plastic cups (500 ml) in the laboratory at ambient temperature and light conditions. The cups contained small (5–10 cm) twigs of eucalyptus or guava with 1–7 leaves and were closed with a mesh. The proximal ends of the twigs were inserted into moist vermiculite to maintain leaf turgor. Fresh twigs were added twice per week. Moth pupae were transferred to a small tree inside a cage (as above) outside the laboratory and were supplied with filter paper moistened with a solution of honey in water (10% v/v). Moths were allowed to emerge, mate, and oviposit inside the cages. Eggs were collected from the cages once a week and were left to emerge in cages containing small trees. The host cultures were frequently supplemented with field-collected individuals.

Recently emerged adult parasitoids, 1 female and 1–2 males, were allowed to mate in a glass tube with a piece of host plant leaf. They were subsequently placed in glass tubes (containing agar and some honey, closed with foam rubber) and either kept in the laboratory when caterpillars were available or stored in a climate box (12 ± 3.0 °C [mean ± standard error of the mean], L12:D12) until provided with caterpillars. Subsequently, the adult parasitoids were incubated for 24 h in a plastic cup (500 ml) containing some leaves and up to 8 first-instar *T. leucocerae* caterpillars of the same age. Parasitoid pupae that had egressed from the hosts were incubated in glass tubes in the laboratory until adult emergence. Parasitoid cultures were frequently supplemented with field-collected individuals.

Field experiments were carried out from 8 January to 28 August 2005, using the same method as the previously published study (Grosman et al. 2008) in 2 small eucalyptus plantations on the campus of the Federal University of Viçosa. The soil was covered sparsely with grasses; the plantations were surrounded by more diverse native vegetation. We obtained parasitized caterpillars in the laboratory following the method described above. Batches of parasitoid pupae that emerged on the same day were placed in the same field within 1 day after egression of the larvae from the host and pupation of the parasitoids. The guarding caterpillar was randomly removed from 37.5% of the batches, and each batch was subsequently attached to a separate tree by stapling the twig (with or without previously parasitized caterpillar, depending on the treatment) to a leaf. In this way, batches of pupae were exposed to the natural community of predators and parasitoids. The number of pupae in batches with and without host did not differ significantly between treatments (with host: 25.0 ± 1.32, without host: 25.8 ± 2.01, *t*-test, *t* = 0.35, degrees of freedom = 109, *P* = 0.73). A total of 127 batches of parasitoid pupae, with a total of 3332 pupae were exposed in the 2 eucalyptus plantations. Batches were recollected after 3 days (ca. half the pupal period), pupae were counted, and the

presence or absence of the caterpillar recorded (except for 17 cases). Pupae were subsequently incubated for 1 month (25 ± 5 °C, 12:12 h light:dark) to allow emergence of parasitoids and hyperparasitoids.

To measure mortality due to causes other than predation and hyperparasitism, an extra 17 batches of pupae (total of 442 pupae) with guarding caterpillar were stapled to a branch of a separate tree, and the branch was subsequently covered with a sleeve cage of fine mesh that prevented predators and hyperparasitoids from entering (referred to below as unexposed batches). Insect glue applied to the base of each branch prevented walking predators and parasitoids from accessing these unexposed batches. These batches of pupae were also recollected after 3 days and treated as above.

The proportion of pupae per batch that were eaten by predators or hyperparasitized was compared between treatments (with or without guarding caterpillar) using general linear models (GLM) with quasi-binomial error distributions to correct for overdispersion (Crawley 2007), using R statistical software (R Development Core Team 2006).

RESULTS

Significantly more pupae were damaged or disappeared from batches of pupae with caterpillars that were exposed to predators and parasitoids than from unexposed batches in sleeve cages (average mortality [± standard error] per batch: unexposed = 0.991 (±0.011), exposed: 0.794 (±0.020), GLM, $F_{1,94} = 23.8$, *P* < 0.0001). We did not correct the mortality of exposed batches for this low background mortality; hence, we scored predation in the exposed batches as the proportion of pupae per batch that had disappeared or were damaged.

