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REVIEW

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Summary

Although host manipulation is likely to be costly for parasites, we still have a poor understanding of the energetic aspects underlying this strategy. It is traditionally assumed that physiological costs are inevitably associated with mechanisms evolved by parasites to induce the required changes in host behaviours. While most energetic expenditures of parasites relate primarily to bringing about the altered behaviours, manipulative parasites also have to consider the condition of their host during the manipulation. Here, we suggest that because of this trade-off, the energy required to accomplish parasite-induced behaviours may represent a key energetic constraint for parasites. Depending on the energetic expenditures specific to each type of manipulation, parasites should undergo selection to secure resources for their host to allow them to perform manipulated behaviours.

Introduction

Parasites, by definition, are organisms that take advantage of their hosts. They do this in many ways, for example through the exploitation of their nutritional resources (e.g. haemolymph, lipid or tissues) and by changing behaviours. From a bio-energetic viewpoint, the host–parasite association can be seen as a perpetual conflict between the needs of the parasite and those of the host for growth, reproduction and survival. Although maximal exploitation of host resources could be advantageous for parasite fitness (e.g. increase in growth rate and/or adult reproductive success), the negative consequences of this strategy could in fact be fatal for parasites if they lead to early host death. Therefore, parasites face competing demands for shared host resources and should evolve to manage this conflict by adopting the most profitable trade-off between the benefits of resource consumption and the costs of reduced host viability (Poulin, 2007).

Many parasites, in order to facilitate their transmission or increase their survival, have the capacity to manipulate the behaviour of their host to their own advantage (for reviews, see Moore, 2002; Poulin, 2010). Although natural selection is expected to retain manipulations that require low, rather than high, physiological costs, host manipulation is unlikely to be free. Manipulative parasites have therefore to 'budget' for such costs when optimizing the exploitation of host resources as they develop. Although many aspects of this strategy are now well known (e.g. diversity, timing, adaptive values) (Lefèvre et al., 2008), the energetic aspects underlying host behavioural manipulations remain poorly understood (Thomas et al., 2005; Poulin, 2010).

It is traditionally assumed that physiological costs are inevitably associated with host manipulation (e.g. the energy required for the production of neuroactive substances), and that the energy spent by parasites for this task would therefore not be available for other functions such as growth and reproduction (Poulin, 1994; Poulin, 1995). Manipulative parasites would then face a trade-off between allocating the energy taken from the host into host manipulation and other functions. Franceschi and colleagues recently provided experimental evidence supporting the existence of trade-offs in manipulative parasites (Franceschi et al., 2010). In the acanthocephalan *Pomphorynchus laevis* parasitizing the gammarid *Gammarus pulex*, manipulated hosts display an aberrant escape response toward the water surface, following a mechanical disturbance, thus increasing the likelihood of predation by waterfowl, the definitive hosts of the parasite. The authors showed that individual parasites that rapidly reach the stage infective to waterfowl do not induce these host behavioural changes, while parasites developing more slowly manipulate the behaviour of their host as soon as they reach the infective stage (Franceschi et al., 2010). This finding suggests that *P. laevis* cannot optimize both their growth rate and the intensity of the behavioural manipulation.

