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Testing adaptive significance of host manipulation with a parasitoid wasp

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Abstract

According to the extended phenotype hypothesis, certain parasites manipulate the host's behaviour which ultimately enhances the transmission of parasite genes into the next generation. The parasitoid wasp *Ampulex compressa* attacks and stings its cockroach *Periplaneta americana* host and lays an egg on the cockroach's leg. Before the wasp's oviposition, the stung cockroach engages in excessive self-grooming for about 30 min. The prey location hypothesis posits that self-grooming may allow the wasp to easily locate its host before transporting it to the nest. To test this hypothesis, we manipulated the mobility of the stung cockroach under different spatial constraints. Latencies to locate stung cockroaches with unlimited movement were similar than latencies to locate stung, but motionless cockroaches irrespectively of spatial constraints. Wasps were less willing to lay eggs and seal an entrance to the burrow in treatments with motionless cockroaches which suggests that if the expected reproductive success is low, then parental investment decreases. Our results provide no support for the location hypothesis and call for further experimental investigation of the extended phenotype hypothesis in parasite–host interactions.

KEYWORDS

Ampulex compressa, cockroach, extended phenotype, jewel wasp

1 | INTRODUCTION

To increase the likelihood of successful transmission, genes of a parasite can affect the host phenotype (Hughes, Brodeur, & Thomas, 2012; Moore, 2002; Poulin, 2010). This concept, well known as the "extended phenotype," has been defined by Dawkins (1982) as anomalous behaviour of the parasitized host resulting from the expression of the parasite's genes ultimately allowing manipulation of the host's behaviour. Textbook examples of manipulations of hosts by their parasites include suicidal jumping of crickets into water to reach the reproductive habitat of a hairworm parasite (Thomas et al., 2002). The intracellular parasite *Toxoplasma gondii* disrupts the basic instincts of rodents, its intermediate hosts, to enhance the chance that the rodent will be consumed by the final feline host necessary for sexual reproduction of *Toxoplasma* (Berdoy, Webster, & MacDonald, 2000; Dass & Vyas, 2014). Mosquito vectors infected

by the parasitic protozoan *Plasmodium falciparum* bite for longer periods of time and more often than uninfected mosquitoes (Koella, Sorensen, & Anderson, 1998; Rossignol, Ribeiro, & Spielman, 1986). As a result, infected mosquitoes are more likely to take larger blood meals (Koella & Packer, 1996).

Although host manipulation by parasites is a fascinating phenomenon, considerable scepticism concerning this hypothesis exists (Heil, 2016; Moore & Gotelli, 1990; Poulin, 2000). The altered behaviour could be an adaptive response on the part of the host to the parasite infection (Bakker, Frommen, & Thünken, 2017; Poulin & Thomas, 1999). For instance, *Toxoplasma* may not directly manipulate its rodent host, but altered host's behaviour could be influenced by neuroinflammation produced by chronic infection rather than by parasite cysts (Martynowicz, Augusto, Wek, Boehm, & Sullivan, 2019). Similarly, enhanced foraging activity by mosquitoes infected by *Plasmodium* need not be a result of manipulation by parasites but is instead likely to be compensation for the increased metabolic

costs induced by the parasites (Cator et al., 2013). In addition, recent reviews stress that experimental manipulations of host traits are scarce, most evidence is correlative, and that theory outruns experimental studies (Bakker et al., 2017; Poulin & Maure, 2015). Critical evaluation of the parasite manipulation hypothesis with experimental methods is therefore required.

