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Exploitation of manipulators: ‘hitch-hiking’ as a parasite transmission strategy

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ABSTRACT

For many parasites with complex life cycles, manipulation of host behaviour is an adaptation to increase the probability of successful transmission. Since manipulation is likely to be costly, other parasites may exploit hosts already manipulated so as to ensure their transmission without investing in manipulation. Such a cheating strategy, called ‘hitch-hiking’, could be adaptive in a range of situations. We first propose and discuss criteria that should be met by any parasite to be considered a hitch-hiker. Then, to understand the evolution of the hitch-hiking strategy, we use simple mathematical models to analyse the influence of several variables on the potential benefits for a nonmanipulative parasite of actively seeking a ride to the definitive host with a manipulative parasite. The models suggest that the prevalence or abundance of manipulative parasites will be a key determinant of whether hitch-hiking can be an advantageous option for other parasites.

For many parasite species, continuation of the life cycle involves a succession of unlikely events. If investment in high fecundity is one way to increase the probability of success, natural selection has also favoured various adaptations that increase the chances of infective stages meeting the next host or being released in a suitable place (see Combes 1991, 1995; Poulin 1995 for reviews). Manipulation of intermediate host behaviour is one such feature that has been suggested in a wide range of parasitic taxa (see Poulin 1994a for a review). Even if they are difficult to quantify, these host manipulations are probably often costly to achieve (Poulin 1994b). Costs are, for instance, likely to exist when the parasites produce chemicals to manipulate the host’s behaviour (e.g. Helluy & Holmes 1990; Hurd 1990). Following this, it is generally assumed that there should be trade-offs between the investments in manipulative effort and other traits such as fecundity (Combes 1991; Poulin 1994b).

In many systems, more than one parasite species with complex life cycles coexist in total sympatry, exploiting the same host species in the same sequence. For instance, many helminths are transmitted to the definitive host in ‘packets’ of species rather than singly because they share

a common intermediate host (Bush et al. 1993; Lotz et al. 1995). If one parasite species is an efficient manipulator of host behaviour, it is expected, under certain conditions, that other parasite species could obtain a high probability of transmission simply by infecting hosts already manipulated, making no investment in manipulation themselves. Energy not invested in host manipulation would be theoretically available for other functions such as growth, and natural selection should thus favour such a cheating strategy. Recently, there has been growing interest in this category of cheating parasites, the so called ‘hitch-hiker’ parasites (Combes 1991; Poulin 1994b; Lafferty & Morris 1996; Thomas et al. 1997). For instance, the trematode *Maritrema subdolum* favours its transmission to aquatic birds (definitive hosts) by preferentially infecting gammarids manipulated by the other trematode *Microphallus papillorobustus* (Thomas et al. 1997). However, there is currently little evidence of this phenomenon and the conditions for the appearance and the evolution of hitch-hiking are not well understood.

In this paper, we first attempt to propose and discuss criteria that must be met by any parasite to be labelled a hitch-hiker. Then, from a theoretical perspective, we use simple mathematical models to investigate the influence of several variables on the potential benefits for a nonmanipulative parasite (NMP) of actively seeking to hitch a ride to the definitive host with a manipulative parasite (MP).

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Changes in animals after infection with parasites are extremely common. It is traditionally viewed that for several reasons (for instance competition or cross-immunity), parasites are likely to have lower fitness by infecting an already parasitized host (Combes 1995). While this is probably true in many cases, a parasite could also, in other circumstances, achieve greater fitness by infecting an already parasitized host than an unparasitized host, simply because any changes induced by one parasite, and/or their consequences, can make the host easier to exploit for a second parasite (e.g. Colwell & Wescott 1973). Based on recent definitions of adaptation (Futuyma 1986; Ridley 1993), infection of hosts already parasitized can be considered as an adaptation if it is a trait that is genetically determined and has become (or is becoming) prevalent in the population because it confers a selective advantage to its bearer through an improvement in some function. The concept of the hitch-hiking strategy relies on this principle but involves only ethological traits that are directly shaped by selection because they improve the function of transmission. Hitch-hiking is thus a particular case of 'Favorization' (in the sense of Combes 1991) where the parasite target is a host already parasitized.