Aside from this proximate-level view of the cost of host manipulation, Poulin and colleagues highlighted that from an ultimate-level perspective, indirect costs linked to the manipulation should be considered as well (Poulin et al., 2005). Manipulative parasites could incur a cost resulting from a higher probability of being killed compared with conspecifics that may benefit from manipulation without inducing it themselves. For example, because of their strategic location in the head of their host, manipulative metacercariae of *Microphallus papillorobustus* are more likely to be killed by the host's immune system (i.e. encapsulation and melanization) than conspecifics encysting in the abdomen (Thomas
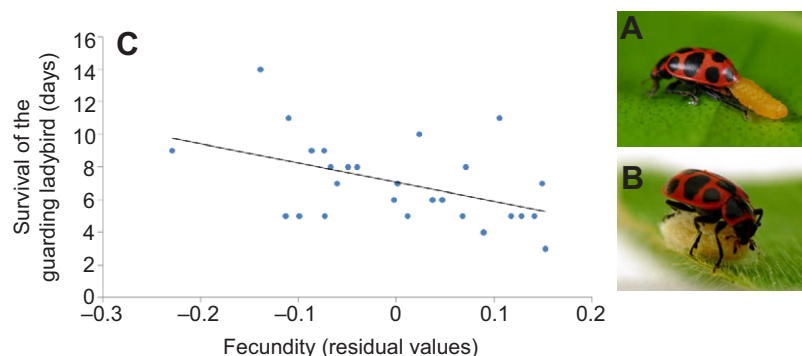
Fig. 1. (A) The parasitoid *Dinocampus coccinellae* and its host the ladybird *Coleomegilla maculata*. The parasitoid larva is shown egressing from the ladybird (photograph by M. Bélanger Morin). (B) Ladybird attending a parasitoid cocoon (photograph by F. Maure). (C) Relationship between the survivorship of attending *C. maculata* ladybirds and the number of mature eggs at emergence of *D. coccinellae* parasitoids. Residuals correspond to fecundity data corrected by the size and the pupal development time of the parasitoid, and the sex and size of the ladybird. R^2=0.219 and P=0.0137 (from Maure et al., 2011).

et al., 2000). Also, manipulative *Curtuteria australis* larvae that encyst in the tip of the food of their cockle host face a greater risk of predation by unsuitable hosts than conspecifics that are found in the base of the foot and do not induce host manipulation (Mouritsen and Poulin, 2003). Although this indirect, probabilistic cost is only paid in the event that the parasite dies during the host manipulation, it is a cost nonetheless, and it is relevant when calculating the net fitness outcome of manipulation (Poulin et al., 2005).

The host energetic resource constraint hypothesis

Here, we suggest that the energy required by the host to accomplish a parasite-induced behaviour represents a key energetic constraint largely overlooked when investigating the cost of host manipulation for parasites. Depending on the energetic expenditures specific to each type of host manipulation, parasites should adaptively leave given amounts of resources to their host to allow them to perform manipulated behaviours. This host energetic resource constraint (HERC) hypothesis has recently been illustrated in the association between the parasitic wasp *Dinocampus coccinellae* and its host, the spotted lady beetle *Coleomegilla maculata* (Maure et al., 2011). Parasitoid females deposit a single egg in the haemocoel of the host, and during larval development the parasitoid feeds on host tissues. At the prepupal stage, the parasitoid egresses from its host by forcing its way through the beetle's abdominal segments (Fig. 1A) and begins spinning a cocoon between the ladybird's legs (Fig. 1B). Remarkably for a parasitoid, *D. coccinellae* does not kill its host during its development but rather partially paralyses the

coccinellid, usurping its aposematic coat and defensive behaviour. The manipulated ladybird is then turned into a bodyguard (*sensu* Maure et al., 2013) that contributes to reduce mortality from natural enemies during parasitoid pupation. The length of the manipulation period is negatively correlated with *D. coccinellae* fecundity (Fig. 1C), suggesting that the parasitoid cannot concomitantly allocate maximal resources for both its reproduction and protection.

Although we consider the HERC hypothesis as conceptually appealing, there is currently no example besides the coccinellid–parasitoid model that supports the idea that manipulative parasites must leave resources to their hosts to successfully achieve their goal through host manipulation. The relevance of the HERC hypothesis in other manipulative parasites therefore invites further exploration.

From our previous findings (Maure et al., 2011), we developed a schema representing the energetic dilemma faced by manipulative parasites as a nested system (Fig. 2). In addition to managing host resources for their direct needs (the 'proximate trade-off' commonly mentioned in the literature; see 'Trade-off 2' in Fig. 2) (Poulin, 1994), parasites should also consider the energetic costs arising from the host manipulation (see 'Trade-off 1' in Fig. 2). Depending on the energetic expenditures involved with this strategy of transmission/survival, predictions can be derived on how the 'host energetic budget' should be managed by the parasite with regards to its fitness (Fig. 3).