A parasitoid is defined as a parasite that kills its host as a normal and required part of its development (Lafferty & Kuris, 2002; Weinersmith, 2019). The emerald jewel wasp *Ampulex compressa* (Hymenoptera: Ampulicidae) is the parasitoid of its host, the American cockroach *Periplaneta americana* (Blattodea: Blattidae). Upon encountering the cockroach, *A. compressa* attacks the cockroach and injects venom directly into the cockroach's subesophageal ganglion, in and around the central complex in the supraesophageal ganglion (Haspel, Rosenberg, & Libersat, 2003). The wasp's venom drastically changes the stung cockroach's behaviour; the cockroach starts to excessively groom itself for about 30 min (Weisel-Eichler, Haspel, & Libersat, 1999). After the wasp returns to the envenomed cockroach, it breaks the cockroach's antennae and sucks up outflowing haemolymph from the broken antennae (Keasar, Sheffer, Glusman, & Libersat, 2006; Williams, 1942). Finally, the wasp grabs one of the cockroach's antennal stumps, drags the stung cockroach into its burrow and lays a single egg on a mesothoracic leg of the host (Williams, 1942). About 1 week after oviposition, the larva enters the still living cockroach's body cavity and feeds on its interior organs which results in the death of the cockroach (Williams, 1942). The larva completes its life cycle after ~45 days (Libersat, 2003), after which the adult wasp abandons the dried exoskeleton of the cockroach.

In this study, we investigated the adaptive significance of self-grooming of the stung cockroach and the drinking of the cockroach's haemolymph by the adult female jewel wasp. According to the prey location hypothesis, excessive self-grooming of the stung cockroach may allow the wasp to easily locate its host before transporting it to the nest (Libersat & Gal, 2014). This hypothesis predicts that it is more difficult for the wasp to locate motionless cockroaches than intact cockroaches. The prey location hypothesis also implicitly assumes that the wasp's visual-spatial abilities are limited and should work better in a spatially limited environment. To test this idea, we performed our experiments in cages of different sizes. We hypothesized that wasps are quicker in locating cockroach in smaller, spatially limited, environments than in larger, spatially, less limited, environments.

2 | METHODS

2.1 | Experimental animals

Experimental *A. compressa* used in this study were third-generation laboratory-reared descendants of individuals obtained from a commercially distributed population reared in Germany, bought in 2018. The adults were reared in 29 × 30 × 20 cm plexiglass cages and provided with honey and water with sugar ad libitum. Pine bark and pumice stones served as substrate. One female and one male were maintained in each breeding cage. Male and female cockroaches were reared together in 6-L plastic containers filled with carton with dry dog food, apples and water ad libitum. All the insects were maintained at room temperature (~24°C and ~50% humidity). The light/dark cycles were 10 and 14 hr. Female cockroaches (*P. americana*) were predominantly chosen for parasitization (88%, *N* = 64 cockroaches). Experiments were made between May and June 2019 in the glass cages with an identical substrate as for breeding purposes. Each cage contained one 50-ml plastic tube serving as the wasp's burrow.

2.2 | Behavioural test

Wasps (*N* = 16) and cockroaches (*N* = 64) were randomly assigned to one of four treatments. Half of the experiments were made in large cages (140 × 50 × 50) and half in small cages (29 × 30 × 20 cm) filled with peat. Cockroaches in both the large cage and small cage treatment were divided into intact (*N* = 16) and frozen (*N* = 16). In the latter group, cockroaches were killed by placing them in a freezer with −80°C for 10 min, then warmed with heater GOODLINE BSC 2000 for 3 min (temperature ~40°C) and subsequently returned back to the experimental cage.

A female wasp was placed inside the cage and given 60 min to habituate. The experiment began after the cockroach entered the cage. Cockroaches from the frozen treatment were gently removed immediately after they were stung by the wasp, killed by freezing and returned back to the same place. We recorded behaviours reported in Table 1 to the nearest 1 min: latency since the start of the experiment until the cockroach has been stung by the wasp (min), distance of the stung cockroach from the wasp's burrow (cm), location of the stung cockroach since the start of the experiment by the wasp (min), occurrence of breaking the cockroach's antennae by the wasp (yes or no), start of the cockroach's escorting since it was located (min), total time the wasp spent with the escorting cockroach (min), total time the wasp spent in the burrow with the stung cockroach (min), occurrence of oviposition by visual inspection of the cockroach's mesothoracic legs after the experiment (yes or no) and sealing of the entrance by substrate (yes or no).

