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Predation by and activity patterns of 'parasitic' beetles of the genus *Amblyopinus* (Coleoptera: Staphylinidae)

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(With 2 plates and 1 figure in the text)

This study explores the relationship between staphylinid beetles of the genus *Amblyopinus* and their small mammal hosts. Previous studies had concluded that these beetles were parasitic and fed directly on blood, skin exudates, or other epidermal derivatives of their hosts. We examined the mode of attachment, behaviour, and feeding activities of 254 *Amblyopinus* (*A. tiptoni* and *A. emarginatus*) on 69 hosts which were captured in Sherman live traps. In addition, similar information and diurnal activity patterns were monitored for 11 beetles kept on two hosts (*Peromyscus nudipes*) over a period of 14 days. Beetles were found to be attached to the host only by grasping clumps of fur in their mandibles. No sign of damage to the skin of the host could be found. Feeding by the beetles on parasitic arthropods was observed and concluded to be the primary feeding habit. Beetles showed a strong circadian activity pattern, in which they are attached to the host during night-time hours and actively hunt in the nest during daylight hours. Attachment to the host is hypothesized to be primarily a vehicle for tracking prey of the beetles within the variety of nests used by any individual host. We conclude that these beetles are not parasitic but, instead, highly specialized predators on ectoparasitic arthropods, with specialized behavioural and morphological adaptations for their unique life style.

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Introduction

Perhaps the most interesting and enigmatic of all host-parasite relationships are those of staphylinid beetles of the tribe Amblyopinini, adults of which are found on Neotropical and Australian mammals, primarily rodents and South American marsupials. Although numerous groups of arthropods have independently evolved an ectoparasitic relationship with vertebrate hosts, this apparently has happened only once in the most diverse family of insects, the coleopteran family Staphylinidae. The vast majority of over 50,000 described species of staphylinids are

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either known or believed to be predators. In contrast, five genera, *Amblyopinus*, *Amblyopinodes*, *Edrabius*, *Megamblyopinus*, and *Myotyphlus*, which constitute the tribe Amblyopinini, appear to have quite different habits. Adults of these beetles are almost always found in the fur of small mammals, though on one occasion they were taken from mammal nests (Seevers, 1955). In addition, amblyopinines have been reported to be attached to the host's skin, where they were believed to cause trauma, by their mandibles (Solsky, 1875), and to be associated with wounds on the host (Vaughan, 1982). Therefore, it generally has been assumed that all amblyopinines are obligate, blood-sucking ectoparasites. Indeed, Seevers (1955:212), in the latest comprehensive revision of the tribe, categorically states: 'There is no doubt that the Amblyopinini are obligatory ectoparasites.' None the less, there are few actual data on the biology of these beetles.

This lack of information about the biology of amblyopinines is especially disturbing because, in recent years, a number of parasitology texts and review papers have fully accepted the Amblyopinini as obligate, blood-feeding ectoparasites (i.e. Askew, 1971; Marshall, 1981; Kim & Adler, 1985). A typical quote from a review monograph on parasitic insects states 'The beetles embed their mandibles deeply into the hosts' skin, and they are removed only with difficulty. They tend to congregate either behind the ears or about the base of the tail. The host's skin swells up around the point of attachment. These Staphylinidae, like *Platypsyllus*, live in all their life history stages upon the host' (Askew, 1971:92). Kim & Adler (1985:166) state 'The adults and larvae occur on the host and are considered obligate parasites. They embed their mandibles deep in the skin, causing irritation. Presumably they feed on skin and body fluids.'

The purpose of this paper is to document the relationship between two species of amblyopinine beetles, *Amblyopinus emarginatus* and *A. tiptoni*, and their mammalian hosts, provide detailed observations on feeding and circadian behaviour of these beetles, and present the hypothesis that the members of *Amblyopinus* and their hosts form a highly evolved and specialized co-evolutionary system which is not a parasite-host relationship.

