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Host manipulation by parasites: a multidimensional phenomenon

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The diversity of ways in which parasites manipulate the phenotype of their hosts to increase their transmission has been well-documented during the past decades. Parasites clearly have the potential to alter a broad range of phenotypic traits in their hosts, extending from behaviour and colour to morphology and physiology. While the vast majority of studies have concentrated on few, often only one, host characters, there is increasing evidence that manipulative parasites alter multiple characteristics of their host's phenotype. These alterations can occur simultaneously and/or successively through time, making parasitically modified organisms undoubtedly more complex than traditionally viewed. Here, we briefly review the multidimensionality of host manipulation by parasites, discuss its possible significance and evolution, and propose directions for further research. This view should prove to be an extremely useful approach, generating a series of testable hypotheses regarding the ecology of parasitized hosts, and leading to a better comprehension of complex host–parasite relationships.

Parasite-induced alteration of host phenotype is a widespread strategy of transmission among pathogens (Moore 2002). It has been reported in viruses, fungi, bacteria, protozoans, nematodes, nematomorphs, trematodes, cestodes, acanthocephalans and parasitoids (Poulin 2007, Lefèvre et al. 2009). Phenotypic changes in parasitized hosts can vary greatly in their magnitude and diversity, from slight shifts in the percentage of time spent performing a given activity to the display of spectacular morphologies or behaviours (Thomas et al. 2002a, Yanoviak et al. 2008). While host-manipulative parasite associations are frequently known for one particularly striking phenotypic change (e.g. ants manipulated by *Dicrocoelium dendriticum* climb to the top of grass blades, crickets parasitized by hairworms jump into water...), it is increasingly recognized that parasitically modified hosts are not merely normal hosts with one or few altered traits, but instead they are deeply modified organisms (Poulin and Thomas 1999, Brodeur and Boivin 2004, Cézilly and Perrot-Minnot 2005, Thomas et al. 2005). One cause of this complexity is that manipulative parasites alter not only one but several phenotypic traits in their hosts (Table 1).

Here, we explore the multidimensional aspect of host manipulation by parasites. After providing definitions and examples, we discuss the extent, significance and evolution of this phenomenon, and show how it provides a new and promising research direction. Specifically, we link multidimensional manipulation with theoretical frameworks already established in other fields, such as the mosaic theory of coevolution, and the hypotheses regarding the evolution of

complex signalling systems that have fuelled recent research in behavioural ecology. We show how the use of conceptual tools borrowed from other fields and applied to a multidimensional view of host manipulation can lead to progress in the study of host–parasite interactions that would otherwise not be possible.

Definition of multidimensionality

Basic considerations

A first condition before a manipulation can be considered as multidimensional is that at least two changes in different phenotypic traits, or in the same phenotypic traits, are observed in the manipulated host. 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. For instance, a behavioural change can be associated with neurological disorders in the brain of the parasitized host, but we cannot consider the atypical behaviour displayed and their associated neurological bases as different dimensions of the manipulation. In addition, since the label manipulation has been restricted to phenotypic changes that are involved in parasite transmission processes (Poulin 1995), we propose to also restrict the label multidimensionality to these specific changes. For instance, if we consider the case of the amphipod *Gammarus insensibilis* parasitized by the trematode *Microphallus papillorobustus* (Table 1), it has been demonstrated that each of the three behavioural changes displayed by parasitized

Table 1. Examples of multidimensionality in host-manipulative parasite systems (the list is not exhaustive).

