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REVIEW

Diversity and evolution of bodyguard manipulation

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Summary

Among the different strategies used by parasites to usurp the behaviour of their host, one of the most fascinating is bodyguard manipulation. While all classic examples of bodyguard manipulation involve insect parasitoids, induced protective behaviours have also evolved in other parasite–host systems, typically as specific dimensions of the total manipulation. For instance, parasites may manipulate the host to reduce host mortality during their development or to avoid predation by non-host predators. This type of host manipulation behaviour is rarely described, probably due to the fact that studies have mainly focused on predation enhancement rather than studying all the dimensions of the manipulation. Here, in addition to the classic cases of bodyguard manipulation, we also review these 'bodyguard dimensions' and propose extending the current definition of bodyguard manipulation to include the latter. We also discuss different evolutionary scenarios under which such manipulations could have evolved.

Introduction

Host manipulation by parasites is one of the most concrete and fascinating examples of the extended phenotype (Dawkins, 1982). Parasites across many taxa, from viruses to parasitoids, have evolved the ability to manipulate their hosts to their own advantage, sometimes inducing spectacular behavioural changes in their hosts (Moore, 2002; Lefèvre et al., 2009; Poulin, 2010; Hughes et al., 2012). Although these phenotypic changes occur only in parasitized hosts, evidence of benefits for the parasites is necessary to allow conclusions to be drawn about their adaptiveness (Poulin, 2010).

Traditionally, parasitic host manipulations have been divided into four general categories, three of which have been well documented (Poulin, 2010). In the first, the parasites can manipulate their hosts in such a way as to favour transmission to their next host, by rendering the former more susceptible to predation. One of the best-described examples is that of amphipods infected with trematode parasites; infected gammarids display an aberrant escape response toward the water surface following a mechanical disturbance, and remain at the air–water interface, thereby favouring the parasite's transmission to the definitive host, a waterfowl (Bethel and Holmes, 1977; Helluy, 1983; Helluy, 1984). The second category involves parasites that must either exit the host or release their propagules in a habitat other than the one in which the host lives. For example, crickets *Nemobius sylvestris* infected with the nematomorph *Paragordius tricuspidatus* were shown to actively jump into pools and streams, where the worms would egress from the host and find mates (Thomas et al., 2002b). The third type of manipulation involves vector-borne parasite transmission. The best-known examples are pathogens transmitted to vertebrate hosts by blood-sucking insects such as mosquitoes (Lefèvre et al., 2006). In this situation, transmission opportunities for the parasite increase with the number of potential hosts visited by the mosquitoes, and parasites have been shown to shorten the duration of individual blood meals to increase the number of hosts attacked (Moore, 1993; Koella et al., 1998).

The last category of manipulation is known as bodyguard manipulation. Although fascinating, it remains largely unstudied, with only a handful of documented cases and even fewer addressing the underlying mechanisms. This type of manipulation is used by insect parasitoids that must exit their host following larval development and pupate on external substrates, and is defined by Poulin as 'a manipulation that alters the behaviour of the host in ways that will provide protection to the parasite pupae from predators or other dangers' (Poulin, 2010), where the host forgoes potential foraging and/or reproductive opportunities. While all of the documented examples of bodyguard manipulation involve parasitoids and more particularly parasitic wasps, induced protective behaviours can evolve in other parasite–host systems. For instance, within the context of multidimensional manipulations, where parasites modify multiple aspects of their host's phenotype (see Appendix), certain dimensions (i.e. aspects) of these manipulations have been shown to reduce predation pressure and therefore the mortality of the immature parasites. Although currently labelled as the 'predation suppression' phase (see Parker et al., 2009), these behaviours ultimately ensure parasite survival. From this point of view, they could be interpreted as 'bodyguard dimensions', where manipulated hosts act as bodyguards only during specific phases of the manipulation.

The present review examines the diversity and evolution of bodyguard manipulation. First, we will give an overview of the textbook cases of bodyguard manipulation. Second, we will highlight the bodyguard dimension that occurs in a great number of biological systems, and discuss its potential inclusion in a broader definition of bodyguard manipulation. We will conclude this paper by discussing the evolutionary process leading to bodyguard manipulation.

Textbook cases of bodyguard manipulation

In contrast to most true parasites, insect parasitoids are of relatively large size and possess a free-living adult stage, and their development almost universally kills the host (but see English-Loeb et al., 1990; Maure et al., 2011). Because of these characteristics, behavioural modifications induced by parasitoids have evolved in a way that increases their survival during pupation (i.e. when the parasitoid is at its most vulnerable), through an efficient protection against natural enemies or abiotic factors (Poulin et al., 1994; Brodeur and Boivin, 2004). The induced protection conferred by the host can be either direct or indirect, depending on whether the onset of manipulation coincides with the period of high vulnerability (direct protection) or occurs just before this period (indirect protection). In the first case, the host is maintained alive, at least until the beginning of parasitoid pupal development, in order to be used as a direct defender of the developing pupae against predators or hyperparasitoids (e.g. Lepidoptera hosts attacked by a braconid wasp display aggressive responses when disturbed; see below). In the second case, the host is manipulated just before parasitoid pupation, in such a way as to either build a shelter or move to concealed refugia, and then is killed by the developing parasitoid (e.g. moribund spiders parasitized by an ichneumonid wasp spin a 'cocoon web' to favour parasitoid survival; see below).

