

Parasite transmission via a vitamin supplement

Parasites that live in the digestive tracts of vertebrates are almost always transmitted to them by an infective process. The infective stage itself can be ingested by the host, but more often the infective stage is attached to or incorporated into a prey item (the intermediate host) that is a component of the definitive host's diet. The nutritional requirements and foraging activities of the hosts therefore exert strong selective pressures on parasite populations (Lozano 1991). If genetic diversity provides the parasite with an opportunity of increasing the probability of an encounter with the definitive host, for instance by a specific association with a preferred prey item of the definitive host, then such a character will be of selective advantage to the parasite.

Some parasites have a further adaptation to increase the probability of transmission: They make the intermediate host more susceptible to predation by the definitive host. For example, the parasite may elicit a modification of intermediate host color or trigger a behavior that makes the intermediate host more conspicuous, thereby increasing the likelihood that the intermediate host will be preyed on by the definitive host (Bethel and Holmes 1977, Dobson 1988, Moore 1984, 1995, Moore and Gotelli 1990). When parasites are highly pathogenic, the definitive hosts may in turn selectively avoid prey items that may be intermediate hosts for such parasites, exhibiting altered behaviors that decrease the cost of being infected (Connors and Nickol 1991) or result in parasite

avoidance (Combes 1991). Although such behavioral "arms races" are not well documented, their potential to influence the evolution of food webs is attracting increased attention from ecologists (Brown et al. in press).

In this article, we describe a process that favors the completion of the life cycle of a parasite. The parasite appears to take advantage of its definitive host's need for an essential vitamin (B_1) to ensure its transmission. Whether this process selects for counter behaviors on the part of the host, however, is not clear.

The *Aporchis massiliensis*/yellow-legged gull system

Yellow-legged gulls (*Larus cachinnans michaellis*) on the shores in the Mediterranean are parasitized by several intestinal trematodes (Figure 1). The life cycle of one of these, *Aporchis massiliensis* (Echinostomatid), has three main stages: cercariae, metacercariae, and adults (Prévot 1971). Cercariae, the free larvae, multiply to high levels by asexual reproduction in the benthic mollusc *Vermetus triqueter*. Once they emerge from the snails, the cercariae encyst on various substrates, in particular algae, and lose their tails to form metacercariae. The gulls become infected by ingesting metacercariae, and the adult worms live in the intestine of the bird. This parasite is apparently cosmopolitan.

The *A. massiliensis*/yellow-legged gull system has several unique features:

- The metacercariae are mainly found on algae (*Cystoseira amentacea* Bory, var. *stricta* Montagne), especially at the extremities of the ramifications, or

fronds. Some metacercariae are also found on the body of various small crustaceans living at the top of the algae (Figure 1). The algae live on rocky substrates, and the fronds are close to the surface of water. The cercariae, after emerging from the molluscs and coming in contact with an alga, actively creep upward and finally encyst near the tops of the algal branches.

- The snails shed cercariae in an unusual seasonal pattern (Figure 2a); whereas the cercariae of most trematode species show peak emergence during the warm season, peak emission of *A. massiliensis* cercariae takes place in autumn and winter.

- Breeding female yellow-legged gulls have significantly higher prevalence and intensity of infection with this parasite than nonbreeding females and males (Figure 2b). Of 26 males examined, 3 harbored a total of 4 parasites, and of 20 nonbreeding females examined, 2 harbored a total of 5 parasites; by contrast, of 10 breeding females examined, 9 harbored a total of 72 parasites.

- Nestling yellow-legged gulls, bred from the egg in the laboratory, die within a week when fed exclusively fresh fish. Nestlings fed exclusively fresh fish are aggressive, vocalize constantly, and exhibit tetanus of nuchal (neck) muscles. These symptoms, similar to those of beri-beri, are indicators of a disease caused by a vitamin B_1 deficiency (B_1 avitaminosis). We found that feeding the nestlings any polyvitaminic formula from a drugstore (e.g., Roche Hydro-sol Polyvitaminé) not only allows them to complete their growth, but also saves individuals that are near death. *Cystoseira*, which is rich in vitamin B_1 , also effectively supplemented a fish diet and promoted survival of young gulls.

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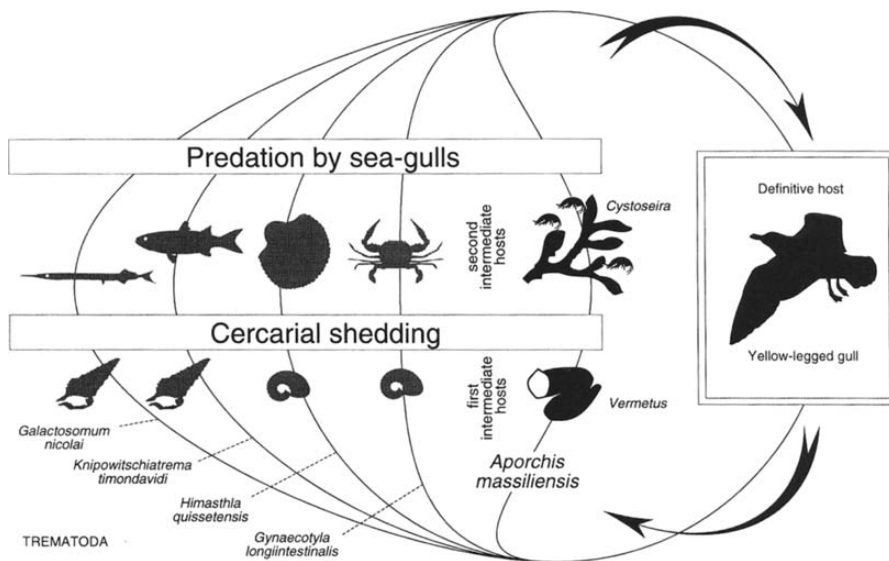


Figure 1. Mode of transmission of some species of trematodes to the yellow-legged gull (adapted from Combes 1995).