Host–parasite systems	Phenotypic alterations	References
Crustaceans–Helminths		
Trematoda		
<i>Gammarus insensibilis</i> - <i>Microphallus papillorobustus</i>	positive phototactism negative geotactism aberrant evasive behaviour higher glycogen content longer intermoult duration reduced fecundity and pairing success	Helluy 1984 Ponton et al. 2005 Thomas et al. 1996 Thomas et al. 1995
Acanthocephalan <i>Gammarus pulex</i> - <i>Pomphorynchus laevis</i>	presence of a new color (orange spot) positive phototactism increased activity reduced oxygen consumption reduced fecundity and pairing success increased glycogen levels increased haemocyanin concentration increased level of fluctuating asymmetry immune depression	Moore 2002 Cézilly et al. 2000 Dezfuli et al. 1994 Rumpus and Kennedy 1974 Bollache et al. 2002 Plaiستow et al. 2001 Bentley and Hurd 1996 Alibert et al. 2002 Cornet et al. 2009
Cestode <i>Artemia parthenogenetica</i> - <i>Confluaria podicipina</i>	increased lipid contents positive phototactism increased carotenoid contents neurological disorders physiology and behaviour	Sanchez et al. 2009a, 2009b and unpubl. data
<i>Gammarus pulex</i> - <i>Cyathocephalus truncates</i>		Franceschi et al. 2007
Insect–Nematomorpha <i>Nemobius sylvestris</i> - <i>Paragordius tricuspidatus</i>	increased activity erratic behaviour water-seeking behaviour	Thomas et al. 2002a
Insect–Fungus <i>Camponotus leonardi</i> - <i>Ophiocordyceps unilateralis</i>	biting behaviour habitat preference	Andersen et al. 2009
Insects–Nematodes <i>Baetis bicaudatus</i> - <i>Gasteromermis</i> sp.	morphology (feminisation of males) behaviour (males undergo complete sex reversal)	Vance 1996
<i>Cephalotes atratus</i> – <i>Myrmeconema</i> sp.	morphology (induce fruit mimicry) behaviour (gasters are held in a conspicuous elevated position, reduced defensive behaviour)	Yanoviak et al. 2008
Insect–Parasitoid <i>Aphidius nigripes</i> - <i>Macrosiphum euphorbiae</i>	negative phototaxis thigmokinesis selection of dark-colored substrate	Brodeur and McNeil 1990
Fish–Cestodes <i>Gasterosteus aculeatus</i> - <i>Schistocephalus solidus</i>	foraging behaviour shoaling behaviour	Barber and Huntingford 1995
<i>Rutilus rutilus</i> - <i>Ligula intestinalis</i>	swim close to the surface aberrant response to stimulus morphology	Loot et al. 2002
Insect–Protozoan <i>Aedes aegypti</i> - <i>Plasmodium gallinaceum</i>	sequential manipulation: reduced and then increased appetite	Koella et al. 2002
Mammal–Virus <i>Canis vulgaris</i> - <i>Lyssavirus</i>	aggressiveness hypersalivation	Rupprecht et al. 2002
Mammal–Protozoan <i>Rattus rattus</i> - <i>Toxoplasma gondii</i>	higher activity level less cautious to novel stimuli attracted by the odour of cat urine	Berdoy et al. 2000

individuals contribute to increase the risk of predation by aquatic birds (definitive host), and hence the transmission of the parasite (Helluy 1984). However, it remains unclear whether the reduced reproductive performance of parasitized individuals and/or their longer intermoult duration also play roles in transmission. It can be advantageous for the parasite to shift host resource allocation from reproduction and growth to survival, since host survival until predation is essential for trophically-transmitted parasites (Poulin 1994, Hurd et al. 2001). In such cases, the reduced reproductive performance and/or growth of parasitized hosts could be considered as a dimension of the manipulation. Otherwise, it should be considered as a pathological consequence of the infection. For example, while the immune depression induced by the acanthocephalan parasite *Pomphorynchus laevis* in its intermediate amphipod host *Gammarus pulex* improves parasite survival within the intermediate host's body cavity, it has apparently no relation to the behavioural alterations that favour transmission to definitive hosts (Cornet et al. 2009). The absence of correlation is however not always evidence for the two altered traits being independent of each other. For instance, different neuro-hormones (affecting specific phenotypic traits) may react differently to an increase in the concentration of a neuro-modulator induced by the parasite in its host.

Can host responses be considered to multidimensionality?