The decision by manipulative parasites to leave a fraction of the resources to their hosts is possibly a one-shot game. In the case
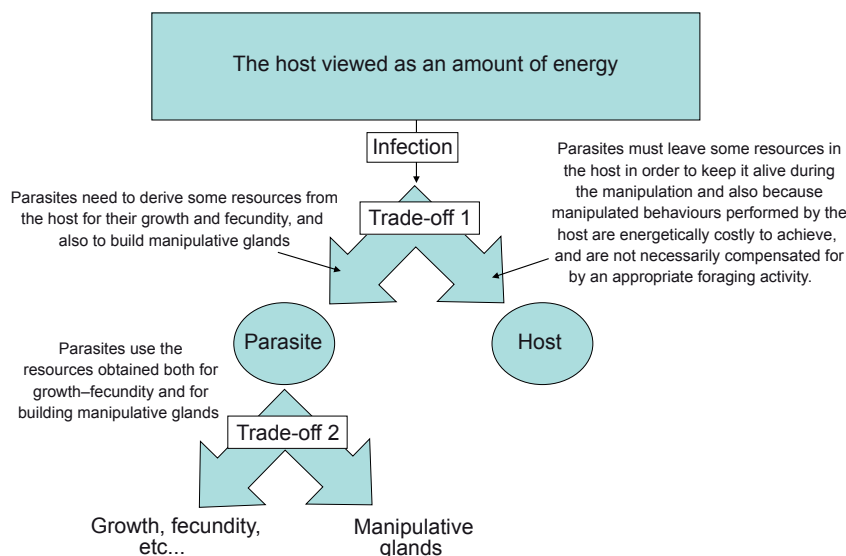

Fig. 2. Schematic diagram of the energetic dilemma faced by manipulative parasites.
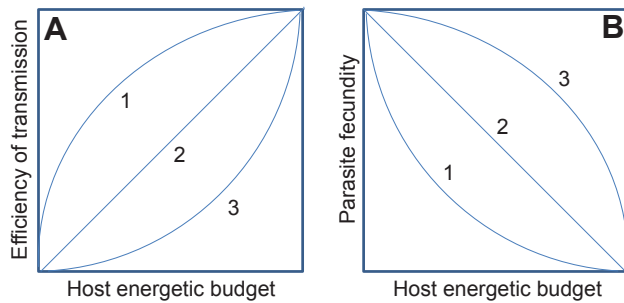
Fig. 3. Predicted relationships between the energetic resources left by the parasite to the host to accomplish manipulated behaviours (the 'host energetic budget') and (A) the efficiency of transmission/survival (hereafter 'transmission') and (B) the fecundity of the parasite. The curves illustrate the three most likely scenarios. For the efficiency of transmission, (1) small increases in the energy left to the host lead to a large increase in transmission, (2) transmission gradually increases as the energy left by the parasite to the host increases, and (3) transmission increases only when the energy left by the parasite to the host is high. For the parasite fecundity, (1) small increases in the energy left to the host lead to a large decrease in fecundity, (2) fecundity gradually decreases as the energy left by the parasite to the host increases, and (3) fecundity decreases only when the energy left by the parasite to the host is high.

described previously (Maure et al., 2011), because the manipulation of the ladybird occurs after the wasp has exited the host, the resource allocation is irreversible as there are no more physical interactions between the two protagonists. Thus, it is during its larval stage that *D. coccinellae* has to 'budget' how much of the resources should be left to the host. In other systems, the resource extraction can be reversible as the host (under its own control or under the control of the parasite) (Roitberg, 2012) continues to forage while being manipulated and this foraging behaviour could potentially fuel the manipulation (i.e. contribute energetically to the cost of the manipulation), at least partially compensating for the energetic expenditures associated with its expression. Whether the decision is reversible or not, reaching the minimal threshold in the host energy level is crucial for the efficiency of the manipulation. For instance, hosts in poor condition will be less subject to intensive manipulation, even if they are genetically sensitive to manipulation and infected with a parasite having strong manipulative abilities (Thomas et al., 2011).