HOW TO TEST FOR 'HITCH-HIKING'

Like Poulin (1995), we propose criteria that must be met if behavioural alteration of a host for transmission is to be adaptive. We suggest and discuss here several criteria to evaluate the adaptive value of behavioural traits in the context of hitch-hiking.

Preferential Infection

One important criterion in demonstrating that a trait is adaptive in the context of hitch-hiking is to show that it leads to preferential infection of a manipulated host. Ideally, this must be tested by experiments that compare the rate of infection of manipulated hosts and that of unparasitized hosts by the supposed hitch-hiker. These tests, although essential, are likely to be difficult to realize since manipulated hosts must come from a previous experimental infection of unparasitized hosts by the MP (manipulated hosts in the field are indeed likely to be already parasitized by the hitch-hiker, Thomas et al. 1997). However, several arguments can serve to evaluate if the infection process of an NMP is biased towards manipulated hosts. First, an obvious and easily measurable consequence of preferential infection is that there should be a positive association between the NMP and the MP in the field (see Janson & Vegelius 1981 for a review of the biological coefficients of association). For an NMP that would infest intermediate hosts at random, and that occasionally achieves higher transmission success by sharing a host with a manipulator (i.e. the coefficient of association is not significant), we reserve the term of 'lucky passenger' rather than 'hitch-hiker'. For instance, this situation could be well illustrated by the nonmanipulative trematode *Microphallus hoffmanni*. The second

intermediate host of both this NMP and the MP *M. papillorobustus* is the amphipod *Gammarus aequicauda* (Helluy 1984), and the definitive hosts of both parasites are several species of aquatic birds (Rebecq 1964). Although cercariae of *M. hoffmanni* should be a priori advantaged when infecting manipulated gammarids, there is no evidence of such a directional infection in the field (F. Thomas & F. Renaud, unpublished data). A positive association is a criterion that must be met by any NMP to be labelled a hitch-hiker, but it is not per se conclusive evidence since several other phenomena can generate positive associations. For instance, although the benefit for an MP of infecting a host previously infected by an NMP is unclear, this is possible if, once infected by an NMP, the host becomes more susceptible to further infections. A positive association between an NMP and the MP may be also coincidentally beneficial. For instance when the infective stages of both the NMP and the MP have little or no dispersal and are released in the same places, those of an NMP previously associated with an MP in the definitive host are more likely to share an intermediate host with the MP, compared with an NMP previously alone in the definitive host. After completing several cycles, a positive association could arise between the two species simply as an artefact of their lack of dispersal ability at the larval stages. Examples of this could be found among helminth species parasitizing terrestrial vertebrates and releasing eggs in the host's faeces.

The absence of dispersal in the NMP can be an adaptation, but it can also arise by chance or be a beneficial side-effect, whereas a specific behaviour is a more complex trait unlikely to be the product of chance. In this context, a second criterion is to evaluate how NMP behaviour fits a purposive design with what is known about the biology of the manipulated host. For instance, in the case of the hitch-hiker parasite *M. subdolum*, cercariae swim high in the water column in search of their next host, gammarid amphipods (Thomas et al. 1997). This is what we would have predicted knowing that gammarids manipulated by the MP *M. papillorobustus* are highly photophilic and geophobic compared with uninfected ones (Helluy 1984). It is probably feasible in many situations to test how the NMP responds to environmental stimuli that would bring it into the microhabitat frequented by manipulated hosts. Convergence between the hitch-hiking behaviour of NMPs phylogenetically distant but evolving under similar selective pressure (i.e. using intermediate hosts similarly manipulated by different MPs) would be a strong argument in favour of adaptation. Although there are some suggestions of convergence in the behavioural alterations of the host induced by MPs (Poulin 1995), further evidence for hitch-hikers is needed before evaluating this criterion.