Poulin and Thomas (1999) argued that the ability of infected hosts to undergo significant phenotypic alterations, such as a change of microhabitat, may depend on the plasticity of some other traits to accommodate this novelty. Manipulative parasites could then act as a developmental switch channelling several associated traits in particular directions (Dingemanse et al. 2009). Because these phenotypic adjustments are host responses, whether or not they could be considered as a dimension in the manipulation is debatable. These changes can be beneficial for parasitized hosts if they allow them to reproduce, at least partially, under their new circumstances. They can also correspond to automatic plastic responses that are not, in the present context, associated with significant fitness benefits for either the host or the parasite. Finally, they can be beneficial for the parasite if they allow the parasitized hosts to cope better with new environmental conditions until events related to transmission (e.g. predation by definitive hosts) occur. This does not necessarily mean that the parasite induces them directly, at best it means that it does not suppress them. We suggest that 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. Lefèvre et al. (2008) proposed that manipulative parasites could affect fitness-related traits in their hosts (e.g. fecundity, survival, growth, competitiveness) in order to stimulate host compensatory responses, when these responses match with the parasites' transmission routes. In that case, the manipulation relies on host responses which are triggered by the parasite. This type of host responses should be included into multidimensionality. Because manipulation *sensu stricto* and exploitation of

host compensatory responses are different but not mutually exclusive scenarios, multidimensionality in host manipulation can also have mixed origins.

Parasite-induced multiple manipulations

Complex alterations of host phenotype can arise from parasites being able to directly manipulate several traits in their hosts. The manipulation of several host traits by parasites is indeed likely to be favoured by selection. For instance, a trophically-transmitted parasite can greatly enhance the detectability and vulnerability of its intermediate host to predation by definitive hosts if it alters simultaneously the behaviour and the colour of its host (Bakker et al. 1997, Sanchez et al. 2009a). Disentangling the exact adaptive nature of each dimension, however, is not always straightforward. Consider for instance the case of crustaceans parasitized by helminths (Table 1) for which, in addition to behavioural changes, an increased level of energetic reserves is observed in these host-parasite associations. These parasites are phylogenetically unrelated but they have evolved under similar ecological pressures for their transmission as they require the predation of the crustacean by a vertebrate predator. If we thus assume that enhanced lipid content in the crustacean host is adaptive for transmission, at least two scenarios can be proposed. First, because displaying an aberrant behaviour can be energetically costly for host species, hosts with a high level of energy reserves could be manipulated for longer periods than those with poor reserves (Ponton et al. 2005). A physiological manipulation of lipid metabolism could then enhance the length, and thereby the chance of success, of the behavioural manipulation. A second, not mutually exclusive, explanation is possible: given that predators foraging on potentially infected prey try to minimise the ratio of cost of infection to energetic benefits (Lafferty 1992), enhancing the nutritive value of the host may be selected as a parasitic strategy to increase transmission to predators that are able to visually discriminate among prey having different energetic values (Sanchez et al. 2009b). It appears important, when feasible, to explore the precise nature and outcome of each alteration on parasite transmission, and the way it interacts with the other dimensions. For example, Kaldonski et al. (2009) tested for an effect of acanthocephalan parasite coloration (in addition to behavioural changes) on increased trophic transmission by painting a yellow-orange spot on the cuticle of uninfected gammarids and by masking the yellow-orange spot of infected individuals with inconspicuous brown paint. They found no evidence for a role of parasite coloration in the increased vulnerability of gammarids to predation by trout.

Simultaneous and sequential multidimensionality

At least two types of multidimensionality must be distinguished: the simultaneous and the successive ones. For instance, while the phenotypic changes reported for *G. insensibilis* (Table 1) occur simultaneously, those mentioned for crickets harbouring hairworms occur in succession. In infected crickets, the first behavioural change (the erratic behaviour) occurs before the worm is fully mature, and apparently serves to increase the probability of encountering a water body suitable for worm emergence and reproduction;

about one week later, the second behavioural change enables the parasite to physically enter water (Sanchez et al. 2008). These behavioural changes are two components of the same transmission strategy but they clearly occur one after the other: crickets displaying the erratic behaviour do not yet enter water (Sanchez et al. 2008). In a related vein, Koella et al. (2002) showed that different stages of the malaria parasite *Plasmodium gallinaceum* differentially affect the host-seeking behavior of its mosquito vector *Aedes aegypti*. Immature stages are expected to increase the vector's survival to increase their chance of becoming mature, while mature stages are potentially confronted with a tradeoff between increasing the vector's lifespan and thus survival on the one hand, and on the other increasing biting frequency at the expense of survival since biting is risky in nature. Accordingly, mosquitoes parasitized with oocysts (which cannot be transmitted) are less likely to seek further probing, conversely to individuals infected with transmissible sporozoites.