Mean body mass of cockroaches (*N* = 64) was *M* = 1.13 g (*SE* = 0.02). There were no significant differences in cockroach body mass across treatments (ANOVA, large versus small cage treatment, $F_{1,60}$ = 2.08, *p* = .15; frozen versus intact cockroaches, $F_{1,60}$ = 3.58, *p* = .06). The body mass of wasps was *M* = 0.14 g (*SE* = 0.06). There were no significant differences in wasp body mass across treatments (GLMM with wasp's ID as a random factor, large versus small cage treatment and frozen versus intact cockroaches, both $F_{1,61}$ = 0.0, *p* = 1.0). Each wasp was used 4 times in total (once per each of the treatments), but no more than once per day to prevent depletion of venom. All the experiments were made between 12:30 and 17:00 p.m. under a natural photoperiod and standard temperature

TABLE 1 Descriptive statistics of examined behaviours. The means are reported with ± SE

| Cockroach | Cage type | | | |
| | Small | | Large | |
	Intact	Frozen	Intact	Frozen
Latency until stinging by wasp (min)	2.6 ± 2.4 (16)	2.6 ± 2.4 (16)	9.2 ± 2.4 (16)	7.9 ± 2.4 (16)
Cockroach's distance from the burrow (cm)	11.7 ± 8 (16)	3.9 ± 8 (16)	55.3 ± 8 (16)	74.7 ± 8 (16)
Location of the stung cockroach (min)	60.1 ± 6.4 (16)	51.8 ± 6.4 (16)	62.4 ± 6.4 (16)	51.9 ± 6.4 (16)
Breaking the cockroach's antennae (Y/N[a])	16/0	13/3	15/1	14/2
Start of the cockroach's escorting since it was located (min)	16.2 ± 2.7 (16)	15.9 ± 2.7 (15)	16.3 ± 2.7 (15)	13.8 ± 3 (13)
Total time of cockroach's escorting (min)	8.7 ± 4.4 (16)	17.7 ± 4.9 (13)	8.4 ± 4.6 (15)	42.4 ± 7.6 (5)
Time the wasp spent in the burrow (min)	11.6 ± 3 (16)	11.8 ± 3.3 (13)	11.1 ± 3 (15)	10 ± 5.3 (5)
Occurrence of oviposition (Y/N[a])	15/1	5/11	15/1	1/15
Sealing the entrance (Y/N[a])	15/1	5/8	15/0	1/4

Note: The values in parentheses are the sample sizes

[a]Binary measures

TABLE 2 Results of GLMM on examined behaviours

	Cage type	Freezing	Interaction term
Latency until stinging by wasp (min)	$F_{1,60} = 8.4, p = .005$	$F_{1,60} = 0.1, p = .75$	$F_{1,60} = 0.08, p = .77$
Cockroach's distance from the burrow (cm)	$F_{1,60} = 46.3, p < .001$	$F_{1,60} = 0.15, p = .7$	$F_{1,60} = 2.9, p = .09$
Location of the stung cockroach (min)	$F_{1,60} = 0.005, p = .95$	$F_{1,60} = 2.71, p = .11$	$F_{1,60} = 0.005, p = .94$
Breaking the cockroach's antennae	$F_{1,60} = 0.05, p = .82$	$F_{1,60} = 1.75, p = .19$	$F_{1,60} = 0.47, p = .49$
Start of the cockroach's escorting since it was located (min)	$F_{1,55} = 0.07, p = .79$	$F_{1,55} = 0.08, p = .78$	$F_{1,55} = 0.12, p = .73$
Occurrence of oviposition	$F_{1,60} = 1.08, p = .3$	$F_{1,60} = 23.4, p < .001$	$F_{1,60} = 1.08, p = .3$

(~24°C) and humidity (~50%). Simultaneous trials were visually isolated from each other by the placement of white paper between the experimental cages. At the conclusion of each trial, all the contents were removed from each cage, the wasps were returned to their housing containers, and the area was cleaned with water.