Direct protection

The first example of this form of protection has been observed in three different Lepidoptera–Braconid wasp models: *Pieris brassicae–Cotesia glomerata* (Brodeur and Vet, 1994; Harvey et al., 2011), *Manduca* spp.–*Cotesia congregata* (Kester et al., 1996) and *Thyrinteina leucocerae–Glyptapanteles* sp. (Grosman et al., 2008) (Table 1). Female parasitic wasps deposit several eggs into the caterpillar host's haemocoel and the parasitoid larvae feed on host tissues throughout their development. Following egression of the parasitoid larvae from the host, the moribund caterpillar remains alive on the pupating parasitoids. Coiled on the cocoon masses, it exhibits violent head-thrashing movements, fending off predators (Kester and Jackson, 1996; Grosman et al., 2008) or hyperparasitoids (Harvey et al., 2011) (Fig. 1A), essentially acting as a true bodyguard as this behaviour results in a reduction in mortality of the parasitic wasp pupae. In addition to displaying this aggressive defence behaviour, it has been shown that *P. brassicae* caterpillars also spin a silk web over the parasitoid cocoons (Fig. 1B), reinforcing the physical barrier covering the parasitoid pupae (Brodeur and Vet, 1994). Interestingly, these two parasite-induced behaviours are normal components of the host's behavioural repertoire but are usurped by the parasitoid to fulfil another purpose. Although the mechanisms responsible for this usurpation of host behaviour were not identified, they are probably induced by the parasitoid larvae, prior to or during egression.

The second example comes from our previous study (Maure et al., 2011), describing an original model associating the parasitic wasp *Dinocampus coccinellae* and one of its hosts, the spotted lady beetle *Coleomegilla maculata* (Table 1). Female wasps lay a single egg in the host and the parasitoid larva grows inside the body cavity of the ladybird until it reaches the prepupal stage. Then, the larva egresses from its host and begins spinning a cocoon between the ladybird's legs (Fig. 1C). Remarkably for a parasitoid, *D. coccinellae* does not kill its host at the end of its development; instead, it partially paralyses the coccinellid upon egression. Thus positioned on top of the parasitic wasp cocoon and displaying little twitching when disturbed, the ladybird acts as a bodyguard for the pupating wasp against predators (Maure et al., 2011). Moreover, it is likely that the aposematic coloration of the ladybirds (Marples et al., 1994) operates as a complementary protection for the parasitoid, depending on the nature of the predators. Thus, *D. coccinellae* could also potentially usurp the natural defences of its host.

Indirect protection

In contrast to the previous examples where manipulated hosts played an active and direct role against natural enemies of the parasitoid, the following studies describe cases where the host is manipulated prior to parasitoid pupation in order to provide shelter against potential biotic and abiotic threats. Although these bodyguards do not directly face the threats, the benefits for parasitoid survival are equally important.

With their studies on the aphid parasitoid *Aphidius nigripes*, Brodeur and McNeil tested the hypothesis that parasitic wasps could avoid natural enemies in time or space through the selection of suitable pupation sites by modifying the behaviour of their host (Brodeur and McNeil, 1989; Brodeur and McNeil, 1992) (Table 1). *Aphidius nigripes*, an endoparasitoid of the potato aphid *Macrosiphum euphorbiae*, completes its pupal development within its eviscerated host (termed 'mummy'). Inside the mummy, the parasitic wasp spins a cocoon and pupates (Fig. 1D). In this state, it remains completely defenceless as the mummy is easily torn apart by the mandibles of invertebrate predators or pierced by the ovipositor of hyperparasitoid females. It has been shown that in order to enhance their survival, parasitoids have the ability to modify the behaviour of *M. euphorbiae*, and that the induced behaviour differs according to the physiological state of the parasitoid (Brodeur and McNeil, 1989; Brodeur and McNeil, 1990). Just prior to death, aphids containing a non-diapausing parasitoid leave the aphid colony and mummify on the upper surface of the leaves (i.e. reducing the impact of predation and hyperparasitism), whereas those containing a diapausing parasitoid leave the host plant and move to more concealed sites (i.e. reducing the negative effects of adverse climatic conditions and the incidence of hyperparasitism). Therefore, it seems that the pressures exerted by natural enemies have influenced the evolution of behavioural modification as a means of defence.

The second example is that of ichneumonid wasps inducing their spider hosts to weave a special web for their own benefit, and is documented in several associations (Nielsen, 1923; Eberhard, 2000; Eberhard, 2001; Matsumoto and Konishi, 2007; Matsumoto, 2009; Eberhard, 2010a; Eberhard, 2010b; Gonzaga et al., 2010) (Table 1). Female parasitoids attack a spider at the hub of its orb, sting it into temporary paralysis and lay an egg on the spider's abdomen. Subsequently, the spider resumes normal activity while the wasp's egg hatches and the larva grows by sucking the spider's haemolymph. On the night that it will kill its host, the larva induces the spider to build a unique 'cocoon web' and once completed the parasitoid larva moults, then kills and consumes the spider. Alterations of the web-spinning spider behaviour are diverse among the different ichneumonid wasps (Fig. 1E–G), but they are

consistently adjusted to details of the host's natural history (e.g. durable *versus* fragile webs, presence or absence of protected retreats) in ways that seem to promote the survival of the wasp's cocoon (Matsumoto, 2009; Gonzaga et al., 2010). Here, the parasitoid usurps the spider's skill in building a sophisticated web but imposes new patterns, rendering it stronger and more durable. This manipulation of the host was shown to be advantageous as it confers added protection to the developing pupae from the frequent heavy rains common to the areas where the species are found (Fincke et al., 1990).

The last example we consider here is, to our knowledge, the only one involving a Diptera parasitoid. Müller investigated the digging behaviour of worker bumblebees *Bombus terrestris* infected with a conopid fly endoparasitoid (Müller, 1994) (Table 1). Dead, parasitized bumblebee workers were found buried in the ground significantly more often than non-parasitized ones. As the bumblebees clearly gain no fitness benefits from digging to their deaths, the behavioural modification observed in parasitized individuals is unambiguously beneficial to the parasitoid only. Analogous to the strategy of aphid parasitoids (Brodeur and McNeil, 1989; Brodeur and McNeil, 1992), by manipulating their hosts into burying themselves just prior to pupation, conopid flies benefit from an increased protection to adverse temperature and natural enemies during hibernation, resulting in higher post-diapausing survival rates and adult size (Müller, 1994). As low levels of juvenile hormone are known to induce digging behaviour in bumblebees, the authors postulated that conopid endoparasites are able to manipulate the production of juvenile hormone in their host to induce this protective behaviour (Müller, 1994).

