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FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.

Optimal foraging theory: a possible role for parasites

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Summary. – The role of parasitism has, to date, been largely ignored in optimal foraging theory. The mechanisms necessary to allow animals to use their diet to protect themselves from potential or actual parasitism have been observed in various species. The inclusion of the effects of parasitism on diet choice may considerably improve the predictive powers of future optimal foraging models.

Traditionally, optimal foraging models have assumed that the maximization of net energy or protein intake was the primary goal of foragers (Stephens and Krebs 1986). Other factors, such as the risk of predation (Milinski and Heller 1978, Krebs 1980, Sih 1980, Edwards 1983, Lima et al. 1985, Abrahams and Dill 1989, Lima and Dill 1990), the effects of intraspecific (Baker et al. 1981, Milinski 1982) and interspecific (Millikan et al. 1985) competition have been recently incorporated into diet choice models to improve their predictive powers. So far however, the possible effects of parasites on optimal foraging have been largely ignored.

It has been long known that parasitized animals may behave differently than uninfected ones (Rothchild 1962). Behavioural changes associated with parasitism by acanthocephalan worms have been studied in amphipods (Bethel and Holmes 1973, 1974, 1977), shrimps (Brown and Thompson 1980), cockroaches (Moore 1983) and isopods (Moore 1984b);other worms have also been known to cause behavioural changes on their hosts (Carney 1969, Brassard et al. 1982, Giles 1987b, Hoogenboom and Dijkstra 1987). Behavioural changes of parasitized intermediate hosts often increase the likelihood that they will be preyed upon by the definitive host of the parasite, thus allowing the parasite to complete its life cycle. It is generally thought that the parasites somehow manipulate the intermediate hosts' behaviour in order to reach its final hosts.

More specifically, the foraging behaviour of hosts can also be affected by parasitism. Giles (1983, 1987a) found that sticklebacks (*Gasterosteus aculeatus*) parasitized with a cestode larvae foraged more actively, recovered faster from a frightening stimulus, and, if deprived of food, suppressed their fright response sooner than uninfected fish. Giles argued that this occurred because the fish had to compensate for the extra nutritional requirements caused by the parasites load. Alternatively, the foraging efficiency of hosts can be reduced by the presence of parasites, as is the case in dace (*Leuciscus leuciscus*), when infected with large numbers of eyeflukes (Crowden and Broom 1980). It has also been determined that parasites may decrease the competitive abilities of their hosts, forcing them to switch their diet choice to what otherwise would be sub-optimal prey (Milinski 1985).

On the other hand, potential or actual hosts can also alter their behaviour to protect themselves from parasitism; preening as well as self and group grooming are obvious examples. Some birds rub crushed ants over their plumage and it has been suggested that this behaviour, known as "anting", occurs because ants produce secretions that are used by the birds to protect their skin from bacteria, fungi and arthropods (Ehrlich et al. 1986). Antibiotic compounds of plants selected for nest material have been found to significantly reduce the effects of fungi, bacteria and ectoparasites on the nestlings of Falconiformes (Wimberger 1984) and starlings (Clark and Mason 1985, 1988). So far, however, diet choice has been largely ignored as a way in which potential hosts could reduce parasitism.

I am suggesting more than just a well balanced diet which would make potential hosts better able to deal with parasitic infections. Generally, a well balanced diet decreases the susceptibility of a potential host to parasites and disease (Beisel 1982a), but extreme malnutrition often decreases the magnitude of the immune response so that the actual damage done by the parasite decreases (Beisel 1982b). I propose that animals could change their optimal diet such that it is not only energetically and nutritionally adequate, but also takes into account the possible harm done by parasites.

Parasites could influence diet choice in three ways: (1) potential hosts could avoid some food items that commonly are sources of parasites; (2) by selectively eating certain food items, an animal could alter its internal environment and make it less hospitable to parasites; and (3) certain foods could be selected because of specific antiparasitic compound(s) that might kill and/or cause the expulsion of parasites already established.

Avoidance of possible parasite sources

A potential host could reduce its risk of parasitism by avoiding, partially or completely, a nutritious food item that is also an important source of parasites. The eating habits of waterfowl provide a good system in which this hypothesis could be tested.