2.3 | Statistical analyses

Generalized linear mixed model with wasp's ID as a random factor was used throughout the analyses. Gamma distribution was used for continuous data and binary distribution for binomial data (yes/no). Satterthwaite approximation for unbalanced samples was used to compare the occurrence of oviposition, because the data were

strongly biased towards frequent oviposition on intact cockroaches. All statistical tests were made with SPSS ver. 23.

3 | RESULTS

Cockroaches were stung by a wasp in small cages significantly sooner than cockroaches in large cages (Tables 1 and 2), irrespectively of whether they were subsequently frozen or not. The interaction term was not statistically significant (Tables 1 and 2). Stung cockroaches in small cages were located closer to wasps' burrow than cockroaches in large cages (Tables 1 and 2), irrespectively of whether they were frozen or not. The interaction term was not statistically significant (Tables 1 and 2). The wasp's location time of the

stung cockroach was not influenced by the cage type, the freezing of cockroaches or by the interaction between variables (Tables 1 and 2), providing no support for the location hypothesis. The wasps almost invariably broke the cockroaches' antennae (Tables 1 and 2) and began to escort them at a similar time since the cockroaches were located (Tables 1 and 2). Only one wasp from the treatment with the small cage and the intact cockroaches stung the cockroach repeatedly, but removing this trial did not influence statistical analyses. The total amount of time the wasp spent with cockroach escorting was apparently longer in large cages, but it was impossible to analyse this difference statistically due to reduced sample size in the treatment with frozen cockroaches in large cages (Table 1). Wasps spent about 10–12 min in burrows (statistics were not provided due to low sample sizes, Table 1). Wasps oviposited on frozen cockroaches significantly less than on intact cockroaches regardless of the effect of the cage or the interaction between variables (Tables 1 and 2). When including only cockroaches which were successfully escorted to the wasp's burrow (frozen in large and small cages, $N = 5$ and 13, respectively, intact in large and small cages, $N = 15$ and 16), occurrence of oviposition on frozen cockroaches (6 of 18, 33%) was less frequent than on live cockroaches (30 of 31, 97%) (Fisher exact test, $p < .001$). Wasps sealed the entrance of burrows with intact cockroaches apparently more frequently then burrows with frozen cockroaches regardless of the type of cage (statistics not provided due to low sample sizes, Table 1). The pooled data from all the treatments revealed that the wasps sealed the entrance in all 36 cases of successful oviposition (100%). In contrast, if the cockroach was escorted to the burrow, but the oviposition did not occur ($N = 13$), the entrance always remains unsealed.

4 | DISCUSSION

This study primarily investigated why cockroaches groom themselves after being stung by a parasitoid wasp. The location hypothesis posits that excessive self-grooming of the stung cockroach allows the wasp to better locate its prey before transporting it to the nest (Libersat & Gal, 2014). Our experiment failed to provide evidence for this hypothesis.

When Libersat and Gal (2014) introduced the location hypothesis, they suggested that wasp behaviour could be induced similarly as in cone snails, where some species induce hyperexcitation of motor circuitry of their prey, which is followed by flaccid paralysis (Olivera, 1999). To date, however, no experimental evidence exists to examine the functional significance of induced hyperactivity caused by cone snails' prey. As far as we are aware, there are no other reported examples of predator–prey interactions supporting the location hypothesis. Orientation based by host movement induced by parasitoid toxins could in all probability be confused by the presence of other living arthropods. Moreover, self-grooming may vary in intensity (pers. obs.) and need not be a clearly visible cue in the heterogenous natural environment. Thus, the wasp might locate the stung prey by the use of a visual representation of the environment near the cockroach prey. Similar cues are used by bees and wasps to guide their return from foraging excursions (Wehner, 1981).