Potential extensions of the bodyguard manipulation

Although not labelled as such, parasitic behavioural modifications satisfying the definition of bodyguard manipulation have been reported in various non-parasitoid systems. An important constraint

Table 1. List of biological systems where textbook bodyguard manipulations have been reported

| Host–parasite systems	Bodyguard behavioural alterations	References
Aphid–parasitic wasp		
Macrosiphum euphorbiae–Aphidius nigripes	Altered microhabitat preference in manipulated hosts results in a reduction in hyperparasitism and increased protection from adverse abiotic factors.	Brodeur and McNeil, 1989; Brodeur and McNeil, 1992
Caterpillar–parasitic wasp		
Pieris brassicae–Cotesia glomerata	Induced web spinning and amplified aggressive/protective behaviour in manipulated caterpillar hosts reduce predation and hyperparasitism on parasitoid pupae.	Brodeur and Vet, 1994; Harvey et al., 2011
Manduca spp.–*Cotesia glomerata*	In addition to protecting parasitoid cocoons by covering them, infected caterpillars jerk their heads backwards and spit at tachinids attempting to larviposit. Therefore, host-attached parasitoids suffer significantly less predation than parasitoids alone.	Kester and Jackson, 1996
Thyrinteina leucocerae–Glyptapanteles sp.	Manipulated hosts cease walking and feeding, and remain near parasitoid pupae and knock off predators with violent head thrashing. This modified behaviour was shown to significantly reduce the mortality from natural enemies during parasitoid pupation.	Grosman et al., 2008
Spider–parasitic wasp		
Plesiometa argyt–Hymenoepimecis sp.	Spider hosts are induced to build an otherwise unique cocoon web to serve as a durable support for the wasp larva's cocoon in order to confer protection from the common heavy precipitation.	Eberhard et al., 2000; Eberhard et al., 2001
Nephila clavipes–Hymenoepimecis sp.	Parasitoid-induced alterations of the web-spinning behaviour of spiders make the webs more resistant to destruction. The cocoon webs include a hub-like platform from which the cocoon is suspended, and are usually protected by a nearby tangle of barrier lines of variable density.	Gonzaga et al., 2010
Theridion evexum–Zatypota petronae	Manipulated host adds more threads on different sections of the retreat (apex, inside and across the retreat opening), making the structure stronger and more durable. The reinforcement of the retreat with additional silk threads possibly increases protection of the cocoon against heavy rain, which is likely to be important for the wasp's survival.	Weng and Barrantes, 2007
Cyclosa octotuberculata–Reclinervellus sp.	The modified web is more robust and better designed to sustain the wasp's cocoon than the normal web.	Matsumoto and Konihi, 2007
Agelena limbata–Brachyzapus nikkoensis	Manipulated spider hosts produce 'veils' of very fine and dense threads covering the spider, and parasitoid larva were observed in the tunnel of the funnel web. The modified web seems resistant against predators and scavengers such as ants.	Matsumoto et al., 2009
Allocyclosa bifurca–Polysphincta gutfreundi	Under the control of the parasitoid, the orb-weaving spider builds a highly modified, physically stable orb web, to which the larva then attaches its pupal cocoon, and adds an otherwise unsual linear silk stabilimentum to this web that may camouflage the cocoon.	Eberhard, 2010b
Anelosimus spp.–*Zatypota nr. solanoi*	Spider hosts are induced to modify their web in such a way as to provide apparent protection and support for the wasp's cocoon by covering the entire web with a protective sheet and adding a central platform, and opening a space below in the enclosed tangle, where the larva suspends its cocoon.	Eberhard, 2010a
Ladybird–parasitic wasp		
Coleomegilla maculata–Dinocampus coccinellae	Partially paralysed on top of the parasitoid cocoon, displaying twitches when disturbed, parasitized ladybirds act as true bodyguards. This manipulated behaviour was shown to provide an efficient protection against predators.	Maure et al., 2011
Bumble bee–endoparasitic fly		
Bumbus terrestris–conopid fly	Induced digging behaviour occurs in infected bumble bees. This manipulated behaviour results in the selection of a hibernation site for the parasitoid pupa and leads to larger and heavier adult flies, showing fewer malformations in their wings than flies hibernating on the ground.	Müller, 1994
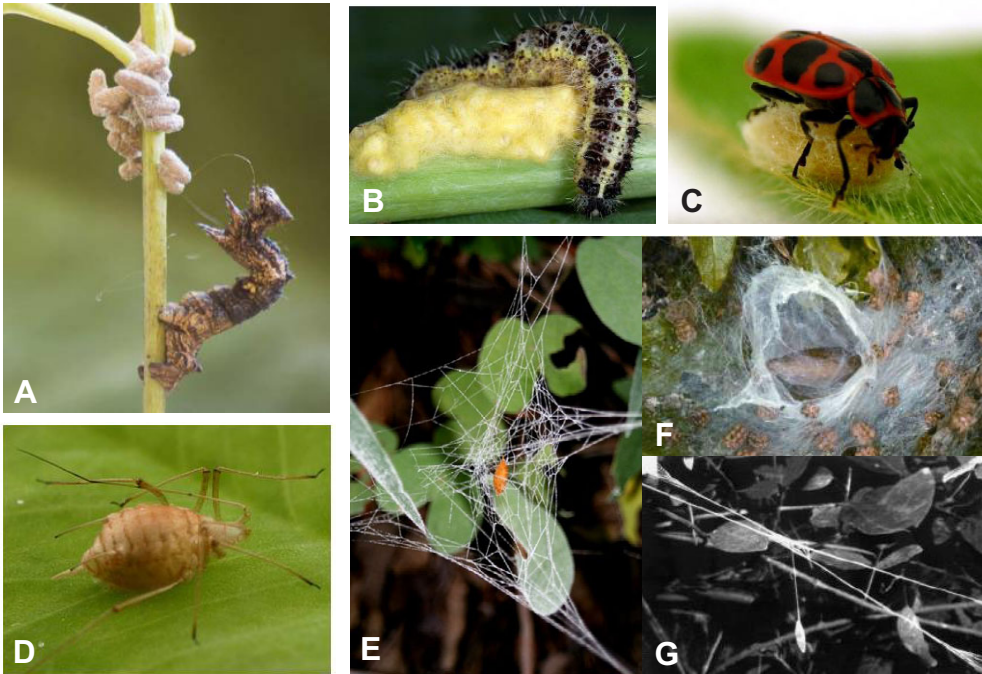
Fig. 1. Illustration of bodyguard manipulation in different host species. (A) *Thyrinteina leucocerae* caterpillar protecting a *Glyptapanteles* sp. parasitic wasp cocoon (photo: J. Lino-Neto). (B) *Pieris brassicae* caterpillar spinning a silk web over the parasitic wasp cocoons of *Cotesia glomerata* (photo: Tibor Bukovinszky). (C) Ladybird *Coleomegilla maculata* attending a cocoon of the parasitic wasp *Dinocampus coccinellae* (photo: F.M.). (D) Mummified aphid remains, hidden under a leaf, after the emergence of the parasitic wasp *Aphidius nigripes* (photo: J.B.). (E) Modified web of *Nephila clavipes* and a larva of the parasitic wasp *Hymenoepimecis bicolor* (photo: M. Gonzaga). (F) A cocoon of the parasitic wasp *Brachyzapus nikkoensis* in the tunnel of the funnel web of *Agelena limbata* (photo: R. Matsumoto). (G) A cocoon of the parasitic wasp *Hymenoepimecis* sp. hanging from a modified orb web of the spider *Plesiometa argyta* (photo: W. Eberhard).

