

Role of parasites and commensals in shaping host behaviour

Maithili Jog and Milind Watve*

Department of Microbiology, Abasaheb Garware College, Karve Road, Pune 411 004, India

The role of parasites in shaping host ecology and behavior is increasingly being recognized over the past three decades. However, we are yet far from understanding all possible consequences of parasite-induced and parasite-selected host behaviour. In this review we attempt to classify parasite-selected and parasite-induced behaviours into eco-epidemiological and evolutionary adaptations. We also speculate on many as yet unexplored possibilities of parasite selected behaviour.

Keywords: Commensals, host ecology, parasites.

PARASITES are marvelously well-adapted organisms. These adaptations are complex since they involve intimate inter-relationship with their host, which is co-evolving¹. The result is a counter-adaptive arms race between host and parasite with far-reaching consequences for the physiology, ecology and behaviour of both. While for a long time conventional parasitology has focused only on the patho-physiological and immunological aspects of host-parasite relationship it is increasingly clear that parasites of all kinds have important consequences for the behaviour of their host on an ecological as well as evolutionary scale^{1,2}. Over the last three decades evolutionary ecology has focused much attention on the role of parasites in shaping animal behaviour. The microbial body flora, on the other hand, has not received sufficient attention of behavioural ecologists. There are recent indications, however, that we have grossly ignored and underestimated their importance in animal behaviour. We intend to bring together in this article some of the important and interesting developments of the last three decades, without pretence of an extensive literature survey. In addition, we will speculate on a number of interesting possibilities and the lines of thinking that may develop in near future.

The large number of case studies and hypotheses for parasite influence on host behaviour can be and have been classified in a number of ways¹. We would prefer a classification based on the ecological and evolutionary consequences for the host and the parasite. A given behaviour might be a consequence of host adaptation or parasite adaptation and the consequences might be apparent on an eco-epidemiological scale or an evolutionary scale. The advantages on an ecological or epidemiological scale are

gained by an individual directly, whereas evolutionary advantages are inclusive genetic fitness advantages gained over generations. As in almost every classification, there are uncertain and borderline cases, but the kind of systematization that we follow here is perhaps the most faithful one for a focus on behavioural ecology.

In the evolutionary arms race one would expect that for every parasite strategy there should be a host counter strategy and vice-versa resulting into a red queen effect. However, this assumption is naïve. Not every behaviour of the parasite is harmful to the host and not every strategy of the host is detrimental to the parasite. An already infected host individual, for example, can help parasite transmission to other individuals without any additional cost. Host and parasite can share the benefits of some behavioural trait. Although it appears contrary to the popular perception of parasitism at a glance, we find a number of examples of it in real life. If a behavioural trait is beneficial to the parasite and neutral to the host individual (and vice-versa), it can evolve without any counterstrategy. It is also possible that a host or parasite trait is beneficial to both. Such a trait can evolve rapidly.

Host adaptations

These are host behaviour modifications to avoid, get rid of the parasite or compensate for their effects. The host may retain or regain its health, or whenever that is not possible try to make the best out of the inevitable bad.

Eco-epidemiological adaptations

Parasite avoidance behaviour: A commonly held belief is that the host should always try to reduce the chances of getting infected by the parasite. A number of examples of parasite avoidance behaviour are known. For ectoparasites a variety of defensive behaviours such as rubbing, scratching, lifting legs, bill snapping, foot stamping and head shaking can be used to protect the body. Some mammals cover their body with mud or water³. Dusting, sunning and anting is reported in several species of birds. Grooming has been observed to be effective in removing ectoparasites from the body of the host³.

For gastrointestinal and visceral parasites that have an oral route of entry, a number of parasite avoidance behav-

*For correspondence. (e-mail: watve@vsnl.com)

hours are reported. Diet choice of the host might change in order to avoid parasitism. Seasonal changes in the eating habits of waterfowl provide a good example of it⁴. Plant matter constitutes the food source of waterfowl throughout the year. Since females require extra protein and calcium during breeding season they switch their dietary habits and consume aquatic invertebrates, especially mollusk that are rich source of calcium, proteins and lipids but they are also intermediate hosts for many digenean flatworms. Since consumption of calcium- and protein-rich invertebrates is associated with high risk of parasitism, it is restricted to only breeding season⁴.