Removal of the caterpillars did not result in a difference in mortality of batches of parasitoid pupae (Figure 1, GLM, $F_{1,126} = 0.050$, *P* = 0.824). There was no difference in predation (Figure 1, $F_{1,126} = 0.035$, *P* = 0.851) or hyperparasitism (Figure 1, $F_{1,126} = 0.013$, *P* = 0.911). Caterpillars disappeared from 27.0% of the batches of parasitoid pupae in the field. This is likely to be due to predation because parasitized

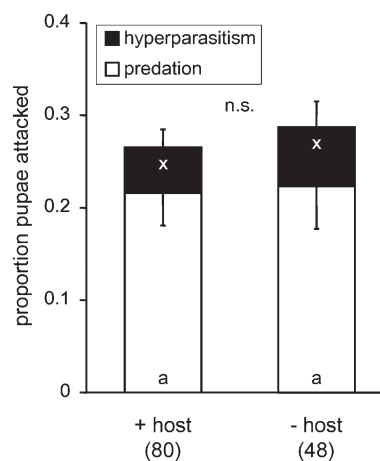


Figure 1 Mortality of parasitoid pupae that were exposed to a natural community of predators and hyperparasitoids in eucalyptus trees in the field with (+ host) or without (– host) their guarding caterpillar. Shown is the total average fraction of pupae that died, broken down into predation (open bars), and parasitism (filled bars) with standard errors of the mean. Numbers under the bars refer to the number of pupal batches per treatment. The difference in total fraction mortality (predation + hyperparasitism) was not significant (n.s.) nor was the difference in predation or hyperparasitism (letters inside the bars).

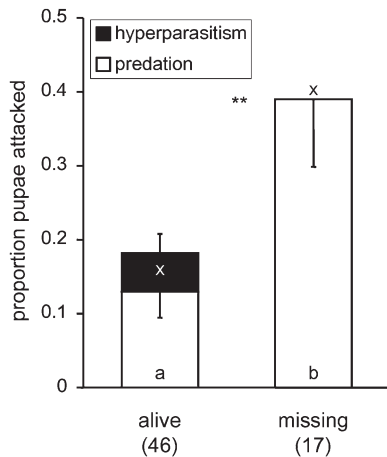


Figure 2
Mortality of parasitoid pupae that were exposed to a natural community of predators and hyperparasitoids in eucalyptus trees in the field with guarding caterpillar (+host from Figure 1), which was either found alive after exposure, or was missing. Shown is the total average fraction of pupae that died, broken down into predation (open bars) and parasitism (filled bars) with standard errors of the mean. Numbers under the bars refer to the number of pupal batches per treatment. Note that the sum of the numbers here is less than the 80 batches of pupae with caterpillars (Figure 1) because the fate of 17 caterpillars was not registered. The difference in the total fraction mortality was significant (**) as was the difference in predation (letters inside bars). The difference in hyperparasitism was bordering significance.

caterpillars hardly move once parasitoid larvae egress (Grosman et al. 2008), and caterpillars inside sleeve cages did not disappear. The mortality in batches of parasitoid pupae from which the caterpillars were missing was significantly higher than the mortality in batches from which the caterpillars survived (Figure 2, $F_{1,61} = 8.98$, $P = 0.0039$). This was due to increased predation (Figure 2, $F_{1,61} = 14.0$, $P = 0.0004$) of pupae in batches where caterpillars were missing. Hyperparasitism of pupae without caterpillars was not significantly different from that of pupae with caterpillars ($F_{1,61} = 3.43$, $P = 0.069$).

The mortality in batches with caterpillars missing was also higher than the mortality in batches from which caterpillars were experimentally removed (cf. Figures 1 and 2), although the difference was just not significant ($F_{1,63} = 3.26$, $P = 0.076$). Predation was significantly higher on batches with caterpillars missing than on batches with caterpillars removed (cf. Figures 1 and 2, $F_{1,63} = 5.67$, $P = 0.020$). This is likely caused by the fact that caterpillars that were missing had been found by predators, which also attacked the pupae, whereas not all batches of pupae without predators were discovered by predators. Parasitism of batches with caterpillars missing was similar to that of batches with caterpillars removed ($F_{1,63} = 3.24$, $P = 0.077$).

DISCUSSION

On guava, a native tree species, we showed that behavioral manipulation in the same host–parasitoid system resulted in a 2-fold reduction of the mortality of parasitoid pupae (Grosman et al. 2008). Here, we did not find such an effect on eucalyptus, an introduced tree species. In theory, this could be caused by effects of the host plant, for example, because plant allelochemicals affect the behavior of the caterpillar. However, the behavioral changes of parasitized caterpillars are equal on both tree species, suggesting a minor effect of the host

plant itself. Hence, the fitness effects of behavioral manipulation are likely to depend on the food web associated with both host plant species, for example, through differences in the community of predators and hyperparasitoids on both host plants species. In a parallel study, we found more ants, spiders, and predatory wasps and bugs on guava but more parasitoids on eucalyptus (Grosman et al., in preparation).