Multidimensional manipulations: evolving from unidimensional ones?

From an historical or phylogenetic perspective, manipulative parasites derive most likely from non-manipulative ones, and it is more parsimonious to assume that the original manipulation involved only one dimension. Any individual parasite able to modify one dimension of its host phenotype with a resulting increase in its transmission success would have been favoured over its conspecifics by natural selection. Given enough genetic variation, what originally may have been an incidental side-effect of infection could then have been shaped by selection into a refined manipulation mechanism (Poulin 1994). Disentangling the mix of adaptive forces that shaped the transition from a simple manipulation to a multidimensional one offers a great challenge. There are indeed several selective forces that can explain why fitness benefits are gained by adding dimensions to a simple manipulation.

The addition of a novel dimension to a simple manipulation is likely to be favoured when the transmission benefits compensate for the extra costs of any new dimension. This situation is particularly likely when the interaction between the two dimensions boosts the transmission in a synergistic fashion. Selection likely favours the addition of novel dimensions when it improves the efficiency of the original one. For instance, in the case of *G. insensibilis* (Table 1), the aberrant escape behaviour displayed by parasitized individuals consists in swimming at the air/water interface each time there is a mechanical disturbance in the water (like a foraging bird walking). Such a behavioural change, on its own, would be likely to increase mortality in parasitized gammarids as mechanical disturbances are not always caused by birds and multiple displacements between the bottom and the surface would result in a waste of energetic reserves. This non-adaptive outcome can be avoided if parasitized gammarids also display a positive phototaxis causing them to stay at the water surface. Although further experimental evidence would be necessary to support this statement, it seems plausible that once a dimension has been retained by selection, then selection is likely to favour adjustments (i.e. other dimensions) that improve its efficiency by reducing the associated costs.

Interestingly, different evolutionary scenarios can be proposed depending on which dimension is considered to be historically the first to arise. In the previous example, it could be that positive phototaxis was the first behavioural change displayed by parasitized gammarids, and the aberrant escape behaviour only appeared subsequently. If so, we could no longer argue that positive phototaxis evolved because it reduced the energetic costs linked to the aberrant escape behaviour. Similarly, in the case of sequential multidimensionality, it is important to keep in mind that the chronology through which successive dimensions are actually observed may, or may not, reflect the order in which they appeared during the course of evolution. For this chronology to be the same as the observed order, it is necessary that each dimension has in itself a positive effect on transmission. Conversely, when the chronology is not the same, the hypothesis that certain dimensions evolved as secondary adjustments becomes a possible scenario. In this case, the first dimensions currently observed do not necessarily have a direct value for transmission.

Another way to improve the efficiency of a given manipulation is to reduce the probability of the intermediate host being eaten by unsuitable species. There are several studies illustrating that certain features of parasite-induced behavioural changes seem more targeted at limiting the risk of predation by the wrong (non-host) predators than at increasing transmission to appropriate hosts (Levri 1998). For instance, the acanthocephalan *Polymorphus minutus*, which completes its life cycle in aquatic birds, does not only alter the behaviour of gammarids in a way that increases their probability of being eaten by birds, it also enhances the escape performance (swimming speed increases of up to 35%) of parasitized individuals when facing non-host predators, especially the crustacean predator *Dikerogammarus villosus* (Medoc and Beisel 2008). Several studies have failed to find adaptive responses of trophically transmitted parasites against non-host predators (Mouritsen and Poulin 2003, Kaldonski et al. 2008). However, recent empirical and theoretical studies show that the avoidance of non-hosts is not always favoured by selection because despite the costs incurred, host manipulation may still be advantageous for the parasite (Seppälä and Jokela 2008, Seppälä et al. 2008, Parker et al. 2009).