Benefits for Transmission

In the context of the hitch-hiking strategy, a trait that leads to preferential infection of manipulated hosts is adaptive only if it also leads to increases in the transmission of the NMP towards a suitable host. Since various

advantages (or sometimes disadvantages) may be associated with infecting a host already parasitized, quantitative demonstrations of transmission benefits are thus essential. Ideally, this would consist of comparing the rate of transmission when the NMP is alone and when it shares the intermediate host with an MP. This is probably difficult in most cases since experimental infections may be difficult to perform, and because of the expected positive association in the field, few hosts are naturally infected by only an NMP (Thomas et al. 1997). An indirect method would consist of comparing the magnitude of the behavioural changes in hosts parasitized by both the NMP and the MP with the magnitude of behavioural changes in those parasitized only by the MP, since this last category of hosts is expected to be more frequent in the field. When the magnitudes of these behavioural changes are similar (i.e. no significant effect of the NMP) and when the transmission exploits a predator-prey system, unparasitized individuals can serve as controls to estimate the probability of transmission of an NMP alone in the intermediate host.

FROM A 'LUCKY PASSENGER' TO A 'HITCH-HIKER'

When an efficient manipulator appears in a parasite community, NMPs that share the same intermediate and definitive hosts are initially likely to be 'lucky passengers' before evolving, perhaps, into hitch-hikers. To understand the conditions that favour evolution towards a hitch-hiking strategy, we examined the influence of several variables on the potential benefits for an NMP of actively seeking to hitch a ride to the definitive host with an MP.

We considered two strategies available to NMPs. First, they can infect intermediate hosts at random, without discriminating between hosts harbouring MPs and unparasitized hosts (i.e. 'lucky passenger'). The parasites opting for this 'passive' strategy occasionally achieve higher transmission success by sharing a host with an MP, but do not incur the costs of actively seeking out manipulated hosts. Second, NMPs can actively search for hosts harbouring MPs, thus infecting a greater proportion of manipulated hosts than expected by chance. These 'active' hitch-hikers regularly benefit from the higher transmission success provided by the MPs, but may suffer from a reduction in overall fitness because of investments into host discrimination or because of greater inter-specific competition for the host's resources. The fitness associated with each strategy is equal to the product of the achieved transmission success and W , the basic reproductive success achieved in the definitive host. The benefits of active hitch-hiking are defined as the difference between the respective fitnesses of the two strategies, that is, $W_{\text{active}} - W_{\text{passive}}$. If the difference is greater than zero, hitch-hiking is the transmission strategy favoured by selection.

In our analysis, we consider the case of two parasite species, one an MP and the other an NMP (with a negligible impact on the host's fitness), both transmitted by predation from the same intermediate host to the

same definitive host. We examine two alternative scenarios, one in which the ability of the MP to increase transmission success is independent of the intensity of infection (i.e. higher transmission success is achieved regardless of the exact number of MPs per host), and one in which manipulation is dependent on intensity.

Manipulation is Intensity Independent

If all hosts harbouring MPs provide higher transmission success to the definitive host, then the prevalence of the MP in the host population, or the proportion of hosts parasitized by the MP, should be the key parameter determining whether active hitch-hiking is advantageous. Other important factors may include the basic transmission rate achieved in the absence of manipulation, and the increase in transmission success obtained by manipulation. We can define the fitness of the two strategies as follows:

$$W_{\text{passive}} = W[m(p+q) + p(1-m)]$$

$$W_{\text{active}} = cW[(m+f)(p+q) + p(1-(m+f))],$$

where m is the prevalence of the MP, p is the basic transmission rate, q is the increase in transmission rate gained from manipulation, and f is the efficiency of the NMP at finding and infecting hosts already harbouring MPs. In practice, f acts to increase the prevalence of the MPs. Because searching for manipulated hosts, competition with MPs and cross-immunization may be costly for NMPs, their fitness is reduced by the factor c , which ranges from 0 to 1. For example, if the value of c is 0.9, the active hitch-hiker incurs a 10% reduction in adult reproductive success that must be compensated by higher transmission success if hitch-hiking is to be favoured by selection.

Analysis of the model indicates that the active hitch-hiking strategy can be favoured only when the prevalence of the MP is not too high. Increases in the efficiency of the NMP at infecting manipulated hosts are beneficial only at low MP prevalence. Even if active hitch-hikers incur costs in reproductive success, hitch-hiking can be favoured if the prevalence of MPs is low. When $c=1$, or when there is no fitness reduction associated with the hitch-hiking strategy, it is favoured for all prevalence levels of the MP except $m=1$, when the NMP relying on chance encounters with manipulated hosts achieves the same fitness as the hitch-hiker.