Comparison of the results obtained here with earlier results on guava may reveal some of the causes for the different effects of behavioral manipulation on the 2 host plants. Total percentage mortality and predation of parasitoid pupae on eucalyptus did not differ from that found earlier on guava (Grosman et al. 2008) (total mortality [predation]: eucalyptus: 0.272 [0.222], guava 0.259 [0.243]), but the percentage hyperparasitism was significantly higher on eucalyptus than was found earlier on guava (Grosman et al. 2008) (eucalyptus: 0.050, guava: 0.015, $F_{1,244} = 5.92$, $P = 0.016$). To allow for more careful comparison of both data sets, we furthermore restricted the comparison to the period in which experiments were carried out on both host plant species simultaneously (30 June–28 August 2005) and found the same results (no difference in total mortality between host plant species but higher hyperparasitism on eucalyptus than on guava). Hyperparasitoids are apparently not deterred by the defensive behavior of the guarding caterpillar (Grosman et al. 2008; Harvey, Kos, et al. 2008; but see Tanaka and Ohsaki 2006, 2009), hence, the higher incidence of hyperparasitism on eucalyptus may be partially responsible for the absence of an effect of the guarding caterpillar on mortality of the parasitoid pupae. However, the levels of hyperparasitism were too low to account for the total difference in effect of the guarding caterpillar on the 2 host plants (Figure 1 and Grosman et al. 2008).

Another reason for differences in the effectiveness of the behavioral change in the caterpillar host might have been higher vulnerability of the guarding caterpillar, that is, the predation risk of the host. To the human eye, the guarding caterpillars closely resemble small dead twigs of guava and are therefore difficult to find on this host plant. In contrast, they are easy to detect in eucalyptus trees; hence, they may be hypothesized to attract more visual-hunting predators and parasitoids, resulting in higher predation of the caterpillars and higher mortality of the parasitoid pupae. Indeed, the higher predation rates of batches of pupae from which caterpillars were missing than of batches with caterpillars removed may have been caused by the guarding caterpillars attracting predators (Figures 1 and 2). Such attraction of predators by the guarding caterpillar would amount a fitness cost of the behavioral manipulation. However, similar percentages of caterpillars disappeared from eucalyptus (17 of 63, Figure 2) and guava (17 of 67, Grosman et al. 2008), suggesting that predation of the guardian caterpillars did not differ between the host plants. When the caterpillars survived, the mortality of parasitoid pupae on eucalyptus was not significantly higher than on guava (0.167 vs. 0.099, respectively). Nevertheless, these mortalities suggest that predators on eucalyptus were less deterred by the caterpillar bodyguard than the predators on guava.

It may not be coincidental that behavioral manipulation of the caterpillar by the parasitoid has no positive effect on parasitoid survival on a novel host tree but that it is effective on a native tree. The behavioral manipulation has evolved vis a vis the community of enemies of the parasitoid pupae that occur on guava, not that occurring on eucalyptus. Although the changed host behavior does not promote survival of the manipulating parasitoid on eucalyptus, there are also no fitness disadvantages, except, perhaps, that the parasitoid has invested in the behavioral manipulation without receiving returns (Parker et al. 2009). In the system studied here, one to a few larvae stay behind in the host, and we hypothesized that

these parasites manipulate the host's behavior. These larvae would, thus, increase the survival of their brothers and sisters outside the host, at the expense of their own survival, and this would be an investment. Furthermore, larger parasitoid clutches could, perhaps, be produced if the host does not need to survive beyond the egression of the parasitoid larvae (Harvey, Bezemer, et al. 2008). Hence, when a host and its manipulating parasitoid or parasite move to a novel environment, it is conceivable that there will be selection against behavioral manipulation when investments of the parasite in behavioral manipulation are high and when the manipulation results in reduced (or even negative) fitness benefits to the parasite in the novel habitat. Alternatively, selection could drive the parasitoid to more effective host manipulation in the novel environment.

Our results illustrate the importance of studying behavioral manipulation in its proper ecological context, not only with respect to the various predators and parasitoids that occur in the field (Mouritsen and Poulin 2003; Tompkins et al. 2004) but also with respect to the host plant of the host.