Many waterfowl feed on plant matter most of the year but switch their diets to include a greater amount of invertebrates during the breeding season; this change is more pronounced in females (Swanson 1985). The change occurs partly because invertebrates are not available during the winter, but also because females need extra protein and calcium for the production of eggs (Ankney 1977, Reinecke and Owen 1980, Alisauskas and Ankney 1985, Ankney and Afton 1988). Aquatic invertebrates, especially molluscs, are an excellent source of calcium, lipids and protein (Reinecke and Owen 1980), but they are also intermediate hosts to many diginean flatworms. In wood ducks (*Aix sponsa*), Drobney et al. (1983) found that the prevalence of infection by platyhelminths was associated with the proportion of invertebrates in the diet, and that the proportion of females infected was greater than that of males. Female wood ducks, when compared to males, also consumed a greater diversity of invertebrates (Drobney and Fredrickson 1979).

This does not necessarily mean that male wood ducks limit their consumption of invertebrates to decrease their risk of parasitic infection. Other factors such as variation in availability or handling time could explain the differences, but given the high risk of parasitic infection associated with consuming invertebrates, and particularly molluscs, it is likely that parasitism does play a role in the diet choice of waterfowl.

As previously mentioned, behavioural changes of intermediate hosts brought about by parasitic infection sometimes increase the chances of them being preyed upon by the final hosts. This, however, does not imply that the final hosts are actively choosing or avoiding parasitized intermediate hosts. While the parasites are altering the intermediate host's behaviour in order to reach their final hosts, the final hosts should avoid parasitized prey if there is a significant cost involved with being parasitized. To test whether the risk of parasitism really plays a role in the diet choice of the final hosts, the availability, conspicuousness and profitability in terms of energy and nutrients of infected and non-infected prey must be assessed independently and then compared to the final host's diet choice. The effects of parasites on diet choice would, of course, only be observed if, in terms of fitness, there is a high cost to being parasitized.

Consumption of prophylactic food items

Another way in which animals could change their diets to protect themselves from parasitism is by consuming certain items, generally plants, which may alter their internal environment, rendering it inhospitable to potential parasites. Because it is directly in contact with all ingested matter, the most likely "internal environment" to be thus influenced would be the intestinal tract, but other tissues can also be affected.

The ability to store ingested plant compounds in body tissues has evolved in several plant – insect associations; the best known example is that of the monarch butterfly (*Danaus plexippus*) larvae storing in their tissues cardiac glycosides obtained from feeding on milkweed (*Asclepias curassavica*) (Brower 1958, Brower 1969, Rothschild 1972). Given that animals can extract secondary compounds from the plants they feed on, it is possible that plant chemicals, or merely different foods, could be used by animals as protection against parasitism.

Parasites can be affected by alterations of the intestinal environment (Trager 1986), and these shifts can be brought about by dietary changes (Mettrick 1971). In cattle, changes in the biochemistry and microfauna of the rumen have been observed following an alteration in the fibre content of the diet (Eadie et al. 1970). Experimental increases in dietary crude protein have experimentally increased the susceptibility of chickens to coccidiosis (Sharma et al. 1973). Molan and James (1984) showed that mice and gerbils (*Meriones unguiculatus*) placed on a milk diet instead of their regular pelleted food were more susceptible to infection by a diginean intestinal parasite (*Microphallus pygmaeus*).

Under field conditions, Taper and Case (1987) studied the community structure of cynipid gall wasps in different oak (*Quercus* spp.) species and found positive correlations among leaf-tannin levels, wasp diversity and abundance. Herbivorous attack sometimes increases tannin levels in plants (McKey 1979) but in Taper and Case's (1987) study the wasps and the tannins were sampled in different individual trees, so the correlations found were not merely caused by a defensive response on the part of the trees. Tannins are known antifungal agents and it has been argued that their primary role is not herbivore defense but rather protection from bacterial and fungal attack (Swain 1979). In a previous study, Taper et al. (1986) determined that fungal infection was the most important factor influencing the emerging success of cynipid wasp pupae. Taper and Case (1987) concluded that, contrary to the idea that tannins reduce herbivorous attack, tannins are used by wasps to reduce their incidence of fungal infestation.

Phillips-Conroy (1986) studied the diet and the incidence of schistosomiasis in baboons (*Papio* spp.) in the Awash River Valley in Ethiopia. The gastropods required as intermediate hosts by *Schistosoma* spp. were not equally abundant throughout the area, so the risk of infection varied for the different baboon populations living along the valley. In areas of high risk of infection, but not elsewhere, baboons consumed the leaves and berries of *Balanites aegyptica*, a shrub that is toxic to *Schistosoma* cercaria and might affect the maturation of the adult worms in the final host (Phillips-Conroy 1986). *Balatines* sp. was common throughout the study area; therefore, the authors concluded it is consumed because of its prophylactic properties.

