# Observations and Ideas

# Parasite transmission via a vitamin supplement

arasites 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 preved 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

#### by Pierre Bartoli, Michèle Bourgeay-Causse, and Claude Combes

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  $(B_{\rm e})$  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, multipy 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.

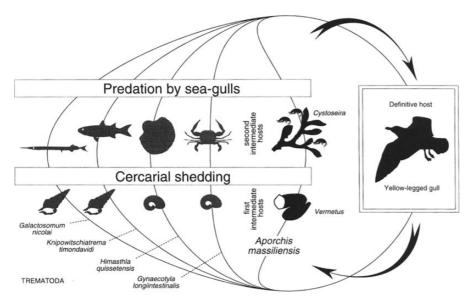
The A. massiliensis/yellowlegged gull system has several unique features:

• 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<sub>1</sub> deficiency (B<sub>1</sub> avitaminosis). We found that feeding the nestlings any polyvitaminic formula from a drugstore (e.g., Roche Hydrosol Polyvitaminé) not only allows them to complete their growth, but also saves individuals that are near death. Cystoseira, which is rich in vitamin B<sub>1</sub>, also effectively supplemented a fish diet and promoted survival of young gulls.



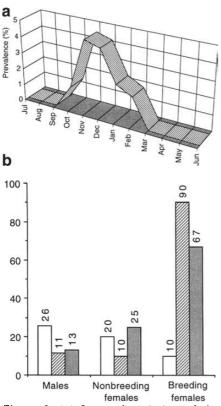


Figure 2. (a) Seasonal variation of the prevalence of snails emitting cercariae of Aporchis massiliensis. Emergence peaks in autumn and winter, rather than in spring and summer, which is more typical of most trematodes. (adapted from Prévot 1971). (b) Distribution of the trematode Aporchis massiliensis 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.

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

# The "vitamin route" to parasitization

These observations can collectively be explained by the following hypothesis. Breeding females give nestlings the necessary supplement of vitamin  $B_1$ , 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.' 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 nonbreeding 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 yellowlegged gulls, contain antithiamine factors, including a thiaminase (Abe et al. 1987) that could destroy much of the vitamin B<sub>1</sub> in algae that is fed to the gulls at the same time. However, there is so much vitamin B<sub>1</sub> 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 wintermaking 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 adults gulls, one dependent on nestling gulls' need for vitamin B<sub>1</sub>. 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 hostswhich 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.

<sup>&</sup>lt;sup>1</sup>J. C. Thibault and P. Beaubrun, 1996, personal communication. Parc Naturel Régionel du Corse, BP 417, and Ecole Pratique des Haute Etudes, Montpellier, France.

#### **References** cited

- Abe M, Ito SI, Kimono M, Hache R, Nishimune T. 1987. Molecular studies on thiaminase I. Biochimica Biophysica Acta 909: 213-221.
- Bethel WM, Holmes JC. 1977. Increased vulnerability of amphipods to predation owing to altered behavior induced by larval acanthocephalans. Canadian Journal of Zoology 55: 110-115.
- Brown JH, Mehlman DW, Stevens GC. 1995. Spatial variation in abundance. Ecology 76: 2028-2043.
- Combes C. 1991. Ethological aspects of parasite transmission. American Naturalist 138: 866–880.
- \_\_\_\_\_.1995. Interactions durables. Ecologie et evolution du parasitisme. Paris (France): Masson.
- Connors VA, Nickol BB. 1991. Effects of *Plagiorhynchus cylindraceus* (Acanthocephala) on the energy metabolism of adult starlings, *Sturnus vulgaris*. Parasitology 103: 395–402.
- Dobson A. 1988. The population biology of parasite-induced changes in host behavior. Quarterly Review of Biology 63: 139– 165.
- Lozano GA. 1991. Optimal foraging theory: a possible role for parasites. Oikos 60: 391–395.
- Moore J. 1984. Altered behavioral responses in intermediate hosts: an acanthocephalan parasite strategy. American Naturalist 123: 572–577.
- \_\_\_\_, 1995. The behavior of parasitized animals. BioScience 45: 89–96.
- Moore J, Gotelli NJ. 1990. A phylogenetic perspective on the evolution of altered host behaviors: a critical look at the manipulation hypothesis. Pages 193-233 in Barnard CJ, Behnke JM, eds. Parasitism and host behavior. London (UK): Taylor & Francis.
- Prévot G. 1971. Cycle évolutif d'Aporchis massiliensis Timon-David, 1955, Digenea, Echinostomatidae, parasite du goéland Larus argentatus michaellis Naumann. Bulletin de la Societe Zoologique de France 96: 197–208.

Pierre Bartoli is a professor at the Unité Nixte de Recherches du Centre National de la Recherche Scientifique Dimar, Centre d'Océanologie de Marseille, Campus Universitaire de Luminy, Case 901, 13288 Marseille Cedex 9, France. Michèle Bourgeay-Causse is a biologist at the Novacité Omega, 8 rue Hermann Frenkel, 69007 Lyon, France. Claude Combes is a professor at the Centre de Biologie et Ecologie Tropicale, Université de Perpignan, 66860 Perpignan Cedex, France. © 1997 American Institute of Biological Sciences.

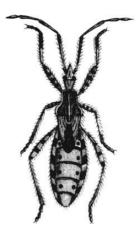


### LAB DIRECTOR

USDA, Agricultural Research Service - Tropical Fruit, Vegetable, and Ornamental Crop Research Laboratory, in Hilo, HI, is seeking a Supervisory Research Entomologist, GS-0414-4/15, to serve as Laboratory Director and provide administrative and technical leadership for all research activities at the Laboratory with facilities in Hilo, Hawaii; Honolulu and Alea. Oahu and Kapaa, Kaui. Research activities of the Laboratory include basic and applied research on: a) the biology and ecology of tephritid fruit flies and other pests to develop biologically-based and environmentallyacceptable suppression, eradication, and commodity quarantine treatment technologies; b) plant molecular physiology to improve and strengthen crop production in tropical regions; and c) to assist in developing appropriate production systems.

Salary range \$60,270 - \$92,161 per annum (plus 15% COLA). The application deadline is 4/21/97. Additional information on job requirements and application procedures can be obtained from the ARS homepage at WWW.ARS.USDA.GOV, or call Barbara Ucda at (808) 959-4301 between 8:00 a.m. and 12 noon, Hawaiian time, Monday through Friday.

ARS is an equal opportunity employer; women and minorities are encouraged to apply, U. S. vitizenship is required.



## plant growth chambers

light

temperature relative humidity co<sub>2</sub> reach-in cabinets walk-in rooms



Environmental Growth Chambers



510 East Washington Street Chagrin Falls, Ohio 44022-4448

> 800.321.6854 216.247.5100 fax 216.247.8710 sales@egc.com

serving your precise controlled environment needs for over forty years with the world's largest selection of options, styles and sizes