Parasite avoidance behaviour may alter the foraging strategies of the host in many other ways. Traditionally, optimal foraging models consider optimization of energy intake and predation risk. Parasite risk is also an important determinant that is seldom taken into account⁴. Hutchings *et al.*⁵ showed that parasitic contamination of pastures via faeces affects grazing decisions. Deposition of faeces tends to increase soil nutrient levels. The nutrient-rich patch on the pasture provides attractive grazing sites for the herbivore at the same time presents a high risk of parasitism. The mammalian herbivores use olfactory cues to assess faecal contamination. The advantage of avoiding faecally contaminated swards outweighed the advantages of increased nutrient intake in sheep⁵.

Freeland⁶ suggested that when an animal or a group of animals continuously use one section of their home range it results in excessive contamination of this area. This results in increased probability of re-infection. He studied the movement pattern of Mangabeys and showed that the shift in the feeding ranges of these animals was not due to non-availability of food but was to avoid the areas for foraging which might be contaminated by their own faeces. Parasite avoidance is also suspected to be one of the factors influencing elephant movement patterns⁷.

Faecal odour of other species is also avoided to varying degrees and it is likely that species with greater chances of cross infection are avoided more. Many prey species avoid faecal odours of their predators⁸. This has been interpreted as mechanism to avoid parasites with prey-predator life cycle⁷. It may be expected that humans have evolved tendency to avoid sources of potentially zoonotic parasites. When human volunteers were asked to rank the faecal odours of 13 species of wild mammals it was observed that the faecal samples of species that had high prevalence of potential zoonotic parasites were ranked among the most obnoxious⁷.

Both macro and microparasites can be transmitted during sexual encounters. Birds and mammals have evolved some behavioural defences which avoid potential partners with signs of harbouring sexually transmitted diseases. In the case of birds, copulation involves cloacal contact which is likely to transmit microparasites to the partner. Cloaca exposure prior to copulation allows the partners to view the visual signs of the disease. Genital inspection is also

seen in mammals which involve visual and olfactory investigations of genitals. Post-copulatory genital licking in mammals is effective in removing pathogens possibly transmitted during copulation^{9,10}. Hart *et al.*¹¹ argued that genital licking by rats mechanically washes off the region and the bactericidal constituents of saliva play an important role in reducing genital infections. This behaviour is also observed in dogs¹¹.

There are some exceptions where the parasite avoidance behaviour seems to have failed to evolve. *Enterobius* is one of the most abundant helminths found in Langurs⁷. The females of this pinworm actively migrate out from the anus to lay eggs on the skin¹². The parasite is transmitted during the act of allogrooming and eating by hands. The life cycle of *Enterobius* has apparently evolved to take advantage of both these behaviours of primates. These behaviours however do not appear to be given up in any species of primates to avoid *Enterobius* infections. Failure to avoid an act which can expose to parasites can result if there are other advantage of the act that outweigh the risk of parasitism.

Therapeutic and vaccination behaviour: Apart from prophylactic behaviours, therapeutic behaviours are also reported. Certain plant products alter the internal environment which affects the growth of the parasite⁴. A wide variety of plant products that are poisonous or repulsive act as a defense against insects or herbivores. These biocidal plant products are generally secondary metabolites which can be used to avoid nest-borne parasites by birds¹⁰. The avian species which used certain green plants to weave the nests showed retarded hatching of louse eggs¹⁰. Chimpanzees have also been observed to eat plants with ethnomedicinal properties¹³. Baboons consumed leaves and berries of *Balanites aegyptica* when they were exposed to high risk of Schistosomiasis. These leaves and berries were toxic to *Schistosoma* sp.⁴. Sick elephants consumed *Terminalia* that is not a part of their normal diet⁷.

Parasite species are likely to compete with each other for the host resources although evidence for such competition is debated¹⁴. Rather than avoiding contact with all parasites, the host might be better off encouraging less harmful parasites or commensals that compete with more virulent ones. Some commensals are known to give cross immunity against pathogens¹⁵ and these organisms would be highly preferred. Acquiring such commensals or milder parasites can be termed as vaccination behaviour. Placental mammals can immunize the foetus with maternal antibodies. The foetus is almost sterile in the womb. The newborn starts collecting commensal and parasitic microorganisms from the physical environment as well as from the other members of the social group, if any. The mother should therefore be exposed to all potential invaders and become immune well in advance so that some placental transfer of immunity to the most likely pathogens is possible.