Thus, both laboratory and field studies show that it is possible to negatively affect a parasite by changing the diet of the host (see Crompton 1987 for further examples). Bundy and Golden (1987), in a review of the effects of nutrition on gastrointestinal helminths, agreed that one way in which the host's diet can affect a parasite is by changing the internal environment of the gut. Crompton (1987) states: "dietary changes may induce...changes in the intestinal environment, and these may lead to alterations in parasite growth and survival". If this is indeed occurring then we should be able to observe deviations from what would be expected if foraging were only based on the optimization of energy and nutrient intake. If it is suspected that certain food items are consumed as prophylactics against parasites, their consumption should be correlated with spatial (Phillips-Conroy 1986) and temporal changes in the risk of parasitism. To be able to conclude that these food items are being consumed because of their prophylactic properties, it would be necessary that they have no other nutritional value.

Consumption of antiparasitic food items

Once parasites manage to establish themselves, the consumption of antiparasitic compounds is one of the few resources available to the host to get rid of or at least slow the growth and development of parasites. Natural medicinal compounds are widely available from plants, especially in the tropics (Caldecott 1987). Many common anthelminthic compounds are derived from plants (Cavier 1973, DeCarneri and Vita 1973, Van den Bossche 1980, Trager 1986), and there are surely many others that remain to be discovered (Caldecott 1987).

Several laboratory studies support the idea that diet changes can suppress parasitic infections. Godfrey (1957, 1958) reported the suppression of several malarial diseases in mice by the addition of cod liver oil to their regular and otherwise nutritionally adequate pelleted diets. Jacobs (1964) showed that *Plasmodium bergei*, a malaria causing organism, requires its hosts to consume para-aminobenzoic acid (PABA), because PABA is needed by the parasites for folate metabolism (Ferone 1977). Crompton et al. (1982, 1983, 1988) placed mice infected with the acanthocephalan worm *Moniliformis* sp. under two diets differing only in the type of the sugar source: glucose and fructose, and found that worms of mice on the fructose diet had a delayed sexual development and a lower growth rate.

If this antiparasitic tactic is to exist in the field, it is first necessary for an animal to recognize it is parasitized and then actively seek antiparasitic compounds. Huffman and Seifu (1989) observed an unhealthy, lethargic, wild female chimpanzee (*Pan troglodytes*) in Tanzania consuming the leafs of a plant known as bitter leaf (*Vernonia amygdalina*). This plant, as its names suggest, has many ethnomedicinal uses and, because of its bitter taste, is seldom consumed by chimpanzees. The female in question appeared to regain her health in two days (Huffman and Seifu 1989).

Chimpanzees have also been observed consuming leaves of plants with known ethnomedicinal value in a very particular manner: by holding them between the tongue and buccal surface for up to 25 seconds before swallowing them (Wrangham and Nishida 1983, Newton and Nishida 1990). Presumably this allows the medicinal substances to enter directly via the buccal mucosa.

This evidence suggests that parasites can be affected by specific diet changes and given the wide availability of naturally occurring antiparasitic compounds, chimpanzees, and probably other animals, have evolved ways to recognize such food items and utilize them in their diets. A more rigorous examination of this idea would involve testing whether unique changes in foraging behaviour follow specific parasitic infections and whether the removal of particular antiparasitic plants from the animal's feeding area affect its parasite load and/or recovery. Stronger support for this hypothesis would be provided if the nutritive value of these plants was found to be relatively poor, thus there would be no other reason for their consumption.

Conclusion

It is therefore possible for an organism to use diet choice as a way reduce the negative effects of parasitism. The mechanisms seem to exist which would make this phenomenon possible and some researchers have previously speculated on the subject (Freeland 1983). Diet choice could have evolved in part to account for the potential reductions of fitness caused by parasites and the costs of protection and prevention via diet changes.

These two factors will differ for each parasite-host-diet system, therefore the dietary responses could vary from mere avoidance of possible parasite sources to actively seeking prophylactic or antiparasitic compounds. In all cases the responses might be obligatory or facultative. An obligatory response would involve an animal changing its diet, perhaps seasonally, regardless of the its present parasite load; it would be favoured in instances where the risk of parasitic infection is fairly constant and/or predictable. A facultative response would require dietary change only upon infection or when the risk of infection is high and it would be favoured in cases where the risk of parasitism is highly variable, thus an animal would not switch its diet unless there is a high risk of parasitism.

A wide variety of responses is therefore possible if parasitism plays a role in diet choice. Future research should perhaps begin with laboratory experiments of cases in which a host response is suspected to occur, parasitism is known to be variable within and between populations and/or current diet choice models have not been satisfactory. The recognition of parasitism as a potential factor influencing diet choice suggests a new approach for future research which would lead to a more complete understanding and accurate modelling of foraging behaviour.

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