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REFERENCES

- Brodeur J, McNeil JN. 1989. Seasonal microhabitat selection by an endoparasitoid through adaptive modification of host behaviour. *Science*. 244:226–228.
- Brodeur J, Vet LEM. 1994. Usurpation of host behavior by a parasitic wasp. *Anim Behav*. 48:187–192.
- Campbell BC, Duffey SS. 1979. Tomatine and parasitic wasps: potential incompatibility of plant antibiosis with biological control. *Science*. 205:700–702.
- Cezilly F, Thomas F, editors. 2005. Host manipulation by parasites. *Behav Process*. 68, p. 185–295.
- Crawley MJ. 2007. *The R book*. Chichester (England): John Wiley & Sons Ltd.
- Eberhard WG. 2000. Spider manipulation by a wasp larva. *Nature*. 406:255–256.
- Elliot SL, Blanford S, Thomas MB. 2002. Host-pathogen interactions in a varying environment: temperature, behavioural fever and fitness. *Proc R Soc Lond B Biol Sci*. 269:1599–1607.
- Grosman AH, Janssen A, de Brito EF, Cordeiro EG, Colares F, Fonseca JO, Lima ER, Pallini A, Sabelis MW. 2008. Parasitoid increases survival of its pupae by inducing hosts to fight predators. *PLoS ONE*. 3: e2276.
- Harvey JA, Bezemer TM, Gols R, Nakamatsu Y, Tanaka T. 2008a. Comparing the physiological effects and function of larval feeding in closely-related endoparasitoids (Braconidae: Microgastrinae). *Physiol. Entomol*. 33:217–225.
- Harvey JA, Kos M, Nakamatsu Y, Tanaka T, Dicke M, Vet LEM, Brodeur J, Bezemer TM. 2008b. Do parasitized caterpillars protect their parasitoids from hyperparasitoids? A test of the 'usurpation hypothesis'. *Anim Behav*. 76:701–708.
- Hauber ME, Moskat C. 2008. Shared parental care is costly for nestlings of common cuckoos and their great reed warbler host. *Behav Ecol*. 19:79–86.
- Hauber ME, Moskat C, Ban M. 2006. Experimental shift in hosts' acceptance threshold of inaccurate-mimic brood parasite eggs. *Biol Lett*. 2:177–180.
- Hohorst W. 1962. Die rolle der Ameisen im Entwicklungsgang der Lanzettgels (*Dicrocoelium dentriticum*). *Parasitol Res*. 22:105–106.
- Lefèvre T, Roche B, Poulin R, Hurd H, Renaud F, Thomas F. 2008. Exploiting host compensatory responses: the 'must' of manipulation? *Trends Parasitol*. 24:435–439.
- Miles CI, Booker R. 2000. Octopamine mimics the effects of parasitism on the foregut of the tobacco hornworm *Manduca sexta*. *J Exp Biol*. 203:1689–1700.
- Moore J. 2002. *Parasites and the behaviour of animals*. Oxford: Oxford University Press.
- Mouritsen KN, Poulin R. 2003. Parasite-induced trophic facilitation exploited by a non-host predator: a manipulator's nightmare. *Int J Parasitol*. 33:1043–1050.
- Parker GA, Ball MA, Chubb JC, Hammerschmidt K, Milinski M. 2009. When should a trophically transmitted parasite manipulate its host? *Evolution*. 63:448–458.
- Ponton F, Lebarbenchon C, Lefèvre T, Biron DG, Duneau D, Hughes DP, Thomas F. 2006. Parasite survives predation on its host. *Nature*. 440:756.
- Poulin R. 1995. 'Adaptive' changes in the behaviour of parasitized animals: a critical review. *Int J Parasitol*. 25:1371–1383.
- Poulin R, Thomas F. 1999. Phenotypic variability induced by parasites: extent and evolutionary implications. *Parasitol Today*. 15: 28–32.
- R-Development-Core-Team. 2006. *R: a language and environment for statistical computing*. 2.3.1. ed. Vienna (Austria): R Foundation for Statistical Computing.
- Tanaka S, Ohsaki N. 2006. Behavioral manipulation of host caterpillars by the primary parasitoid wasp *Cotesia glomerata* (L.) to construct defensive webs against hyperparasitism. *Ecol Res*. 21: 570–577.
- Tanaka S, Ohsaki N. 2009. Does manipulation by the parasitoid wasp *Cotesia glomerata* (L.) cause attachment behaviour of host caterpillars on cocoon clusters? *Ethology*. 115:781–789.
- Thomas F, Adamo S, Moore J. 2005. Parasitic manipulation: where are we and where should we go? *Behav Process*. 68:185–199.
- Thomas F, Schmidt-Rhaesa A, Martin G, Manu C, Durand P, Renaud F. 2002. Do hairworms (Nematomorpha) manipulate the water seeking behaviour of their terrestrial hosts? *J Evol Biol*. 15: 356–361.
- Tompkins DM, Mouritsen KN, Poulin R. 2004. Parasite-induced surfacing in the cockle *Austrovenus stutchburyi*: adaptation or not? *J Evol Biol*. 17:247–256.