for developing parasites is that their survival in their intermediate hosts is contingent on the survival of the hosts themselves. Decreasing the predation risks of the intermediate hosts could be an adaptation for immature, non-infective parasites to increase their fitness. For instance, within the context of multidimensional manipulations (Thomas et al., 2010a) (see Appendix), there exists in certain host–parasite models a 'bodyguard dimension' to the parasite manipulation, currently termed 'predation suppression' by Parker and colleagues (Parker et al., 2009). In a recent theoretical model, they demonstrated that it is an evolutionary stable strategy for parasites to switch from predation suppression, during the non-infective phase, to predation enhancement, when the infective stage is reached and the parasite can be transmitted. Interestingly, according to Parker and colleagues (Parker et al., 2009), this parasite-induced predation suppression should evolve more easily than enhancement, as the former does not need to be host specific, unlike the latter. To date, there are several well-documented examples of such a behaviour that could be comparable to bodyguard dimensions of the manipulation (Table 2); we will overview two of the most compelling cases.

It is well established that *Anopheles* mosquitoes infected with the transmissible stage of the malaria parasite *Plasmodium* spp. have more frequent and longer feeding bouts than non-infected mosquitoes, thereby increasing parasite transmission (Koella and Packer, 1996; Koella et al., 1998). However, further investigation of the behaviour of parasitized mosquitoes during the non-infective developmental stage of the parasite's life cycle revealed that the parasites, in order to increase the mosquito's survival during this non-infective period, have the capacity to manipulate their host in a way that reduces the host's mortality associated with blood feeding (Anderson and Brust, 1996; Anderson et al., 1999). Indeed, it has been reported that the duration and number of feeding bouts are significantly lower when *Plasmodium* is non-infective (Anderson et al., 1999; Koella et al., 2002), suggesting that the parasite protects its host at least until its maturity. Although the host mosquitoes benefit from an increased survivorship, their ultimate fitness is greatly reduced, as they have significantly reduced

fecundity as a consequence of the low blood intake (Rossignol et al., 1986; Koella et al., 2002). The mechanisms that control blood-feeding behaviour in *Anopheles* are not completely understood, although both endocrinological and neuro-physiological components have been detected in other mosquitoes (Lehane, 1991; Clements, 1992).

Acanthocephalans have a long and well-documented history of host manipulation (reviewed in Moore, 2002; Kennedy, 2006). They have been shown to modify several host phenotypes (reviewed in Thomas et al., 2010a), serving as a prime example of the multidimensionality of parasitic manipulation (Thomas et al., 2010b). To date, the majority of the identified phenotypic manipulations have been linked to increased trophic transmission to the final host. However, alterations of the intermediate host's phenotype can also potentially lead to increased predation by a large range of non-host predators. In a series of first-rate studies, Médoc and colleagues (Médoc and Beisel, 2008; Médoc and Beisel, 2009; Médoc et al., 2009) identified new dimensions of acanthocephalan manipulation in their amphipod host. They demonstrated that the amphipod *Gammarus roeseli* infected with the acanthocephalan *Polymorphus minutus* (1) had superior average and maximum swimming speeds in the presence of non-host predators, (2) spent significantly more time at the air–water interface (negative geotaxis) and (3) remained significantly longer in refugia when exposed to non-host predator chemical cues, compared with non-infected *G. roeseli*. These multiple manipulated traits act synergistically, significantly reducing predation of infected hosts by non-host predators in both the laboratory and the field. As with most host–parasite associations, the benefits conferred to the amphipod host in this context are outweighed by the costs of such behaviours as parasitic manipulation invariably leads to complete and partial castration in the female and male amphipod, respectively (Ward, 1986; Bollache et al., 2001).

Having overviewed some of the 'bodyguard dimensions', the question that we now ask is, can these behavioural modifications be considered as bodyguard manipulations? According to the definition proposed by Poulin, 'a bodyguard manipulation is a

Table 2. List of biological systems where 'bodyguard dimensions' have been reported