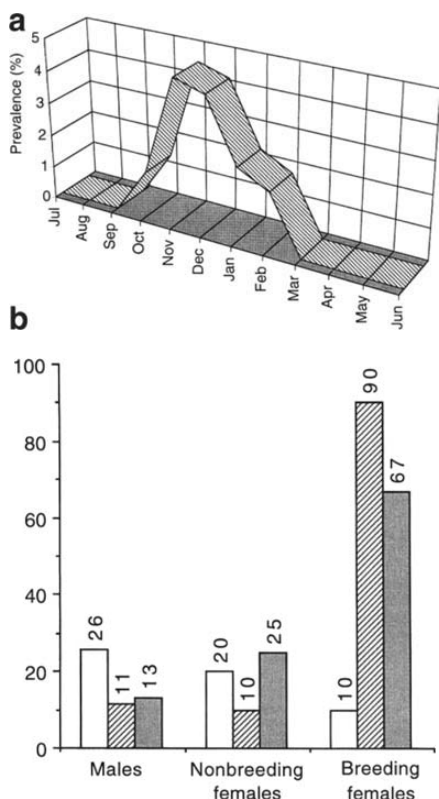


Figure 2. (a) Seasonal variation of the prevalence of snails emitting cercariae of *Aporchis massiliensis*. Emergence peaks in autumn and winter, rather than in spring and summer, which is more typical of most trematodes. (adapted from Prévot 1971). (b) Distribution of the trematode *Aporchis massiliensis* in yellow-legged gulls. White bars indicate number of individuals examined; striped bars indicate percentage of individuals that were infected; shaded bars indicate mean intensity of infection (i.e., mean number of parasites per individual bird). Breeding females are more heavily infected than nonbreeding females or males.

The “vitamin route” to parasitization

These observations can collectively be explained by the following hypothesis. Breeding females give nestlings the necessary supplement of vitamin B₁, which they obtain by eating algae, and the parasite has adapted its behavior such that during the winter, the metacercariae use algae as an intermediate host.

Although it has not been reported that gulls regularly pick off the tips of the algae and feed them to their young, the fact that adult gulls are parasitized by *A. massiliensis* suggests that the tips of the algae make up at least part of their diet. Moreover, two ornithologists who specialize in Mediterranean sea gulls consider the ingestion of the algae consistent with the general biology and ecology of these birds.¹ They note that *Cystoseira* grows frequently just beneath the cliffs where the sea gulls build their nests, and that breeding females collect food for their young only a short distance from the nests. Males and non-

¹J. C. Thibault and P. Beau brun, 1996, personal communication. Parc Naturel Régional du Corse, BP 417, and Ecole Pratique des Haute Etudes, Montpellier, France.

breeding females forage farther away, thus explaining their lower incidence of infection (Figure 1). Fish, which are also a significant part of the diet of young yellow-legged gulls, contain antithiamine factors, including a thiaminase (Abe et al. 1987) that could destroy much of the vitamin B₁ in algae that is fed to the gulls at the same time. However, there is so much vitamin B₁ in the algae that the effects of the fish thiaminase are most likely negligible.

From these observations, we conclude that *A. massiliensis* takes advantage of the feeding strategy of its host: It encysts on the extremities of the *Cystoseira* fronds, thereby increasing considerably the probability that it will be consumed by its definitive host. Also, *A. massiliensis* colonizes the algae during winter—making them highly infective during the breeding season of gulls (approximately April). If our hypothesis is correct, then the higher prevalence and intensity of infection with *A. massiliensis* in breeding females is easily explained because they contribute to brood care more than males.

The parasite *A. massiliensis* thus employs a unique set of adaptations that ensures the infection of adult gulls, one dependent on nestling gulls' need for vitamin B₁. These adaptations confer an enormous selective advantage to the parasite because its survival depends strictly on the host encountering infective stages (Combes 1995). The adaptations also explain why individual parasites are distributed in an aggregative fashion within the host population: different behaviors (males versus females, breeding versus nonbreeding, nestlings versus adults) expose the individual definitive hosts to different levels of contamination. If *A. massiliensis* reduces the fitness of its bird hosts—which may well be the case, both because the intensities of infection can be high and because a different kind of parasitic helminth has been shown to disrupt energy flow in birds (Connors and Nickols 1991)—then foraging on algae to provide the nestlings with vitamins may place a significant cost on breeding females.

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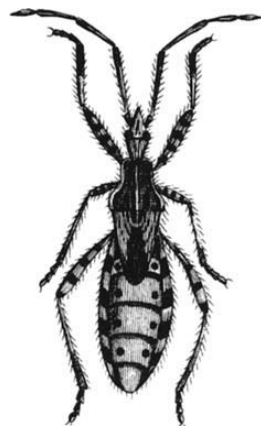
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