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SHORT COMMUNICATION

# Probable mutualistic association between staphylinid beetles *(Amblyopinus)* and their rodent hosts

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The nature of the relationship between amblyopinine staphylinid beetles and the mammals upon which they are found has been an enigma since the group was first described in 1875 (Solsky 1875). The Amblyopinini include some forty species placed in five genera, and have been found almost exclusively in the fur of small mammals in the Neotropics and Australia (Seevers 1955). This habit differs significantly from that of other members of the large and diverse family Staphylinidae, most of which are free-living predators. As a result of this, and reports of epidermal damage to the host, amblyopinines have been accepted to be obligate blood-feeding ectoparasites (Seevers 1955, Marshall 1981, Kim & Adler 1985). However, many reported behavioural facets appear to be inconsistent with this conclusion. For example, it has been reported that hosts ignore both the presence and movements of these beetles through their fur and across highly sensitive areas such as the eyes and vibrissae (P. Hershkovitz, quoted in Seevers 1955). This suggests that the interaction between amblyopinines and their hosts cannot be simply interpreted as adversarial.

We investigated the ecology and host-beetle interactions among populations of highland rodents in Costa Rica during March-May 1986. Some aspects of these interactions were reported in Ashe & Timm (in press). These results are outlined here and additional information is provided which allows us to pro-

pose a preliminary hypothesis about the nature of the rodent-amblyopinine interaction.

Detailed observations were made of host-beetle interactions by observing individuals of *Amblyopinus tiptoni* Barrera and their host, *Peromyscus nudipes*, in captivity over a two week period. Number, position, attachment and behaviour of the beetles, as well as activities of hosts were recorded periodically during the day and night. The response of beetles to other ectoparasites was tested by placing them together in petri dishes with ectoparasites taken from naturally shared hosts.

A total of 326 wild caught rodents were examined for amblyopinines and associated epidermal damage. Seven species of rodents were collected; *Amblyopinus emarginatus* Seevers was found only on *Oryzomys albigularis*, and *A. tiptoni* primarily on *Peromyscus nudipes*, with a few specimens on *Reithrodontomys creper*. Detailed observations were taken on position, attachment and activities of 254 amblyopinines from 69 hosts. An average of 3.7 beetles were found per infested host, with a range of 1 to 13. Beetles were consistently observed grasping clumps of fur with their mandibles. In no instance were the mandibles found to be embedded in the skin of the host. Additionally, close examination of both infested and uninfested hosts revealed no epidermal damage that could be attributed to beetle activity.

Since amblyopinines previously had been found only in the fur of their hosts, it was inferred that they spend most of their time either feeding on the host or attached to it. We tested this hypothesis by observing patterns of activity in two captive *Peromyscus nudipes* and 11 *Amblyopinus tiptoni*. Numbers of beetles on two hosts at each observation period over 12 days are presented in Figure 1. A striking circadian rhythm is indicated. Beetles were attached to hosts only during night-time hours. During daylight hours they were observed to be active within the nesting material (see also Ashe & Timm in press).