Grooming other members of the group or other body contact behaviours would play a crucial role in foetal vaccination. Testable predictions of the 'grooming as vaccination' hypothesis are that allogrooming should be more common in placental mammals, females should more actively engage and seek allogrooming, it should be more pronounced in the breeding age and should be directed more towards individuals that are more likely to be in close contact with the infant⁷.

Best of bad strategies: Once parasitized, a host individual should try to rescue some fitness gains by suitably modifying its survival strategies. It is an attempt to make the best of the inevitable bad. This can be achieved by changing the foraging, mating or social strategies. In stickle-backs, for example, the good competitors feed on larger prey as it is more profitable. The poor competitors feed on smaller prey as it is easy to capture. When stickle-backs are parasitized they shift their diet preference from larger prey to less profitable smaller prey. This shift in diet must be helping them under natural conditions to avoid competition with stronger individuals¹⁶.

Evolutionary adaptations

Parasite spreading behaviour: Every host individual should try to avoid getting parasitized. However, once parasitized the host may or may not have additional costs in spreading the parasite around. Evolution of parasite spreading behaviour in the host would depend on the social environment of the host and whether the new recipients of infection are likely to be random, self, kin or non-kin.

The difference in defaecation behaviour of different species exemplifies this well. How should a territorial animal choose the defaecation site? An ideal site should be such that transmission of parasites from that site to the food resources should be difficult. At the same time it may be better if parasite transmission can be specifically directed against other unrelated conspecifics. In that case one should defaecate in other's territory. This however may not be affordable because of higher energy inputs needed for movement and the direct conflicts arising due to intrusion into other territories. An optimum solution can be the territorial boundaries. Marking of territorial boundaries by defaecation may thus arise as a parasite-selected behaviour. Here one is likely to see a herbivore–carnivore dichotomy for a number of reasons. (i) The food resources of herbivores are much more dispersed than carnivores. (ii) The prey species of carnivores are known to avoid predator scats⁸, a factor which may affect parasite transmission. The food species of herbivores do not do so. (iii) Carnivores have a low and intermittent turnover of food which can lead to more flexibility and choice for the defaecation time. Herbivores feed more continuously and have a more continuous passage of food in the gut and thereby not only is

the defaecation frequency high, but the interval between defaecations is less flexible. Therefore, defaecation at territorial boundaries is more likely to evolve in carnivores than herbivores. Carnivores such as wolves do most of their hunting towards the centre of their territory and avoid hunting at the periphery. However they regularly visit the periphery for urine and faecal scent marking^{17,18}. This means that the major defaecation sites are away from the major feeding sites. Also, by defaecating at the periphery, the parasite transmission is directed relatively more towards neighbours than it would have been by defaecating near the centre. Herbivores on the other hand need not feed more at the centre and avoid the periphery. Food resources being scattered, it would be prudent to defaecate in one or a few places rather than scattered all over. This would avoid contaminating the entire food resource. This, however, is possible if there is a flexibility of defaecation interval and going to the nearest defaecation site not too costly. Probably as a result of this, among herbivores, there are some species which apparently do not show any specific defaecation pattern while some others have specific 'latrines' where repeated defaecations result into large dung piles which are not necessarily situated at the periphery or the centre, but grazing in the vicinity is usually avoided¹⁹.

Certain resource sites such as water holes and salt licks can be potential foci for transmission and behaviour at such sites can be crucial in spreading and acquiring infections. The defecation frequency of elephants is reported to be significantly higher near water holes and salt licks as opposed to other large mammals in southern Indian forests⁷. The elephant behaviour can be interpreted as a spiteful parasite spreading behaviour. Spite is a behaviour that harms other individual(s) at a cost to the actor. Although the members of the elephant herd defaecating in water are likely to get infected by this act, elephant movement patterns in relation to the larval development of their nematode parasites suggests that the parasites are more likely to infect non-self and non-kin⁷. A spiteful parasite spreading behaviour can evolve if transmission is more likely to be directed to non-kin²⁰. Elephants have large home ranges and a given group does not use the same water body on consecutive days after having contaminated it⁷. This reduces the probability that members of the kin group get infected, however, transmission to other groups moving into the area is possible. Habitual contamination of resources can further reinforce nomadic movements in elephants. One can therefore expect a positive feedback cycle between nomadic and 'unhygienic' or spiteful parasite spreading behaviour. Sedentary animals that use the same resource consecutively for a long time are more likely to evolve a 'hygienic' behaviour reflected in avoidance of defaecation on and near critical resources⁷.