The basic transmission rate, p , and the extent to which it is augmented by host manipulation, q , are also important (Fig. 1). When the basic transmission rate is relatively high, hitch-hiking is never favoured. If sharing a host with an MP leads to moderate increases in the rate of transmission, hitch-hiking can be strongly favoured. The influence of the prevalence of the MP remains the key parameter, however. For instance, a large value of q , that is, a large increase in transmission success resulting from manipulation, strongly favours hitch-hiking at low

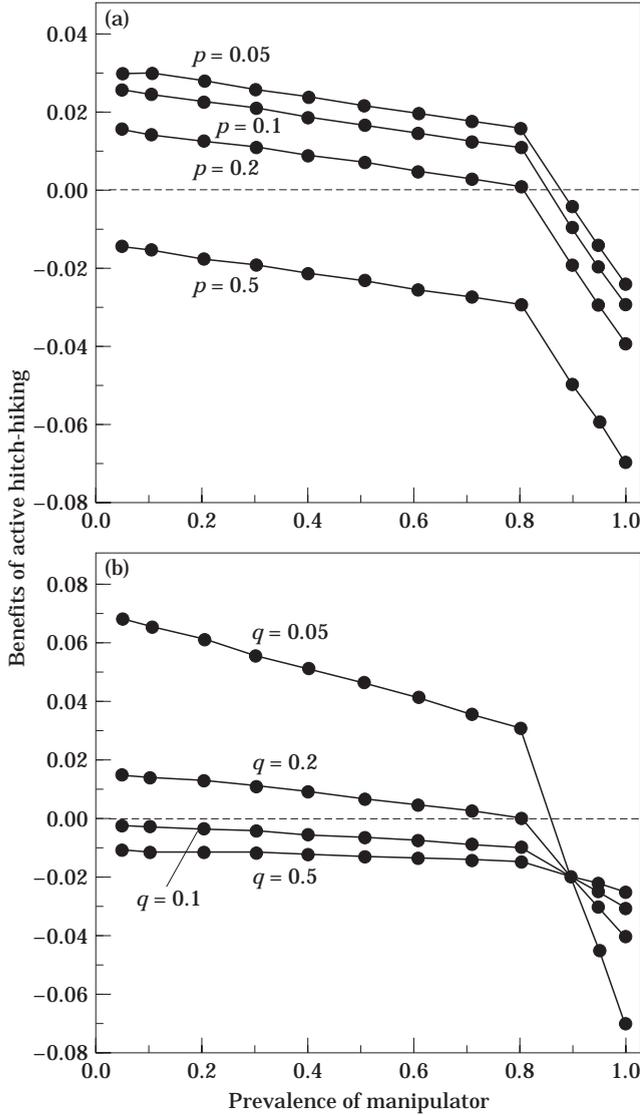


Figure 1. The relationship between the fitness benefits of active hitch-hiking for a nonmanipulator parasite, measured as $W_{\text{active}} - W_{\text{passive}}$, and the prevalence of a manipulator parasite in the host population: (a) for different values of p , the basic transmission rate (other parameters: increase in transmission rate obtained from manipulation $q=0.2$; efficiency of the nonmanipulator parasite at finding and infecting hosts already harbouring manipulator parasites $f=0.2$; fitness reduction $c=0.9$); (b) for different values of q (other parameters: $p=0.2$; $f=0.2$; $c=0.9$). The hitch-hiking strategy is favoured when the expected benefits are positive, that is, above the broken line.

prevalence of the MP, but it greatly disadvantages hitch-hiking at high prevalence (Fig. 1).

Manipulation is Intensity Dependent

The ability of the MP to manipulate host behaviour and increase transmission success may be dependent on the number of conspecific MPs sharing a host. In this situation, we must consider how q varies with the number of MPs per host, and how MPs are distributed among hosts.