Within an evolutionary perspective, the capacity to manipulate several host traits could be inherited from an ancestor of the parasite (Moore and Gotelli 1990). For this reason, the evolution of multidimensionality must be envisaged within a phylogenetic context, just like simple manipulations (Poulin 1995). In cases where multidimensional manipulations did not evolve independently (i.e. they are ancestral legacies), their adaptive value can however be maintained since they still increase significantly the probability of successful transmission. When similar traits are induced by phylogenetically unrelated parasites experiencing comparable selective pressures (see for instance Crustaceans and manipulative helminths, Table 1), convergence is a reasonable explanation since a similar manipulation of host behavior could have arisen independently in different parasite lineages.

Multidimensionality from a mechanistic perspective

One way to explore how different dimensions could be mechanistically related would be to study correlations between

the extent of modification in different altered traits. Such an approach has rarely been adopted until very recently. Benesh et al. (2008) studied five traits from individual isopods infected by the acanthocephalan *Acanthocephalus lucii* (hiding, activity level, substrate colour preference, anterior and posterior body colorations). Infected isopods hid less and had darker abdominal coloration than uninfected isopods. However, these two modified traits were not correlated, which suggests they may have arisen via independent mechanisms. Similarly, in laboratory experiments Helluy (1984) showed that in *G. insensibilis* parasitized by *M. papillorobustus* (Table 1), negative geotaxis, positive phototaxis and aberrant escape behaviour can all occur separately.

At the moment, it is unknown for the vast majority of multidimensional manipulations whether multiple changes in host phenotype are mechanistically related or independent. Positive correlations could indicate that parasites affect one particular component of the host's physiology which results in a cascade of effects. In such a case, all alterations might not be equally efficient in enhancing transmission to appropriate final hosts, some of them eventually making parasitized intermediate hosts more vulnerable to predators that are inappropriate final hosts (Cézilly and Perrot-Minnot 2005). For this reason, it appears important, when possible, to explore the independent effects of each alteration on parasite fitness. Manipulative parasites can also alter several physiological pathways independently. Unless parasites are limited in their ability to alter more than a single dimension in their intermediate hosts, no significant correlation in magnitude are expected between traits (Cézilly and Perrot-Minnot 2005). The majority of studies assume that costs are inevitably associated with manipulation. Although this assumption is reasonable, at this stage, speculation has proven more attractive than data collection. This gap currently limits our understanding of the evolution of manipulative processes (uni- or multidimensional ones) based on this assumption.

Conclusion and future directions

Compared to the important effort invested in the study of host manipulation by parasites, relatively few studies have explored its multidimensional character. At the moment, this phenomenon is mainly known from a descriptive point of view, and probably also only refers to biological models for which its detection was easy. An immediate challenge will be then to gather more systematic information on the range of host-manipulative parasite systems in which multidimensional manipulation is manifested, and on the range of traits that are altered in each case. Because multidimensional manipulations are diversified and complex phenomena, one single method or model cannot totally describe them. Researchers interested in multidimensional manipulation must engage in greater exchanges and collaborations with colleagues who understand how physiology, neuroanatomy and 'omics' contribute to phenotypic trait expression. This step is essential before generalisations can be made. Then, a first exciting research direction would be to explore, via comparative studies, whether the nature of altered trait combinations is linked to the phylogenetic affinities of hosts, of parasites and/or to the ecological constraints linked to

transmission processes. A second promising research direction would be to determine the precise function of each trait in multidimensional manipulations, as well as the way their interaction (additive or synergistic) boosts transmission success. This would then also allow us to evaluate the relevance of the hypothesis according to which certain dimensions evolved not because they increase transmission, but because they reduce the cost of previous dimensions.