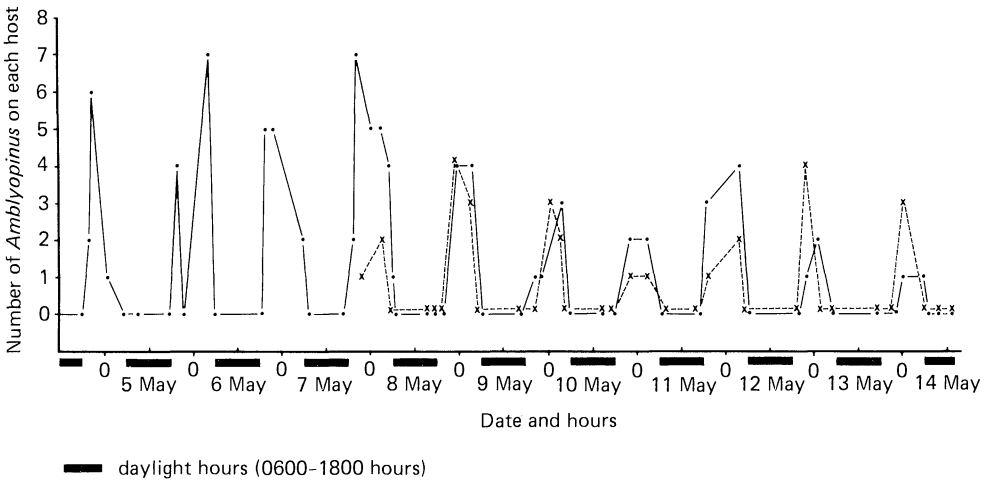


Figure 1. Circadian pattern in number of *Amblyopinus tiptoni* on two captive *Peromyscus nudipes* in each 24 hour period over 12 days (beetles added to second host on 7 May).

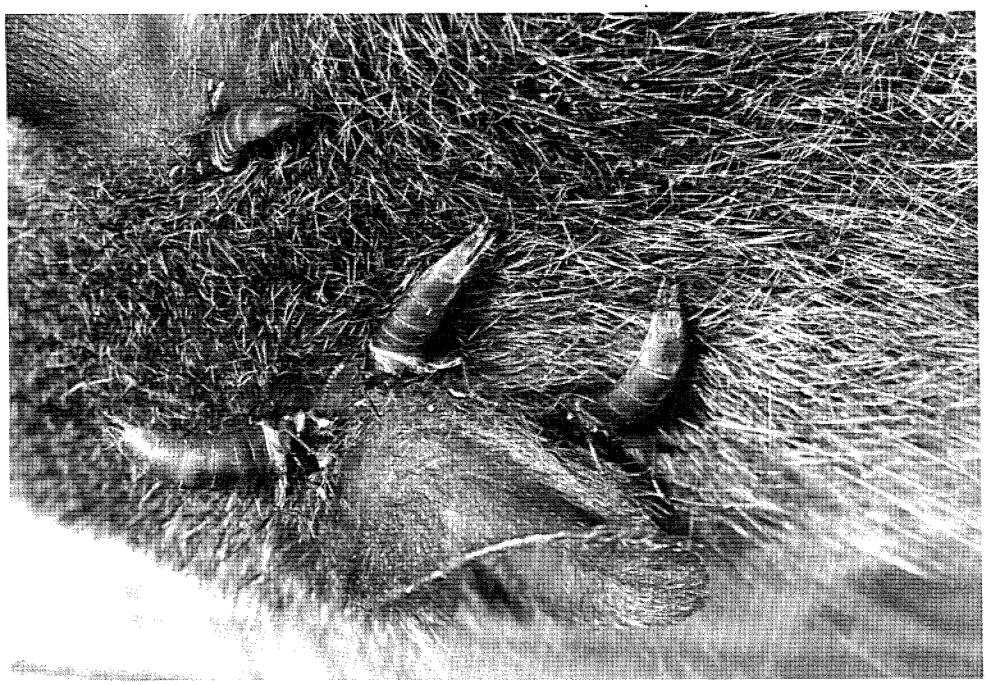

Figure 2. Four *Amblyopinus emarginatus* in a typical position behind the ears of an *Oryzomys albigularis*. Photograph by Barbara Clauson.