Parasites in general tend to be aggregated among their hosts, with the majority of hosts harbouring few or no parasites and a few hosts harbouring many parasites (Crofton 1971). The negative binomial distribution provides a good fit to most observed parasite distributions, and allows us to define the proportion of hosts harbouring X MPs, or $Pr(X)$, for all values of X :

$$Pr(X) = \frac{(k+X-1)!}{X!(k-1)!} \left(\frac{k}{\bar{X}+k}\right)^k \left(\frac{\bar{X}}{\bar{X}+k}\right)^X$$

where \bar{X} is the mean number of MPs per host, and k is a coefficient of aggregation: aggregation increases as k tends towards zero. Next we define $q(X)$, the value of q as a function of the number X of MP per host:

$$q(X) = 0.1(q_{\text{max}})X$$

for all $X < 10$. Thus $q(X)$ increases linearly until, at intensities of 10 or more MPs per host, the value of q_{max} is reached. This relationship is used as an example, and could be substituted by others without any great influence on the results (i.e. only the slope but not the shape of the relationships would be changed). The equations for $Pr(X)$ and $q(X)$ can be used to generate the distribution of q values encountered by NMPs.

For the sake of simplicity, we assume that hitch-hikers can distinguish only between hosts harbouring MPs and those uninfected by MPs, and that they are not capable of discriminating between parasitized hosts harbouring different numbers of MPs. The fitnesses associated with the two strategies considered here are then:

$$W_{\text{passive}} = W \sum_{X=0}^{X_{\text{max}}} Pr(X) (q(X) + p)$$

$$W_{\text{active}} = cW \left[(Pr(0) - f)p + \sum_{X=1}^{X_{\text{max}}} \left(Pr(X) + \frac{Pr(X)f}{1 - Pr(0)} \right) (q(X) + p) \right],$$

where again f , the efficiency of the NMP at infecting hosts already harbouring MPs, acts to increase the prevalence of the MPs. It represents a proportion of the nonmanipulated hosts that is missed by the hitch-hikers, and is redistributed among the manipulated hosts according to the frequency of their load X of MPs.

In the case where manipulation is dependent on intensity, just as in the previous scenario where it was independent of intensity, the parameters c , f , p and q are important determinants of whether hitch-hiking will be the favoured strategy. As earlier, however, the abundance and distribution of MPs among hosts is the key factor. A low basic transmission rate will favour hitch-hiking but especially if the MPs are either very abundant or, for a given abundance, highly aggregated. High aggregation levels in the MP population mean that prevalence is low and that heavily infected hosts are rare, so that NMPs relying on the passive strategy will only rarely achieve the