Host–parasite systems	Bodyguard behavioural alterations	References
Fish–microsporidia		
Gasterosteus aculeatus–Glugea anomala	Increased anti-predator behaviours were observed in infected sticklebacks.	Milinski, 1985
Snail–trematode		
Potamopyrgus antipodarum– Microphallus sp.	Manipulation by *Microphallus* sp. results in altered foraging behaviour in infected snail hosts. The movement of infected snails from the top to the bottom of rocks corresponds to the peak in activity of the non-host fish predator. The behavioural change was shown to reduce the probability of encounter between infected snails and fish.	Levri, 1998; Levri et al., 2007
Mosquito–plasmodium		
Anopheles stephensi–Plasmodium yoelii nigeriensis	Here, 'predation suppression' consists of decreased feeding persistence of female *Anopheles* towards a human host and was induced only by *Plasmodium* at oocyst stage (which cannot be transmitted).	Anderson et al., 1999
Anopheles gambiae–Plasmodium gallinaceum	Mosquitoes infected with oocysts (which cannot be transmitted) had a smaller threshold volume and were less likely to return for further probing.	Koella et al., 2002
Amphipod–acanthocephalan		
Gammarus roseli–Polymorphus minutus	Despite the encystment of *P. minutus* in the abdomen of its intermediate host, infected amphipods had significantly higher swimming speeds than non-infected ones. Furthermore, when interacting with the non-host predator, the highest escape speeds and greatest distances covered by invertebrates were observed for parasitized animals.	Médoc and Beisel, 2008; Médoc and Beisel, 2009; Médoc et al., 2009
Gammarus pulex–Polymorphus laevis	Increased anti-predator behaviour in gammarids parasitized by the non-infective stage of *P. laevis* (acanthella) results in a decrease in mortality by predation.	Dianne et al., 2011
Copepod–cestode		
Cyclops srenuus–Triaenophorus crassus	Increased antipredator behaviour in infected copepod (reduced activity and increased time to recover) reduces its likelihood of being eaten by the stickleback.	Hammerschmidt et al., 2009

manipulation that alters the behaviour of the host in ways that will provide protection to the parasitoid pupae from predators or other dangers' (Poulin, 2010). But why should we limit this manipulation to insect parasitoids? All examples described in the previous section (including those listed in Table 2) were shown to reduce predation on the host organism or protect it from adverse environmental conditions. Furthermore, the modified hosts all forfeited at least one fitness-related trait as a consequence of accomplishing these behaviours. Therefore, this leads us to suggest that bodyguard manipulations have evolved across different parasite taxa; in certain cases the induced protection conferred by the host represents a single dimension of a more complex manipulation, and in other cases the induced protection constitutes the complete manipulation. Bodyguard manipulations should be defined more generally and concern all manipulations – or dimensions of manipulations – that alter the behaviour of the host in ways that will provide protection to the parasite.

Evolution of bodyguard manipulations

In nature, all organisms cope with environmental pressures acting on their survival (e.g. predation, parasitism and adverse abiotic conditions) and therefore they have evolved numerous defence mechanisms to reduce mortality. Parasites (developing within their intermediate host) and parasitoids (pupating either within or outside their host) do not possess the ability to directly defend themselves. Natural selection should therefore favour manipulative parasites that usurp the behaviour of their host as means of defence (Brodeur and McNeil, 1989; Brodeur and Vet, 1994).

Another possibility lies in the fact that hosts in nature are often parasitized by a community of phylogenetically distinct parasites, which may have a conflict of interests (Brown, 1999; Lafferty et al., 2000). Under such conditions, interactions between parasite species having different life cycles (e.g. a simple *versus* a complex

life cycle or trophically *versus* not trophically transmitted) constitute important selective pressures and could give rise to novel types of manipulation. For instance, the amphipod *Gammarus insensibilis*, can be simultaneously infected by a manipulative trematode, *Microphallus papillorobustus*, that induces strong behavioural alterations making them more vulnerable to predation, and by a non-manipulative nematode, *Gammarinema gammari*, that benefits maximally when the host behaves normally (Thomas et al., 2002a). Thomas and colleagues reported that the nematode is able to manipulate the host's behaviour by negating the effects of the manipulator that would lead it to an early death (Thomas et al., 2002a). Furthermore, in the case of parasites with simple life cycles, which complete their development in one host, selection should favour any manipulative trait that would reduce host mortality associated with predation. We therefore postulate that bodyguard dimension/manipulation could have been selected for within these contexts and evolved as local adaptations depending on parasitic and predator communities, even in parasites with a simple life cycle.

An important constraint for the success of this manipulation is the match between the appropriate parasite developmental stage and the onset of the manipulated behaviours. Within the parasitic wasp models that benefitted from an induced direct protection from their host, manipulation is especially necessary at the pupal stage, when parasitic wasps are particularly vulnerable to danger (Brodeur and Vet, 1994). For instance, in the biological model described previously (Maure et al., 2011), if the paralysis of the ladybird, which inhibits ladybird foraging, is initiated prior to wasp egression, the resulting costs to the developing wasp would be significant: (1) the already limited energetic resources within the host would become even more limited because of the inability of the insect to feed, which would negatively affect wasp fitness; and (2) the unprotected parasitoid pupae would be completely exposed
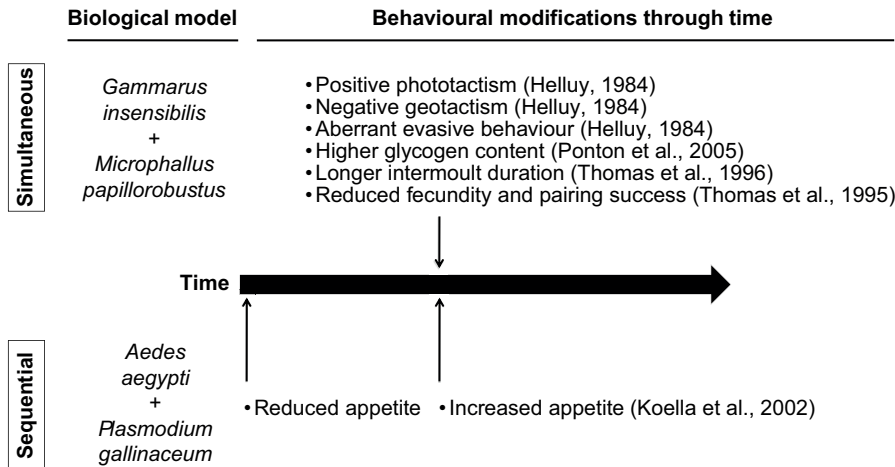
Biological model   **Behavioural modifications through time**

Fig. A1. Schematic diagram of the two categories of multidimensional manipulations: simultaneous and sequential.