Our observations of beetles on both captive and field caught hosts concurred with earlier observations that hosts ignore beetle activity. Movements of the beetles through the fur, around very sensitive areas such as the eyes and vibrissae, and prolonged attachment near the base of the ears (Figure 2), consistently elicited no response from the host. Additionally, the beetles are large, up to 10.0 mm in length, and observations suggest that their movements in the fur should be a considerable disturbance to the host. Still, the possibility that activities of the beetles are unapparent to the host must be considered. To test the hypothesis that rodents are not aware of the presence of the beetles, we placed several *Amblyopinus tiptoni* into the fur of captive *Scotinomys teguina*. This mouse is similar in body size and fur type to normal hosts of this amblyopinine, but beetles are not naturally found on *Scotinomys*. *Scotinomys* immediately responded to these beetles as a source of irritation, and actively attempted to remove them by vigorous grooming. If the rodent was able to dislodge the beetle, it immediately killed it; if not, it continued attempting to dislodge the beetle until we removed it. Similar behaviour was illicited in trials with three different individuals of *S. teguina*.

Throughout all of our observations, we found no evidence that amblyopinines feed on blood, epidermal derivatives, or body secretions of their hosts. Nor was there an indication of epidermal damage to hosts attributable to feeding activities of amblyopinines, even among hosts which had heavy infestations of 10 to 13 beetles. Additionally, when on the host, amblyopinines were

almost always attached and stationary, and were not observed in any behaviour which could be interpreted as feeding or related activites.

Since we were unable to confirm that amblyopinines derived any nutrients directly from their hosts, we tested their response to associated ectoparasites. We observed amblyopinines to readily feed on fleas and mites in typical staphylinid predatory manner, both in the nests of captive hosts and in petri dishes.

We concluded that members of *Amblyopinus* are not ectoparasites, but rather specialized predators upon ectoparasites of their hosts. Earlier literature statements that these beetles are parasitic are erroneous and appear to have been based upon faulty assumptions and observations. Barrera's report (1966) of a positive benzidine test for occult blood in gut contents of some *A. tiptoni* is more correctly interpreted as secondary ingestion of blood from guts of the beetles' prey (Ashe & Timm in press).

The interpretation most consistent with observed behaviours of both hosts and these amblyopinines is that both parties benefit. Under this interpretation the interaction is one of mutualism. Clearly the beetles benefit by maintaining contact with their host and its parasites which form their prey. For hosts to benefit, the beetles must have a significant impact upon the total ectoparasite load. This level of impact seems likely. Average number of beetles per infested host is 3.7, and each of these probably requires several ectoparasites per day as food. Indifference of hosts to activites of these beetles must be interpreted as an active response to presence of beetles, and is strong circumstantial evidence that hosts recognize presence of amblyopinines as a benefit.

Structural and behavioural characteristics of amblyopinines appear to be associated with efficient attachment to and transport by the host, rather than with parasitism. Known rodent hosts are nocturnally active, and amblyopinine behaviour reflects this host activity pattern. Attachment of beetles during night-time hours assures that they will be transported among currently used nest sites, an important factor to animals which feed primarily in the nest. A necessary prediction of these results is that the nesting behaviour of hosts is an important factor in determining evolution of this mutualistic interaction, and suggests that hosts use more than one nest in a way that is unpredictable to beetles. Under these circumstances, use of hosts as transport vehicles among nesting sites would be a considerable advantage. If true, then the selective force controlling evolution of a circadian behaviour pattern by amblyopinines would be the necessity for maintaining contact with the host during its nocturnally active period.

Coevolution resulting in mutualistic interactions between vertebrates and macroscopic invertebrates are rare, and, to our knowledge, all prior examples were limited to aquatic ecosystems.

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# Book review

SIBLY, R. M. & CALOW, P. 1986. *Physiological ecology of animals: an evolutionary approach.* Blackwell Scientific Publications, Oxford. 179 pages. ISBN 0-632-01494-6 (hardback), 0-632-01495-4 (paperback). Price £26.00 (hardback), £11.95 (paperback).

This book is to physiology what *Behavioural ecology: an evolutionary approach* (Krebs & Davies 1978) has been to ethology. It dissects and explores some constraints on animal function in the wild and attempts to predict how animals might respond under changing circumstances. The two books share this rationale, as well as many of their broad assumptions and techniques. They also have the same subtitle, signalling a common interest in