Importantly, wasps in large cages did not spend more time locating stung cockroaches than wasps in small cages, suggesting that experimental conditions did not limit wasps' location behaviour. While the cockroach engages in self-grooming, the wasp waits nearby (Williams, 1942), perhaps in order to minimize the chance of losing its stung prey.

Drinking the cockroach's haemolymph by the adult parasitoid wasp after breaking its antennae could be explained by gauging the effectiveness of the sting. Although this hypothesis has never been formally introduced in scientific literature, it appears to be popular in natural history movies (video, 00:02:30). This "neurotoxin concentration hypothesis" predicts that if the concentration of the neurotoxine is low, the wasp should repeat the envenomation of the cockroach prey. Keasar et al. (2006) suggest that drinking of haemolymph by the wasp might serve to probe host suitability to oviposition, thus sometimes resulting in refusal. We observed that the haemolymph of the frozen cockroach apparently did not leak out, meaning that the wasp could not fully detect the neurotoxin concentration nor could the haemolymph serve as a food source. Furthermore, no repeated envenomation occurred in frozen cockroaches as could be predicted according to "the neurotoxin concentration hypothesis" nor were there any differences in latency before transport with respect to treatment. The latter argument suggests that wasps were "satisfied" with their prey irrespective of the amount of haemolymph. Although we did not directly manipulate neurotoxin concentration in the cockroach's haemolymph, our preliminary observations cast doubt on the supposed role of breaking the antennae and drinking the cockroach's haemolymph by the wasp.

Wasps apparently spent more time with escorting stung, but frozen, cockroaches than with escorting stung, but living, cockroaches. We suggest that the wasp is too small to carry relatively larger and heavier cockroaches; thus, the guided escorting of the stung, but docile, cockroach to the wasp's burrow is necessary. This can be apparent particularly in natural conditions, where cockroaches could be attacked by the wasp further from the burrow, similarly like in our large cages treatment. A dead, frozen cockroach cannot respond to the wasp's guidance; thus, the wasp spends more time and energy with escorting it. Cockroach escorting was completed more frequently in small cages, where cockroaches were stung closer to wasps' burrows due to spatial constraints. Interestingly, however, even when the frozen cockroach was successfully escorted to the wasp's burrow, the likelihood of oviposition was significantly smaller than the oviposition on stung, but living cockroaches. The host's movement can be an important cue facilitating oviposition, because the stung cockroach serves as a living food storage for developing parasitoid larva for several days (Libersat & Gal, 2014; Williams, 1942). Certain parasitoid wasps similarly avoid laying eggs on motionless host larvae (Howard, Charlton, & Charlton, 1998; Wang, Yang, Gould, Wu, & Ma, 2010; Yamamoto, Chau, & Maeto, 2009). In addition, jewel wasps which did not lay eggs also did not seal the entrance of the burrow providing evidence that if the expected

reproductive success is low, then parental investment decreases (Sargent & Gross, 1985).

Self-grooming of the stung cockroach is induced by dopamine in the wasp's venom (Banks & Adams, 2012) which is a proximate explanation of behavioural changes in the wasp's host. The ultimate explanations of behavioural changes in the parasitized cockroach host are, however, still largely unclear. The location hypothesis failed to uncover the significance of self-grooming of stung cockroaches; thus, other explanations should be considered. Libersat and Gal (2014) have suggested that self-grooming might help remove pathogens from the cockroach's cuticle, which may finally improve the fitness of developing larva. Future research should be focused on this possibility as another viable explanation of host behaviour in order to acknowledge whether host's behaviour results from expression of the parasite's genes (extended phenotype, Dawkins, 1982) or whether it is self-defence of the host against parasite manipulation.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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