Simultaneous

Gammarus insensibilis + *Microphallus papillorobustus*

- Positive phototactism (Helluy, 1984)
- Negative geotactism (Helluy, 1984)
- Aberrant evasive behaviour (Helluy, 1984)
- Higher glycogen content (Ponton et al., 2005)
- Longer intermoult duration (Thomas et al., 1996)
- Reduced fecundity and pairing success (Thomas et al., 1995)

Time

Sequential

Aedes aegypti + *Plasmodium gallinaceum*

- Reduced appetite   • Increased appetite (Koella et al., 2002)

to predation. Similarly, in parasites with complex life cycles, the induction of a bodyguard dimension is only advantageous at a precise developmental stage, prior to the parasites becoming transmissible to the next host. If predation suppression was induced when the parasite was infective, transmission would therefore be greatly reduced; such behaviour should be selected against. The success of this manipulation is dependent on a fixed timing of the onset of the host bodyguard behaviour.

Conclusions and perspectives

In its most general sense, the bodyguard manipulation consists of modified host behaviours that provide protection to the developing parasite/parasitoid against biotic or abiotic factors. Although few induced protective behaviours are explicitly labelled as such, this original survival strategy seems to have evolved in many parasite taxa, sometimes as a sole dimension of more complex manipulations. To enhance our comprehension of the inherent mechanisms governing behavioural manipulations, further experimental evidence of efficient host protection of parasites/parasitoids is necessary. Another avenue of research that has already proven fruitful in a parasitoid model (Maure et al., 2011) but that remains poorly understood in the context of manipulative parasites in general, is the exploration of trade-offs between the benefits conferred by the bodyguard manipulations and the direct costs to fitness-related traits (e.g. longevity, size, fecundity). Indeed, Parker and colleagues postulated that one of the reasons why 'predation suppression' is so seldom observed as compared with 'predation enhancement' is that suppression may be more costly to the parasite (Parker et al., 2009). Furthermore, this type of behaviour may also be rarely described as a consequence of research bias; research investigating parasitic manipulations has either only focused on predation enhancement rather than including all the dimensions of the manipulation or focused on parasites with complex life cycles as opposed to those with simple life cycles.

In addition, the full understanding of these fascinating biological systems necessitates studying the mechanisms underlying host manipulation. Until now, these approaches were regarded as unfeasible in most of the biological models that are described in the present manuscript because of the lack of molecular data in the corresponding species. But recent progress in omics approaches and the emergence of next-generation sequencing offer the opportunity to study in detail the effect of these different parasites on their host physiology. The proliferation of these approaches in these different models could help us to better understand the evolution of this kind of manipulation.

Appendix
The multidimensionality of parasitic manipulation

It is increasingly recognised that parasitically modified hosts are not merely normal hosts with one or a few altered traits, but instead are greatly modified organisms. Indeed, many parasites alter not one but several phenotypic traits in their hosts, significantly increasing the transmission or survival of the parasite (as distinct from the 'infection syndrome') (see Cézilly and Perrot-Minnot, 2010; Thomas et al., 2010b).

Defining multidimensional manipulation

A manipulation may be considered as multidimensional when at least two changes in different or in the same phenotypic traits are observed in manipulated hosts. These changes can occur within or between trait categories (behaviour, morphology and/or physiology), and must not correspond to different ways of measuring the same alteration. Traits that are merely host responses should not be considered as part of multidimensional manipulation unless one can demonstrate that they are adaptively maintained by parasites because of transmission benefits. For instance, Lefèvre and colleagues (Lefèvre et al., 2008) proposed that manipulative parasites could affect fitness-related traits in their hosts (e.g. fecundity, survival, growth) in order to stimulate host compensatory responses, when these responses match with the parasite's transmission route.

Two categories of multidimensional manipulations have been observed: those where the manipulated behaviours occur simultaneously and those where they occur sequentially. For example, all the behavioural changes in the amphipod host *Gammarus insensibilis* infected with the trematode *Microphallus papillorobustus* occur simultaneously, whereas the behavioural changes in the mosquito vector *Aedes aegypti* infected with the malaria parasite *Plasmodium gallinaceum* appear sequentially (Fig. A1).

References

Anderson, R. A. and Brust, R. A. (1996). Blood feeding success of *Aedes aegypti* and *Culex nigripalpus* (Diptera: Cullicidae) in relation to defensive behavior of Japanese quail (*Coturnix japonica*) in the laboratory. *J. Vector Ecol.* **21**, 94-104.

Anderson, R. A., Koella, J. C. and Hurd, H. (1999). The effect of *Plasmodium yoelii nigeriensis* infection on the feeding persistence of *Anopheles stephensi* Liston throughout the sporogonic cycle. *Proc. Biol. Sci.* **266**, 1729-1733.

Bethel, W. M. and Holmes, J. C. (1977). Increased vulnerability of amphipods to predation owing to altered behavior induced by larval acanthocephalans. *Can. J. Zool.* **55**, 110-115.

Bollache, L., Gambade, G. and Cézilly, F. (2001). The effects of two acanthocephalan parasites, *Pomphorhynchus laevis* and *Polymorphus minutus*, on pairing success in male *Gammarus pulex* (Crustacea: Amphipoda). *Behav. Ecol. Sociobiol.* **49**, 296-303.

Brodeur, J. and Boivin, G. (2004). Functional ecology of immature parasitoids. *Annu. Rev. Entomol.* **49**, 27-49.

Brodeur, J. and McNeil, J. N. (1989). Seasonal microhabitat selection by an endoparasitoid through adaptive modification of host behavior. *Science* **244**, 226-228.

Brodeur, J. and McNeil, J. N. (1990). Overwintering microhabitat selection by an endoparasitoid (Hymenoptera: Aphidiidae): induced phototactic and thigmokinetic responses in dying hosts. *J. Insect Behav.* **3**, 751-763.

Brodeur, J. and McNeil, J. N. (1992). Host behaviour modification by the endoparasitoid *Aphidius nigripes*: a strategy to reduce hyperparasitism. *Ecol. Entomol.* **17**, 97-104.

