Parasite-induced changes in host behaviour

Parasite-Induced Changes in Host Behaviour: Is it Truly Parasitic Manipulation?

Introduction

Behavioural changes in the host when infected with a parasite were first observed in 1952, when van Dobben discovered that fish caught by cormorants (waterbird) were more likely to play intermediate host to the cestode, *Ligula intestinalis* than fish caught by fishermen (cited in Thomas *et al* ., 2005). However it wasn’t until 1972 that the ability of parasites to manipulate their host’s behaviour in order to facilitate their transmission was discovered and demonstrated by Holmes and Bethel (cited in Poulin, 2000). They showed that infection of the parasite, *Polymorphus paraoxus* caused the amphipod, *Gammaeras lacustris* to display abnormal behaviours that led to an increase in its predation by ducks, the definitive host of the parasite. Since then there has been considerable research carried out in this area supporting the idea that parasites have adapted in order to manipulate their host, with a large number of parasites now known to cause changes to their hosts behaviour. There is a wide array of influenced behaviours from anti-predator behaviour e. g. mice infected with the tapeworm, *Taenia crassiceots* show no stress response to predation (Wheat, 2009); to reproductive behaviour e. g. female mice infected with the nematode, *Trinchinella spiralis* show inhibition of their sexual behaviours, limiting possible mate response (Kavaliers *et al.* , 2000). In a few cases completely new behaviours in infected hosts have been observed, for example orb-weaving spiders infected by a parasitic wasp build unusual webs that are designed to protect the emerging larva once the host spider dies (Eberhard, 2010). More recently, the idea of parasitic manipulation has come under criticism, due to the lack of supporting evidence demonstrating that these behavioural changes provide parasites with a fitness benefit (a prerequisite of an adaptive trait), either in the form of increased transmission or survival (Poulin, 1998) and has therefore been suggested that the observed changes may just be an inevitable consequence of infection, or in some cases mediated by the host itself in order to counteract the negative fitness effects of parasitic infection. Understanding the origin of these behavioural changes is of great importance as there are many manipulative parasites that have implications for human health, such as malaria which alters the behaviour in the mosquito in order to increase transmission to humans (Lynch *et al.,* 2014) and *Toxoplasma gondii* which can alter the personality of infected individuals (Worth *et al* ., 2014). Manipulative parasites are also seen as playing as important a role as predation in shaping biological communities, even having an influence on non-host species (Hatcher *et al* ., 2014).

Adaptive vs. Non-adaptive Behavioural Change

The argument that some of the previously observed behavioural changes of the host during parasitic infection are non-adaptive and just a consequence of infection generally refers to three different kinds of phenomena (Thomas *et al* ., 2005). The first is the idea that the behavioural changes are just a side-effect of parasitic infection and confer no adaptive value for either the parasite or its host. However this is a questionable explanation as it is highly unlikely that any such change in behaviour will not provide a positive effect for either organism. Therefore this explanation should only be used if there is strong supporting evidence and not used as a default explanation, for example the parasitic cestode, *Hymenolepis diminuta* was shown to cause reduced fecundity in females of the beetle intermediate host, *Tenebrio molitor* and was seen as a side-effect, until further research discovered that the parasite produced a substance that inhibited vitellogenin uptake (Moore, 2012). Secondly some behavioural changes may be considered beneficial to the parasite, but are not due to manipulation by the parasite in order to do so, for example when the parasite *Ligula intestinalis* infects the Roach (*Rutilus rutilus*) a change in host migration to areas where predation by the parasites definitive host, ichtyopahgous predatory birds, are more common is observed (Loot et al., 2001). However it was found that these areas are more productive and it is therefore more likely that the increased energy demands caused by the parasitic infection had caused the Roach to migrate to these areas in order to negate this negative effect of the parasitic infection and increase its own fitness. Thirdly other adaptations by the parasite may have coincidentally caused behavioural changes in the host which unintentionally led to an increase in the transmission of the parasite to its definitive host, for example Fathead minnows (*Pimephales promelas*) are commonly infected by the trematode, *Ornithodiplostomum ptychocheilus* which caused a reduction in behaviours associated with host vision by the encystment of the parasite in the optic lobes, which leads to an increase in its predation by piscivorous birds. However this encystment in the eye may originally been favored by selection as it offers the parasite protection from the host’s immune system and not because it increased the transmission of the parasite to its definitive host (Shirakashi and Goater, 2005)

On the other hand the argument for the adaptive nature of behavioural changes of the host during parasite infection is normally supported by the idea that it should show some degree of specificity in the intermediate host, for example *P. laevis* induces various behavioural and physiological changes in the crustacean amphipod, *Gammarus pulex,* such as altered drifting behaviour, altered anti-predator behaviour, partial castration and lower immune activity. These changes are not observed in *Gammarus roeseli* a closely related species, showing that the alterations by the parasite are specific to *Gammarus pulex* (Lagrue *et al* ., 2007) Examinations on the effect of the acanthocephalan parasite, *Moniliformis moniliformis* on the behaviour of different species of cockroaches by Moore and Gotelli found that different behavioural changes had evolved for different species of cockroach supporting the adaptive nature of the host behavioural change (cited in Poulin, 1998). Indirect methods have also been used to demonstrate the adaptive nature of altered behaviours in the host by determining whether the timing of observed behavioural changes coincide with the period when the parasite is infective to its next host. For example *Tribolium confusum* beetles infected with the nematode, *Protospirura muricola* only show observable changes in the behaviour of the beetles that make them more vulnerable to predation when the parasite has developed to the third larval stage. No behavioural change is observed in beetles home to the first and second larval stage. (Schutgens *et al* ., 2013)

Behaviour as a Form of Host Defense

Not all changes in behaviour can be attributed to the manipulation of the host by the parasite as they do not benefit the parasite. The host is under selection to avoid parasites, and when possible to compensate for the negative effects of infection. Behaviour is often used in order to achieve this and is the first line of defence against parasites as it allows animals to avoid becoming infected in the first place (Moore, 2012). Animals may avoid infection by parasite propagules through behavioural means such as territoriality, site-specific defecation and mate selection. More drastic measures may be taken when trying to avoid ectoparasites, including migration, shifting habitats and lethal combat e. g. howler monkeys invest a significant proportion of their energy to slap at flies, and execute over 1500 slaps in a 12 hour resting period. Once a host becomes infected with a parasite, its behaviour will also be altered in order to minimise damage caused by the parasite. For example animals display sickness behaviours e. g. fever and behavioural chills, which may help in obtaining the benefit of increased care from other members of a group/population. Some animals, for example Chimpanzees, show self-medicating behaviour in which infected animals may consume medicinal plants that are not part of their usual diet. It is also possible in some cases that both parasite and host are shown to benefit from a change in host behaviour, in these cases it can be difficult to determine which organism is responsible for change, or whether it is a shared adaptation, for example caterpillars of several butterfly species play host to braconid wasp parasitoids and unlike non-parasitised individuals they perch at the top of high branches. It has been suggested this benefits the host by making itself more likely to eaten by a predator, killing both the parasitoid and host, but protecting its nearby relatives from the parasite. However it may also help the parasite by reducing the risk of hyperparasitism and therefore increasing its chance of survival. (Poulin, 1998).

Conclusion

Up to this point mainly laboratory based studies have been carried out in order to assess host behavioural changes due to parasite infection. Future research into the area needs to include field based studies in order to fully assess these changes in the natural environment. Currently very little is known about the molecular and genetic mechanisms underlying these changes. Therefore the basis as to how parasites cause these behavioural changes in there host is an area that needs to be addressed in order for these behavioural changes to ever be fully understood.

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