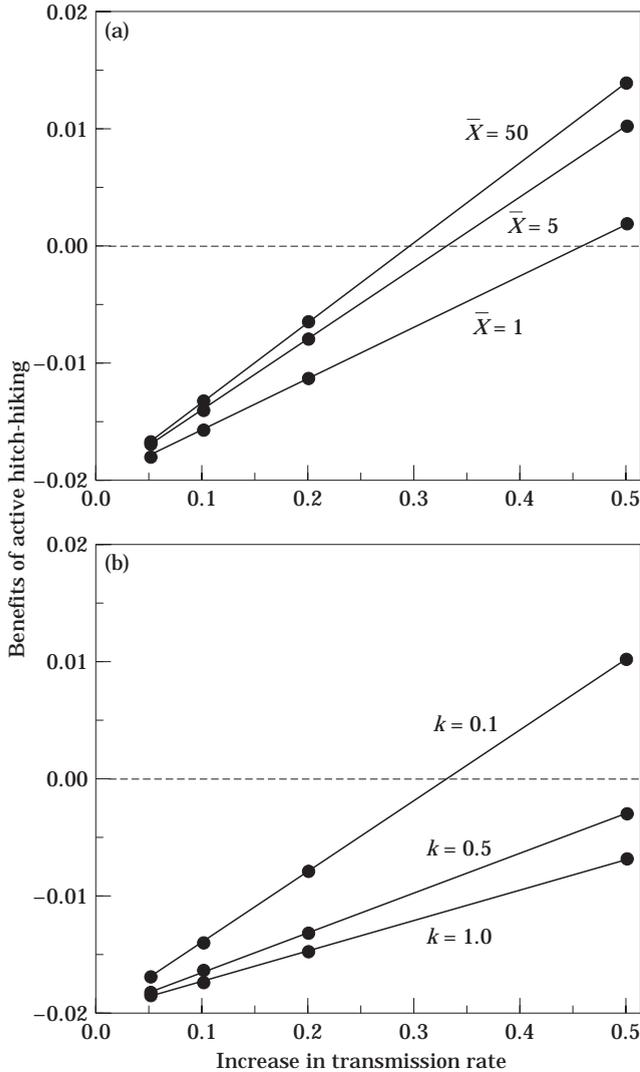


Figure 2. The relationship between the fitness benefits of active hitch-hiking for a nonmanipulator parasite, measured as $W_{\text{active}} - W_{\text{passive}}$, and q , the increase in transmission rate obtained from manipulation: (a) for different values of \bar{X} , the mean number of manipulators per host (other parameters: basic transmission rate $p=0.2$; efficiency of the nonmanipulator parasite at finding and infecting hosts already harbouring manipulator parasites $f=0.15$; fitness reduction $c=0.9$; coefficient of aggregation $k=0.1$); (b) for different values of k (other parameters: $p=0.2$; $f=0.15$; $c=0.9$; $\bar{X}=5.0$). The hitch-hiking strategy is favoured when the expected benefits are positive, that is, above the broken line.

high transmission success provided by manipulated hosts. Even if the increase in transmission success provided by manipulation is substantial, hitch-hiking is favoured only if MPs are either abundant or highly aggregated (Fig. 2). If there is no fitness cost associated with actively seeking manipulated hosts in the hitch-hiker strategy (i.e. if $c=1.0$), hitch-hiking is always favoured among NMPs but it gets more advantageous if the MPs are both abundant and highly aggregated.

The way in which host manipulation varies with the number of MPs per host can follow relationships other than linear. For instance, there may be a threshold

number of MPs necessary to cause a host manipulation. Hosts harbouring fewer MPs than the threshold number would not be manipulated. This scenario, not illustrated here, would make hitch-hiking less advantageous unless active hitch-hiker parasites could avoid hosts harbouring too few MPs.

DISCUSSION

Because changes in parasitized hosts are sometimes substantial, it is not unrealistic to consider that, in certain circumstances, a parasitized host can be a new type of host for other parasites, that is, with new properties and new consequences for transmission. Several fitness benefits can be associated with infecting hosts already parasitized. The preceding models show that hitch-hiking can evolve under a range of conditions, provided that its higher transmission success outweighs any reductions in reproductive success that hitch-hikers may incur.

The prevalence of the MP was shown to be a key parameter since the hitch-hiking strategy can be favoured only when it is not too high. The frequency of manipulated hosts in nature may rarely attain high levels for several reasons. First, at any time, once manipulated, parasitized hosts are expected to disappear more rapidly from the population than nonmanipulated hosts. Second, the demographic impact of MPs on their intermediate host population (e.g. Thomas et al. 1995; Rousset et al. 1996) is likely to generate cyclic regulations of the intermediate host and parasite populations (Dobson 1988). In addition, since MPs are expected to evolve particularly when definitive host populations are unstable (Dobson 1988), the population dynamics of MPs are likely to vary over time. Empirical studies that have compared parasitological parameters of one MP in several host species that differ in the magnitude of their behavioural changes after infection allow us to test these assumptions. For instance, Thomas et al. (1995), comparing the profiles of infection by an MP on two sympatric host species, showed that MPs were considerably less abundant in the host that displayed the stronger behavioural alterations after infection.

Increases in the NMP transmission success achieved by infecting manipulated hosts depend on the passive transmission rate and on the efficiency of manipulation. When the passive transmission rate is high, lucky passengers are advantaged over hitch-hikers since they achieve the same transmission rate without paying any costs. In such situations, however, MPs are not expected to appear either since NMPs achieve a similar transmission rate without making any investment in manipulative effort (Poulin 1994b). When the passive transmission rate is low, many changes induced by parasites are likely to influence positively the transmission rate for other parasites. For instance, a reduced vigour in infected hosts frequently increases their probability of predation, even when this is not adaptive for the parasite responsible for this effect (e.g. Hudson et al. 1992). In other cases, changes that are observed in parasitized hosts have directly evolved because they initially favoured transmission. These situations appear to promote the evolution of