Another possible reason for the evolution of spiteful parasite-spreading behaviour seems to have been largely ignored. If the fitness of individuals is dependent on the relative rather than absolute health, an infected individual

can regain its fitness by spreading the parasite to others. This is a more likely case for males whose access to females is decided by their relative ranking. Therefore males should be more interested in spreading parasites than females. Interestingly there are reports of pharmaceutical and biotech companies preferring female workers than males in clean rooms, since males have a greater rate of shedding bacteria through aerosols and skin contact²¹. It is a common observation that coughing and sneezing is more violent in men as compared to women.

Traditionally infections are studied under the branch of medicine and not ecology. Therefore most of the effects of the parasite on the host are treated as symptoms of the disease. Many symptoms, however, make sense from the behavioural ecology point of view²². Diarrhoea, for example, facilitates the transmission of the pathogen and therefore can be viewed as a parasite-induced behavioural change in the host. To a limited extent the host body may also be benefited by diarrhoea since it is an act of washing off the pathogen from the gut. Coughing and sneezing offer similar benefits to both parasite as well as host. In both the examples the interests of the parasite as well as host are served by the same behavioural act.

The role of fever, however, is debated. Fever is believed to enhance host resistance or immunity²². Fever is a typical symptom in warm-blooded animals that possess body temperature regulation mechanisms. Interestingly, there are records of temperature rise accompanying infection in cold-blooded animals too. Klugger²³ observed that desert iguana keep their body temperatures constant and warm by shifting between warm and cool microhabitats. When infected with *Areogenosa hydrophilia* they did run high fever by moving into warmer microhabitats. The infections became more severe when iguanas were kept at lower temperatures.

Fever does not always function as a defense. Some pathogens could be more resistant to higher temperatures. Pathogens that are not suppressed by the fever could benefit from it as the metabolic processes generally speed up at higher temperatures and hence produce more progeny per unit time. At present the evidence is controversial and it is not clear whether fever helps the host or the parasite. However, fever is certainly not a parasite-induced behaviour alone, since the warm-blooded hosts give fever response to a number of biochemical stimuli, collectively called pyrogens. Pyrogens do not necessarily come from parasites, they are released from lysis of host cells as well. For the fever response it is important that the pyrogens are released free in blood²⁴. We suggest an ecological role for fever. Elevated body temperatures attract blood-sucking arthropods such as 'seed ticks'¹² by means of which blood-borne pathogens are likely to be transmitted. This is certainly beneficial to the parasite, but is also likely to have evolved as a spiteful parasite-spreading behaviour in the host. If this is true, following the above hypothesis males should have a greater tendency to develop fever

than females for comparable severity of infections. This hypothesis needs to be tested.

It is suggested that an infected individual moving out from a kin group can be interpreted as an altruistic suicidal behaviour if it exposes itself to increased risk of predation²⁵. In this act the parasites are killed along with the host, reducing the chances of their spread to kin²⁵. If the emigrated infected individual tries to enter another unrelated group, it can be labelled spiteful since this results in redirecting the flow of pathogens from kin to non-kin²⁰. Xenophobia is a counter-adaptive strategy that is aimed at prohibiting immigration of heavily infected individuals into a group. Freeland²⁶ argued that in primate groups, xenophobia primarily evolved to prevent entry of novel pathogens.

Sex and parasites: Hamilton²⁷ suggested that sexual reproduction evolved as an adaptation to resist parasites. Parasites have considerably short generation time as compared to their hosts. They can evolve faster and overcome the host resistance mechanisms. This hypothesis views sex as a host adaptation that creates new recombinant genotypes in every generation. Recombination of parasite resistance genes can be an effective means to counter the faster evolving parasite strategies. The parasite theory is among the most promising theories of the evolution and stability of sex.