Brodeur, J. and Vet, L. E. M. (1994). Usurpation of host behaviour by a parasitic wasp. *Anim. Behav.* **48**, 187-192.

Brown, S. (1999). Cooperation and conflict in host–manipulating parasites. *Proc. R. Soc. Lond. B* **266**, 1899-1904.

Cézilly, F. and Perrot-Minnot, M. J. (2010). Interpreting multidimensionality in parasite-induced phenotypic alterations: panselectionism versus parsimony. *Oikos* **119**, 1224-1229.

Clements, A. N. (1992). *The Biology of Mosquitoes: Development, Nutrition and Reproduction*, Vol. 1. London: Chapman & Hall.

Dawkins, R. (1982). *The Extended Phenotype.* Oxford: Oxford University Press.

Dianne, L., Perrot-Minnot, M. J., Bauer, A., Gaillard, M., Léger, E. and Rigaud, T. (2011). Protection first then facilitation: a manipulative parasite modulates the vulnerability to predation of its intermediate host according to its own developmental stage. *Evolution* **65**, 2692-2698.

Eberhard, W. G. (2000). Spider manipulation by a wasp larva. *Nature* **406**, 255-256.

Eberhard, W. G. (2001). Under the influence: webs and building behavior of *Plesiometa argyra* (Araneae, Tetragnathidae) when parasitized by *Hymenoepimecis argyraphaga* (Hymenoptera, Ichneumonidae). *J. Arachnol.* **29**, 354-366.

Eberhard, W. G. (2010a). Recovery of spiders from the effects of parasitic wasps: implications for fine-tuned mechanisms of manipulation. *Anim. Behav.* **79**, 375-383.

Eberhard, W. G. (2010b). New types of behavioral manipulation of host spiders by a parasitoid wasp. *Psyche* **2010**, Article ID 950614, doi:10.1155/2010/950614.

English-Loeb, G. M., Karban, R. and Brody, A. K. (1990). Arctiid larvae survive attack by a tachinid parasitoid and produce viable offspring. *Ecol. Entomol.* **15**, 361-362.

Fincke, O. M., Higgins, L. and Rojas, E. (1990). Parasitism of *Nephila clavipes* (Araneae, Tetragnathidae) by an ichneumonid (Hymenoptera, Polysphinctini) in Panama. *J. Arachnol.* **18**, 321-329.

Gonzaga, M. O., Sobczak, J. F., Penteado-Dias, A. M. and Eberhard, W. G. (2010). Modification of *Nephila clavipes* (Araneae Nephilidae) webs induced by the parasitoids *Hymenoepimecis bicolor* and *H. robertsae* (Hymenoptera Ichneumonidae). *Ethol. Ecol. Evol.* **22**, 151-165.

Grosman, A. H., Janssen, A., de Brito, E. F., Cordeiro, E. G., Colares, F., Fonseca, J. O., Lima, E. R., Pallini, A. and Sabelis, M. W. (2008). Parasitoid increases survival of its pupae by inducing hosts to fight predators. *PLoS ONE* **3**, e2276.

Hammerschmidt, K., Koch, K., Milinski, M., Chubb, J. C. and Parker, G. A. (2009). When to go: optimization of host switching in parasites with complex life cycles. *Evolution* **63**, 1976-1986.

Harvey, J. A., Tanaka, T., Kruidhof, M., Vet, L. E. M. and Gols, R. (2011). The 'usurpation hypothesis' revisited: dying caterpillar repels attack from a hyperparasitoid wasp. *Anim. Behav.* **81**, 1281-1287.

Helluy, S. (1983). Relations hôtes-parasite du trematode *Microphallus papillorobustus* (Rankin, 1940) II – modifications du comportement des *Gammarus* hôtes intermédiaires et localisation des métacercaires. *Ann. Parasitol. Hum. Comp.* **58**, 1-17.

Helluy, S. (1984). Relations hôtes-parasites du trématode *Microphallus papillorobustus* (Rankin, 1940) III – facteurs impliqués dans les modifications du comportement des *Gammarus*, hôtes intermédiaires et tests de prédation. *Ann. Parasitol. Hum. Comp.* **59**, 41-56.

Hughes, D. P., Brodeur, J. and Thomas, F. (2012). *Host Manipulation by Parasites.* Oxford: Oxford University Press.

Kennedy, C. R. (2006). *Ecology of the Acanthocephala.* Cambridge: Cambridge University Press.

Kester, K. and Jackson, D. (1996). When good bugs go bad: intraguild predation by *Jalysus wickhami* on the parasitoid *Cotesia congregata*. *Entomol. Exp. Appl.* **81**, 271-276.

Koella, J. C. and Packer, M. J. (1996). Malaria parasites enhance blood-feeding of their naturally infected vector *Anopheles punctulatus. Parasitology* **113**, 105-109.

Koella, J. C., Sörensen, F. L. and Anderson, R. A. (1998). The malaria parasite, *Plasmodium falciparum*, increases the frequency of multiple feeding of its mosquito vector, *Anopheles gambiae. Proc. Biol. Sci.* **265**, 763-768.

Koella, J. C., Rieu, L. and Paul, R. E. L. (2002). Stage-specific manipulation of a mosquito's host-seeking behavior by the malaria parasite *Plasmodium gallinaceum. Behav. Ecol.* **13**, 816-820.

Lafferty, K. D., Thomas, F. and Poulin, R. (2000). Evolution of host phenotype manipulation by parasites and its consequences. In *Evolutionary Biology of Host-Parasite Relationships: Theory Meets Reality* (ed. R. Poulin, S. Morand and A. Skorping), pp. 117-127. Amsterdam: Elsevier Science.

Lefèvre, T., Koella, J. C., Renaud, F., Hurd, H., Biron, D. G. and Thomas, F. (2006). New prospects for research on manipulation of insect vectors by pathogens. *PLoS Pathog.* **2**, e72.

Lefèvre, T., Roche, B., Poulin, R., Hurd, H., Renaud, F. and Thomas, F. (2008). Exploiting host compensatory responses: the 'must' of manipulation? *Trends Parasitol.* **24**, 435-439.