Table 1. Estimates of the increase in transmission success to the definitive host resulting from intermediate host manipulation by manipulator parasites, obtained from published experimental studies

Parasite	Intermediate host	Definitive host	Laboratory (L) or field (F) study	Increase in transmission rate*	Source
Protozoan	Mammal	Bird	F	0.134	Hoogenboom & Dijkstra 1987
Digenean	Crustacean	Bird	L	0.224	Helluy 1984
Digenean	Insect	Mammal	L	0.243	Webber et al. 1987
Digenean	Fish	Bird	F	0.497	Lafferty & Morris 1996
Cestode	Insect	Mammal	L	0.196	Blankespoor et al. 1997
Cestode	Crustacean	Fish	L	0.348	Poulin et al. 1992
Cestode	Crustacean	Fish	L	0.078	Urdal et al. 1995
Cestode	Crustacean	Fish	L	0.081	Wedekind & Milinski 1996
Acanthocephalan	Crustacean	Fish	L	0.270	Camp & Huizinga 1979
Acanthocephalan	Crustacean	Fish	L	0.500	Brown & Thompson 1986
Acanthocephalan	Crustacean	Fish	L	0.179	Bakker et al. 1997
Acanthocephalan	Crustacean	Bird	L	0.520	Holmes & Bethel 1972
Acanthocephalan	Crustacean	Bird	L	0.380	Hindsbo 1972
Acanthocephalan	Crustacean	Bird	F	0.275	Moore 1983

*Increases were calculated as the difference between the proportion of parasitized intermediate hosts captured by the predator (definitive host) and that of unparasitized intermediate hosts.

Table 2. Examples of systems in which several parasite species with similar life cycles, one of which is a manipulator, use the same intermediate host population

Intermediate host	Number of parasite species	Manipulator	Source
Snail (<i>Ilyanassa</i>)	8 digeneans	<i>Gynaecotyla adunca</i>	Curtis 1987
Amphipod (<i>Hyalella</i>)	6 cestodes+1 acanthocephalan	<i>Corynosoma constrictum</i> *	Bush & Holmes 1986
Amphipod (<i>Gammarus</i>)	3 cestodes+1 acanthocephalan	<i>Polymorphus marilis</i> *	Bush & Holmes 1986
Amphipod (<i>Gammarus</i>)	4 digeneans	<i>Microphallus papillorobustus</i>	Helluy 1981
Crab (<i>Pachygrapsus</i>)	6 digeneans+1 cestode	<i>Microphallus</i> sp.†	Bush et al. 1993
Snail (<i>Potamopyrgus</i>)	≥12 digeneans	<i>Microphallus</i> sp.	Levri & Lively 1996
Fish (<i>Fundulus</i>)	2 digeneans	<i>Euhaplorchis californiensis</i>	Lafferty & Morris 1996

*See Bethel & Holmes (1973).

†See Helluy (1984) for demonstration that certain species of *Microphallus* are capable of manipulation.

the hitch-hiking strategy in co-occurring parasite species since manipulative changes are expected to be an efficient way of transmission for hitch-hiker parasites. From estimates of the increase in the transmission success resulting from alteration by MPs (Table 1), the efficiency of manipulation appears quite high in certain cases, suggesting that hitch-hiking by co-occurring parasites is likely to evolve. There are numerous examples of NMPs that share intermediate and definitive hosts with such efficient MPs (Table 2). It is likely that in these situations, certain NMPs could benefit from the presence of the MPs for their transmission. We should be cautious, however, before assuming that they are hitch-hikers rather than lucky passengers before applying the criteria suggested in the first part of this paper.