Parasitism is a potential selective force in the evolution of host mating systems¹⁰. Sexually transmitted diseases can be one of the factors selecting for monogamy. Interestingly parasites and pathogens can also exert a selective force for polygamy. If for a female it is impossible to assess genetic contribution of potential mates prior to mating, multiple matings can be a good strategy. Multiple mating or polyandry increases genetic diversity of offspring^{28,29}. As a result, at least some of the offspring will be resistant to any prevailing parasite genotype¹⁰. Polyandry can be a good strategy for a female with large number of offspring. However if the female produces fewer offspring with more investment in each, choosing one or a few males with 'good genes' would work better than polyandry. Freeland³⁰ suggested that the mate choice by females may be related to parasites and pathogens carried by males. Hamilton and Zuk³¹ further developed the concept that host-parasite coevolutionary cycles might drive the evolution of female preferences for extreme male displays. Males carrying resistance genes will be healthier and in a better condition to grow plumage or perform strenuous displays. Females by preferring these males ensure 'good genes' for their offsprings. However unlike other good gene hypotheses, the resistance genes will be constantly changing since the parasites are also evolving, and thus the system remains dynamic maintaining the importance of female choice. A number of empirical studies have supported the hypothesis by showing correlations between parasite loads and secondary sexual characters^{32,33}. Interestingly, some recent data indicate that non-parasitic microorgan-

isms associated with the body also influence secondary sexual characters³⁴.

The parasite-imposed selection can lead to modifications in the mate choice behaviour in three different ways. (i) The animals might avoid mating with individuals infected with contact-transmitted pathogens. (ii) In the case of species where males provide parental care, females choose healthy and vigorous males. In both these cases the choice is for healthy phenotypes and may not have any genetic basis. (iii) The genetic benefits in choosing parasite-resistant males would have far-reaching consequences.

There are several pathogen-related cues that might be used in mate choice. Male–male competition can be a mode to reveal the disease state of potential mates³¹. Females may avoid diseased males by observing direct external signs of infection. Costly secondary sexual characters give an honest signal of male health³⁵. Finally chemosensory cues to the genetic composition of males are also known to help female choice. Pheromones are known to be involved in mate choice and mate choice by olfaction is related to immune mechanisms of the body in an interesting way.

The modification of human pheromones by bacteria associated with skin is perhaps the most intriguing example of how the host and microbial evolution has worked together to generate complex consorted behaviours. The demonstration of human pheromones is recent and research on it is yet to pick up speed. However, the few facts revealed so far raise exciting possibilities. The major histocompatibility complex (MHC) genes are known to influence mate choice in mammals¹⁰. MHC comprises immunity related genes and females are shown to prefer males with different MHC composition. Interestingly, mate choice for these genes is based on olfactory cues³⁶. How immunity-related genes can be perceived by olfaction is still unclear, but the only sensible hypothesis is that MHC genes influence the body flora and the composition of the body flora decides the body odours³⁷. Singh *et al.*³⁸ demonstrated apparent absence of body odours in germ-free animals strengthening the hypothesis. In at least one case the chemistry of human pheromones and the role of skin flora is clearly demonstrated. Aerobic bacteria mainly belonging to the genus *Corynebacterium* oxidize odourless precursors androstadienol and androstadienone secreted by human skin to give two odorous compounds³⁶. Androstamol (5-androst-16en-3ol) has a musk-like scent and is perceived as an attractant by females. However, androstamol is a relatively unstable compound and is oxidized to the ketone from Androstamol. Androstamol (5alpha androst-16en-3-one), on the other hand, has somewhat urinous smell and is repellent. However, during the menstrual cycle, ovulating females found androstamol more pleasant than on other days³⁶.

The female response to androstamol and androstamol suggests a revolutionary hypothesis about mate choice in humans that is likely to raise fierce debates and controversies. In the last two decades there have been extensive studies on extra-pair-matings in species of birds and