Lefèvre, T., Lebarbenchon, C., Gauthier-Clerc, M., Missé, D., Poulin, R. and Thomas, F. (2009). The ecological significance of manipulative parasites. *Trends Ecol. Evol.* **24**, 41-48.

Lehane, M. J. (1991). *Biology of Blood-Sucking Insects.* Cambridge: Cambridge University Press.

Levri, E. (1998). The influence of non-host predators on parasite-induced behavioral changes in a freshwater snail. *Oikos* **81**, 531-537.

Levri, E. P., Lunnen, S. J., Itle, C. T., Mosquea, L., Kinkade, B. V., Martin, T. G. and DeLisser, M. A. (2007). Parasite-induced alteration of diurnal rhythms in a freshwater snail. *J. Parasitol.* **93**, 231-237.

Marples, N. M., Van Veelen, W. and Brakefield, P. M. (1994). The relative importance of colour, taste and smell in the protection of an aposematic insect *Coccinella septempunctata. Anim. Behav.* **48**, 967-974.

Matsumoto, R. (2009). 'Veils' against predators: modified web structure of a host spider induced by an Ichneumonid parasitoid, *Brachyzapus nikkoensis* (Uchida) (Hymenoptera). *J. Insect Behav.* **22**, 39-48.

Matsumoto, R. and Konishi, K. (2007). Life histories of two ichneumonid parasitoids of *Cyclosa octotuberculata* (Araneae): *Reclinervellus tuberculatus* (Uchida) and its new sympatric congener (Hymenoptera: Ichneumonidae: Pimplinae). *Entomol. Sci.* **10**, 267-278.

Maure, F., Brodeur, J., Ponlet, N., Doyon, J., Firlej, A., Elguero, É. and Thomas, F. (2011). The cost of a bodyguard. *Biol. Lett.* **7**, 843-846.

Médoc, V. and Beisel, J. N. (2008). An acanthocephalan parasite boosts the escape performance of its intermediate host facing non-host predators. *Parasitology* **135**, 977-984.

Médoc, V. and Beisel, J. N. (2009). Field evidence for non-host predator avoidance in a manipulated amphipod. *Naturwissenschaften* **96**, 513-523.

Médoc, V., Rigaud, T., Bollache, L. and Beisel, J. N. (2009). A manipulative parasite increasing an antipredator response decreases its vulnerability to a nonhost predator. *Anim. Behav.* **77**, 1235-1241.

Milinski, M. (1985). Risk of predation of parasitized sticklebacks (*Gasterosteus aculeatus* L.) under competition for food. *Behaviour* **93**, 203-216.

Moore, J. (1993). Parasites and the behavior of biting flies. *J. Parasitol.* **79**, 1-16.

Moore, J. (2002). *Parasites and the Behavior of Animals.* Oxford: Oxford University Press.

Müller, C. B. (1994). Parasitoid induced digging behaviour in bumblebee workers. *Anim. Behav.* **48**, 961-966.

Nielsen, E. (1923). Contributions to the life history of the Pimpline spider parasites (Polysphincta, Zaglyptus, Tromatobia) (Hym. Ichneum.). *Entomol. Medd.* **14**, 137-205.

Parker, G. A., Ball, M. A., Chubb, J. C., Hammerschmidt, K. and Milinski, M. (2009). When should a trophically transmitted parasite manipulate its host? *Evolution* **63**, 448-458.

Ponton, F., Biron, D. G., Joly, C., Helluy, S., Duneau, D. and Thomas, F. (2005). Ecology of parasitically modified populations: a case study from a gammarid-trematode system. *Mar. Ecol. Prog. Ser.* **299**, 205-215.

Poulin, R. (2010). Parasite manipulation of host behavior: an update and frequently asked questions. *Adv. Stud. Behav.* **41**, 151-186.

Poulin, R., Brodeur, J. and Moore, J. (1994). Parasite manipulation of host behaviour: should hosts always lose? *Oikos* **70**, 479-484.

Rossignol, P. A., Ribeiro, J. M. C. and Spielman, A. (1986). Increased biting rate and reduced fertility in sporozoite-infected mosquitoes. *Am. J. Trop. Med. Hyg.* **35**, 277-279.

Thomas, F., Renaud, F., Derothe, J. M., Lambert, A., Meeüs, T. and Cézilly, F. (1995). Assortative pairing in *Gammarus insensibilis* (Amphipoda) infected by a trematode parasite. *Oecologia* **104**, 259-264.

Thomas, F., Verneau, O., Santalla, F., Cézilly, F. and Renaud, F. (1996). The influence of intensity of infection by a trematode parasite on the reproductive biology of *Gammarus insensibilis* (Amphipoda). *Int. J. Parasitol.* **26**, 1205-1209.

Thomas, F., Fauchier, J. and Lafferty, K. D. (2002a). Conflict of interest between a nematode and a trematode in an amphipod host: test of the 'sabotage' hypothesis. *Behav. Ecol. Sociobiol.* **51**, 296-301.

Thomas, F., Schmidt Rhaesa, A., Martin, G., Manu, C., Durand, P. and Renaud, F. (2002b). Do hairworms (Nematomorpha) manipulate the water seeking behaviour of their terrestrial hosts? *J. Evol. Biol.* **15**, 356-361.

Thomas, F., Poulin, R. and Brodeur, J. (2010a). Host manipulation by parasites: a multidimensional phenomenon. *Oikos* **119**, 1217-1223.

Thomas, F., Poulin, R. and Brodeur, J. (2010b). Infection syndrome and multidimensionality: two terms for two different issues. *Oikos* **119**, 1230.

Ward, P. I. (1986). A comparative field study of the breeding behaviour of a stream and a pond population of *Gammarus pulex* (Amphipoda). *Oikos* **46**, 29-36.

Weng, J. L. and Barrantes, G. (2007). Natural history and larval behavior of the parasitoid *Zatypota petronae* (Hymenoptera: Ichneumonidae). *J. Hymenopt. Res.* **16**, 326-335.