An obvious cost for a hitch-hiker parasite is that of searching for manipulated hosts. If the models show that hitch-hikers are advantaged over lucky passengers when the prevalence is low, search costs to find manipulated hosts are, however, expected to increase when the prevalence of the MP decreases. Hitch-hikers may, for instance, be selected to respond to environmental stimuli in ways

that bring them into the microhabitat frequented by manipulated hosts. Search costs to locate manipulated hosts can be minimal when the free-living stages of the hitch-hiker benefit from external processes to change the microhabitat. In the case of the trematode *M. subdolum*, for instance, the swimming effort of cercariae that allows them to reach the space occupied by gammarids manipulated by *M. papillorobustus* could be trivial if cercariae use the vertical currents of diffusion in the water (Thomas et al. 1997). In such a case, a small investment in hitch-hiking effort may in return result in a high transmission success. The larval stages of many parasites display precise behavioural patterns serving to bring them within close range of their target host (Combes et al. 1994). Similar low-cost adaptations could be used by hitch-hikers to locate the subset of the intermediate host population that they target, that is, those parasitized by MPs. Alternatively, since hitch-hikers are expected to invest relatively more in fecundity than MPs, search costs may be compensated by the production of more infective stages. Finally, search costs also depend on the mechanism involved, for instance improved fitness for the NMP may

arise partially through the MP reducing host immunity and then making easier the infection by the NMP.

Competition with the MP for the resources inside the manipulated host may strongly limit the possibility of hitch-hiking. For instance, when this competition inevitably results in the elimination of the NMP or the MP, the hitch-hiking strategy cannot evolve. The competition could also decrease the efficiency of the MP to alter the behaviour of the host and/or increase the probability of nonadaptive mortality of the host. Competition for resources may also occur in the next hosts of the complex life cycle. These situations are likely to reduce the potential benefits for an NMP of actively seeking to hitch a ride to the definitive host with an MP. In addition, it is expected that MPs would evolve mechanisms preventing the association with a costly hitch-hiker.

In many complex life cycles, competition between parasites is more likely to occur in certain hosts than others. For instance, interspecific competition between trematode larvae is known to be strong in the mollusc first intermediate host (Kuris & Lafferty 1994; Lafferty et al. 1994) while there is less evidence of this in the second intermediate host of most trematodes. There is also evidence of competition between larval cestodes in their intermediate host. The rat tapeworm, *Hymenolepis diminuta*, and the chicken tapeworm, *Raillietina cesticillus*, have different definitive hosts but use the same range of coleopterans as intermediate hosts. Both species are MPs and they induce similar changes in their intermediate host (Graham 1966; Hurd & Fogo 1991; Robb & Reid 1996). Presumably, the changes induced by both cestodes increase the predation rate on infected beetles by both rats and chickens, so that one parasite could potentially benefit from the manipulative effort of the other. However, cysticeroids of *H. diminuta* often fail to establish in beetles previously infected with *R. cesticillus* (Gordon & Whitfield 1985). In this example, competitive interactions may have prevented one MP from turning into a hitch-hiker. Because of interspecific competition, hitch-hiking is probably less likely to appear in hosts that are used as resource bases in complex life cycles, except if the NMP is taxonomically distant from the MP and is therefore less likely to exploit the same resource.

In addition to a low probability of competing with the MP for host resources, there are other traits that a hitch-hiker must possess. For example, since a hitch-hiker that infects a manipulated host will immediately have a high transmission rate to the next (definitive) host, it must quickly become infective to that next host. We might expect the developmental rates of the hitch-hiker in the intermediate host to be faster than those of the MPs they join. Hitch-hikers must also be able to exploit the definitive host spectrum of their MP. Finally, hitch-hikers, like MPs, must not be pathogenic for the definitive host, otherwise selective pressures to avoid manipulated prey should evolve in definitive hosts (Lafferty 1992). Features like these could have evolved after the adoption of the hitch-hiking strategy, or they could have predisposed certain NMPs to become hitch-hikers.

In conclusion it seems that the conditions for the evolution of hitch-hiking in parasites could be met in

several assemblages of parasites with complex life cycles, but more evidence based on rigorous criteria is needed before generalizations can be made. Real evidence for manipulative costs also appears crucial for a full understanding of the conditions favouring the evolution of hitch-hiking strategies. Although the possible evidence for hitch-hiking concerns parasites that are trophically transmitted, we believe that the hitch-hiking strategy can evolve under a wide range of behavioural alteration of hosts induced by MPs. It could also be an alternative strategy not adopted by all the members of an NMP population. The role of MPs in the population dynamics of NMPs in general and in the evolution of cheating strategies of transmission is currently underestimated. We thus encourage future investigators to examine the entire community of parasites in manipulated hosts.

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