mammals (including humans) where biparental care necessitates long-term pairing of males with females^{39,40}. The evolutionary argument is that the best mating strategy for a female is to pair with a faithful male that gives good inputs for child-care, but seek opportunistic mating with a male that is genetically superior and more popular among other females⁴¹. Mating with such a male can enhance the evolutionary fitness of females through a 'sexy son'. Data on extra-pair mating in birds as well as humans are in support of this argument^{40–44}. The question of interest here is how would females select these two types of males in the two situations. Our interpretation is the following. Males should produce androstamol in spurts when they interact with females since androstamol is a perceived female attractant. However, since its oxidation to androstamol is inevitable, males that interact with females very frequently will have a high androstamol to androstamol ratio. On the other hand a male that has not had encounters with other females recently will have a low ratio and this is more likely to be a faithful male. A female should choose a faithful male for long-term pairing, but seek mating with a more 'sexy' male during ovulation. The increased tolerance to androstamol during ovulation is likely to induce the choice of a more 'sexy' male for mating when the probability of conception is at its peak⁴⁵. In this system bacteria on the skin is an indispensable component and the co-evolution of such a system is an interesting problem to investigate.

Group living and sociality: In the evolution of group living and sociality one of the major costs of aggregation is believed to be increased risk to parasitism⁴⁶. Inter-group transmission may be substantially lower than intra-group transmission^{27,46–49}. Some empirical studies and theoretical models point in the opposite direction⁵⁰. Freeland⁵¹ showed that polyspecific groups in primates reduced the number of blood-sucking insects per individual. Grouping can be an effective behaviour for protection from parasitic flies in the case of birds and some ungulates. Encounter dilution effect reduces the chances of attack by biting flies⁵². The positive effects of grouping may not be restricted to ectoparasite avoidance. Watve and Jog⁵³ using spatial stochastic simulation model showed that at a given host population density, aggregation into groups increased within-group transmission but decreased between-group transmission. In a wide range of parameters the net rate of transmission reduced with group size and there was an optimum group size that ensured minimum chances of infection. Wilson *et al.*⁵⁴ reconfirmed the theoretical results and also found that in lepidopterans solitary species had to invest more in parasite defense than gregarious ones contrary to common belief. Parasites therefore must have played a complex role in the evolution of group living and sociality.

Avoidance of disease is the factor promoting multiple matings in social insects as stated above. However, multiple

matings reduce the average relatedness in a colony. This is a potential problem in explaining hymenopteran sociality by kin selection alone. While kin selection requires high genetic relatedness in cooperating individuals⁵⁵, multiple matings decrease it. The need to secure the colony from parasites and diseases seems to have overpowered the need to maintain high genetic relatedness in social hymenopterans⁵⁶.

Parasite adaptations

The parasites can take over partial control of the host behaviour and these parasite-induced behaviours help their own transmission⁵⁷. Some of the symptoms of infection are likely to be parasite adaptations. There has been a debate on whether a given change in the host physiology or behaviour is merely an inevitable physiological effect of the growth of the parasite or is a specific parasite-induced change¹. The debate is perhaps unnecessary and as long as a given behavioural change in the host helps the pathogen, we would classify it under parasite-induced behaviour irrespective of the mechanism.

Ecoepidemiological adaptations

Susceptibility to predation: Some parasite species with a complex life cycle rely on predation of their intermediate host for its own transmission to the definitive host. These parasites would be benefited by an increased rate of predation specifically of the infected individuals by the definitive host. A number of examples of parasite-induced susceptibility to predation are well documented. This is brought about often by change in behaviour of the intermediate host. The changes in the behaviour of the intermediate host may take several forms. An infection might result in reduced activity that results in increased vulnerability of the intermediate host to predation. It can be due to weakness or reduced stamina or due to specific parasite-induced behavioural changes that make the parasite individual more conspicuous for the predator⁵⁸. The parasite can manipulate host's decision making ability for example by suppressing the fear response or the ability to recognize predator. This is demonstrated by three spined stickle backs infected with plerocercoids. The fishes did not change their feeding behaviour in response to predator as opposed to healthy individuals that avoided the predator. The increased food requirement in the presence of the parasite apparently outweighed the risk of predation. The activity of parasitized lemmings (*Dicrostonyx richardsoni*) increased upon infection by a protozoan *Sarcocystis rauschorum*. The hosts became more noticeable and as a result the risk of predation by snowy owls increased⁵⁹. Perhaps the most dramatic example of parasite-induced behaviour is that of *Dicrocoelium dendriticum*. This is a

liver fluke of ruminants which affects the second intermediate host, formicine ants. The metacercariae of the fluke are ingested by the ant which penetrate into the abdominal coelom and are encysted. One (occasionally two or three) of the cercariae migrates to the suboesophageal ganglion. The infected ants hang on the tips of grass blades with locked mandibles during cooler parts of the day. This behavioural change is associated with temperature. As the temperature decreases during evenings and early mornings, the ants migrate up the vegetation. During mid day their behaviour is similar to the uninfected ants. This keeps the infected ants near the top of the vegetation during the early morning and late evenings which are the grazing periods of the definitive hosts.