A full understanding of the evolution of the multidimensionality of manipulation also requires knowledge of the selective pressures experienced by both the host and the parasite. We thus encourage researchers to consider the ecological context in which multidimensional manipulations occur (Thomas et al. 2005). This is critical to our understanding of the costs and the benefits of parasitic manipulation. In some cases, certain features of parasite-induced behavioural changes seem more relevant to limiting the risk of predation by the wrong (non-host) predator than to increasing transmission to appropriate hosts (Levri 1998). There are other ways in which environmental forces can drive multidimensional manipulation. For example, on a geographical scale, populations of the same parasite species infecting different host populations will experience different selective forces, because of regional variation in community composition. In some areas, one species of definitive host may be the dominant predator of intermediate hosts; in another area, another suitable definitive host species may be numerically dominant, and in yet another locality suitable definitive hosts may be outnumbered by non-host predators. Similarly, the variety of microhabitats available to manipulated intermediate hosts may vary greatly among localities, such that one altered trait that works efficiently for the parasite in one area may be ineffective or costly (in terms of ingestion by non-hosts) elsewhere. Parasites coevolve with their hosts in a heterogeneous environment, following the general principles of the geographic mosaic theory of coevolution (Thompson 2005). Therefore, multidimensional manipulation may have evolved, and may be maintained, in response to spatially variable external conditions affecting the probability of transmission. The panoply of traits manipulated by a parasite may increase the probability that at least one of these manipulated traits will fit the current local conditions. Measuring the benefits of different altered traits under different external conditions would provide a promising way to assess the adaptiveness of multidimensionality.

Hosts in nature are usually infected by multiple phylogenetically unrelated parasites, which may have opposing interests in their use of the host. In certain cases, parasites have been shown to sabotage the manipulation exerted by other parasites, reverting the phenotype of an infected hosts to its 'normal' uninfected state (Thomas et al. 2002b, Haine et al. 2005, Rigaud and Haine 2005). It would be interesting in these situations to explore whether or not sabotages apply to all the dimensions of a multidimensional manipulation, or only those that are the most critical for the transmission interests of the sabotaging parasite.

From a mechanistic perspective, nothing is known concerning the way multidimensional manipulation occurs. This research direction therefore has huge potential, and could benefit from sophisticated approaches such as the incorporation of post-genomic tools for determining the

genetic basis of manipulation. This will help to predict if host traits modified by manipulative parasites should covary positively or negatively in magnitude. An interesting avenue will also be to explore the possible mechanistic links between the multidimensionality of host manipulation and the host immune system.

Host manipulation as a scientific field has, until now, developed in relative isolation from behavioural ecology approaches. This is unfortunate since links between these fields have the potential to reveal new perspectives and lines of research. Complex signal function has indeed been studied in many species by behavioural ecologists, and therefore, examples of animals in which signallers use more than one display to advertise their qualities are common (Møller and Pomiankowski 1993). Three hypotheses are usually invoked to explain why these complex signals evolve. First, the redundant signal hypothesis suggests that although each signal transmits on average the same information, redundant signals evolve because 1) this enhances the detectability of the signal, 2) it improves the accuracy with which receivers assess a single quality given imperfect correlations between signals and individual quality, and 3) it insures that the information will be transmitted despite environmental unpredictability because different signals vary in their transmission capacities in different environments. A second hypothesis proposes that different signals provide information about different qualities (the 'multiple messages' hypothesis) (McGraw and Hill 2000, Doucet and Montgomerie 2003). Finally, different signals may have evolved because they are addressed to different receivers (Coleman 2004). Trophically transmitted parasites using a multidimensional manipulation to increase their transmission can be viewed as signallers sending multiple signals (through their extended phenotype in the host) to other species, including predatory definitive hosts. Therefore, the previous conceptual framework and its hypotheses could well be applicable in the context of multidimensional manipulation. We believe that the traditional separation between sub-disciplines that leads to different perspectives on the same ecological reality is a fundamental limitation that needs to be overcome if complex processes, like multidimensional host manipulation, are to be understood. Answers to many current and future questions about multidimensionality might come as a result of convergence between these disciplines. Presently, this promising area of research is in its infancy and clearly, a much larger global research effort is required to 'calibrate' the methodology and concepts. We believe that the multidimensionality of manipulation is one of the most exciting research directions on manipulative parasites for the near future.

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