There are at the moment no available data to test the HERC hypothesis and quantify the energetic costs required to accomplish manipulated behaviours. However, this hypothesis should be relevant in many systems as manipulated hosts obviously perform activities requiring energy. For instance, the aberrant escape behaviour of gammarids parasitized by *M. papillorobustus* consists of swimming from the bottom toward the surface following a mechanical disturbance and then remaining at the air–water interface for a period of several seconds or even minutes (Helluy, 1983). In response to the attack of *Cotesia glomerata* parasitoid cocoons, manipulated caterpillar hosts behave as a bodyguard, spinning a silk web over the parasitoid cocoons and displaying violent head thrashing to knock off natural enemies (Brodeur and Vet, 1994). Also, in addition to turning the abdomen of its ant intermediate host bright red, the nematode *Myrmeconema neotropicum* drives the ant to perch itself, abdomen raised, among patches of small red berries, waiting to be eaten by frugivorous birds, the definitive hosts of the parasite (Yanoviak et al., 2008). In other systems, the altered parasite-induced behaviours seem to be

associated with low or no significant energetic cost, for instance when manipulated hosts, once in a given microhabitat, do not accomplish particular activities [e.g. ants parasitized by the trematode *Dicrocoelium dentriticum* climb to the tip of grass blades and stay there waiting for a grazing sheep (Carney, 1969)]. However, such alterations, even though they are undoubtedly less energy consuming than active manipulated behaviours, probably come with an energetic cost, at least because foraging opportunities are absent or reduced during these periods.

The relevance of the HERC hypothesis possibly lies in the fact that it may help us to understand different aspects related to the evolution of host manipulation by parasites, and more specifically to the evolution of 'multidimensional manipulations' (Thomas et al., 2010). It is increasingly recognized that manipulative parasites alter several phenotypic traits in their hosts, these alterations occurring simultaneously and/or successively (Thomas et al., 2010). For example, several bird helminths (trematodes, acanthocephalans and cestodes) parasitizing crustaceans from the genus *Gammarus* and *Artemia*, in addition to modifying the behaviour of their host, are able to increase the host's level of energetic resources (glycogen and especially lipids) (Amat et al., 1991; Plaistow et al., 2001; Ponton et al., 2005). Although experimental evidence is still lacking, these findings suggest that these parasites physiologically manipulate their hosts in a way that will compensate for the energetic expenditures associated with manipulated behaviours. Complete or partial castration induced by trophically transmitted parasites in an intermediate host could also have evolved in this context; because of the trade-off between reproduction and longevity, the energy saved could be used by the host to fuel manipulative changes (e.g. the host lifespan) (Hurd et al., 2001). The HERC hypothesis also provides a possible explanation for the important intraspecific variability observed in host manipulation in nature (Thomas et al., 2011) as the intensity of the manipulation could be related to the host condition.

Empirical data on energetic costs associated with manipulated behaviours in different systems are clearly required. The HERC hypothesis constitutes a novel and promising research direction. Exploring this topic will require collaborations between parasitologists and researchers from other disciplines, especially physiology, biochemistry and bioenergetics. One conceivable approach to test the HERC hypothesis would be to experimentally manipulate the expression of induced behaviours in parasitized hosts. Measurement of the energetic expenditure of the hosts under different conditions of manipulation (e.g. level of intensity) would provide a concrete illustration of the energetic constraints for manipulative parasites. Hoover and colleagues have recently identified a gene responsible for the manipulation of gypsy moth behaviour by a baculovirus (Hoover et al., 2011). Following deletion of this specific gene, infected caterpillars do not express the altered behaviour consisting of climbing to the top of their host tree to die, liquify and then release millions of infective virus particles. Such a system could be a good candidate for investigating how much energy manipulative parasites must leave to their hosts to accomplish altered behaviours.

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