If the parasites make the predator job easy, the question arises whether there can be a mutualistic relationship between the predator and the parasite⁶⁰. A mutualistic relationship can be said to exist between a predator and a parasite if the cost of harbouring the parasite is less than the benefit of greater success in catching the prey. Such a mutualism is likely in a mammalian prey–predator with a protozoan parasite⁷. The prey–predator parasite system comprises Chital (*Axis axis*), dhole or Indian wild dog (*Cuon alpinus*) and a protozoan parasite *Sarcocystis axicuonis*⁶¹. Dhole preferentially take chital infected with *Sarcocystis*. There is evidently a division of labour among the dhole pack. Only a few members of a pack carry the parasite and at any given time a few parasite-free members are always present that may be more active in hunting. This division of labour can reduce the cost of carrying the parasite substantially, making it a more likely case of predator–parasite mutualism.

Evolutionary adaptations

If sex, recombination, polygamy are the adaptations by the host to resist parasitism, parasites also have evolved certain strategies to counteract them. Vertically transmitted bacterial species are known to induce parthenogenesis in insect hosts⁶². Prevention of cross breeding due to cytoplasmic incompatibility is another way to minimize new gene combinations in the next generation of the host. *Wolbachia* in insects and other invertebrates is the most striking and well-studied example of 'selfish' cytoplasmic elements⁶². These are intracellular bacteria transmitted within the egg cytoplasm. Species of *Wolbachia* in some host species seem to induce cytoplasmic incompatibility by some kind of encryption of the sperm in infected males. The same strain of *Wolbachia* should then be present in the egg to decode the encrypted sperm. Therefore sperms from an infected male cannot fertilize eggs from a female that is either uninfected or infected with a different strain of *Wolbachia*. This results into reproductive isolation within a host population that can effectively enhance speciation. It is speculated that the widespread occurrence of *Wolbachia*

and other microbial species in insects might be responsible for the exceedingly large species diversity among them. In some species of insects development and reproduction have become dependent on the presence of *Wolbachia*. In the wasp species *Asobara tabina*, if *Wolbachia* are removed by antibiotic treatment, the females fail to develop ovaries⁶². When a host cannot live without a parasite owing to take over of certain metabolic controls by the parasite, we can label this curious phenomenon as 'parasite addiction'.

Maternally transmitted microorganisms typically cause female biased sex ratios since that facilitates their transmission^{63,64}. For example, cytoplasmically transmitted spiroplasmas kill males in several species of *Drosophila*. *Rickettsia tsutsugamushi*, the causative agent of scrub typhus, produces all female progeny in its mite host. The strategies that cause female bias generally range from cytoplasmic incompatibility⁶³ to male killing^{64,65} or feminization of genetic males. In a species of African butterflies the highly skewed sex ratio due to male killing has resulted into female leks. While leks of males is the evolutionary rule, role reversal of sexes is caused by bacteria⁶². The effects of *Wolbachia* and other cytoplasmic microorganisms in invertebrates are being unearthed only in the last two decades and what has been found is perhaps the tip of an iceberg. The effects of *Wolbachia* on invertebrate behaviour discovered so far deserve a separate review. But the influence of microorganisms on reproductive behaviour of invertebrates is perhaps far more diverse and widespread than what we know today.

Over the last two decades a large number of theoretical as well as empirical studies have demonstrated that parasitic and commensal organisms associated with animal bodies are players of immense importance in behavioural evolution. They have some or the other role to play in almost every aspect of behaviour ranging from foraging to mating or sociality. They were ignored prior to the 1980s owing to their inconspicuousness and subtle mechanisms of action. Parasite theories offer better explanations for a number of behavioural phenomena that were poorly explained before. They also open up entirely new lines of thinking that would have extensive ramifications. Compared to parasites the role of commensals has been ignored so far, but it can be said with confidence that parasites and commensals together would continue to occupy the central stage in behavioural evolution research for several decades to come.

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