Methods

During the period of 27 April to 13 May, an extensive live-trapping study of rodents and their associated ectoparasite fauna was carried out at 3 elevational ranges (1,320–1,380 m, 1,520–1,580 m and 1,780–1,820 m) around the community of Monteverde in Costa Rica [Prov. Puntarenas, 10°18′N, 84°48′W]. Amblyopinines were found only at the 2 higher sites. Five species of rodents, *Heteromys desmarestianus* (122), *Oryzomys albigularis* (7), *Peromyscus nudipes* (121), *Reithrodontomys creper* (1) and *Scotinomys teguina* (20), which could serve as potential hosts, were captured at these sites, comprising a total of 271 individual animals. Among these potential hosts, 33 individuals were infested with a total of 117 amblyopinines. In addition, 2 nights of trapping at 2,440–2,670 m near Cerro de la Muertè [4 km S. and 2 km E. of Ojo de Agua, Prov. San José, 9°34′45″N, 83°48′06″W], yielded 44 potential hosts of 5 species; *Heteromys desmarestianus* (1), *Oryzomys albigularis* (1), *Peromyscus nudipes* (33), *Reithrodontomys* sp. (1) and *Scotinomys xerampelinus* (8). Of these, 28 had a total of 114 amblyopinines attached to them. In a separate survey of mammal parasites conducted in the 'Zona Protectora' (Prov. Heredia; Parque Nacional Braulio Carrillo) at 5 elevational sites (300 m, 700 m, 1,000 m, 1,500 m and 2,050 m), amblyopinines were only collected from the 2,050 m site. At this elevation, 18 potential hosts of 4 species, *Oryzomys albigularis* (3), *Peromyscus mexicanus* (6), *Reithrodontomys* (7) and *Scotinomys teguina* (2) were captured, of which 8 yielded 23 beetles.

All mammals (except for some collected in the 'Zona Protectora') were captured unharmed in Sherman live-traps and examined for beetles as well as other parasites. Mode of attachment and position of beetles were noted in each instance. Additionally, infected hosts were carefully examined for any sign of feeding or other cuticular damage that could be associated with activities of the beetles. Voucher specimens from each trapping site were prepared and are deposited in the collections of the Field Museum of Natural History, Chicago or Universidad Nacional de Costa Rica, Heredia.

More detailed observations were made of the behaviour of the beetles by keeping 11 *Amblyopinus tiptoni* and 2 *Peromyscus nudipes* in aquaria. Both hosts were known to have previously harboured *A. tiptoni* under natural conditions. Observations on the number, position, attachment and behaviour of beetles on each host were made periodically during the day and night over a 2-week period (1–14 May, 1986). Two or more observations were taken during each 12-hour period, although the exact timing of the observations varied. In addition, position and attachment of beetles on the hosts were photographed using high resolution macrophotography techniques for later analysis.

Hosts were housed in 5-gallon clear glass aquaria, provided with cotton and paper towels for bedding, and supplied with food and water *ad libitum*. Beetles were added to the first *P. nudipes* beginning on 1 May. Additional beetles were added to this host as they became available from field captures until 5 May, when there were a total of 7 beetles present on this host. On 6 May, 4 additional beetles were added to a second *P. nudipes*. Observations were then taken on the activities of the beetles on both hosts through 14 May.

Beetles were associated with the captive host by placing each medially on the back of the host. In most instances, beetles immediately assumed the typical attachment posture. In a few instances, the beetles crawled from the host into the nesting material.

Beetles were easily observed on the host or in the nesting material through the clear glass bottom, sides, and open top of the aquarium. On 2 occasions during daylight hours, the nests were disturbed by searching for and observing beetle activity.

Other beetles were placed with parasites (with fleas or mites of the genus *Gigantolaelaps*) from the appropriate host in petri dishes, and their response to these observed over several days. Periodically, fleas were added to each host and response of the beetles monitored.

Results and observations

Two species of *Amblyopinus* were collected from the three study areas, *A. tiptoni* Barrera and *A. emarginatus* Seevers. *Amblyopinus tiptoni* was found primarily on *Peromyscus mexicanus* and *P. nudipes*, with a few specimens on *Reithrodontomys* sp. *Amblyopinus emarginatus* (Plate I) was found exclusively on *Oryzomys albigularis*. Behaviour of both species of *Amblyopinus* appeared to be similar.

Mode of attachment of the beetles

Because earlier workers have consistently stated that the mandibles of amblyopinines were embedded in the skin of their hosts, we paid particular attention to the precise mode of attachment of the beetles. Our detailed observations on 254 individuals of two species of *Amblyopinus* demonstrate that beetles are consistently, and only, attached to the host by grasping clumps of fur in their mandibles. Clumps of fur are typically grasped at the base, very near the skin. Superficial examination could easily lead to the mistaken impression that the mandibles are actually implanted into the skin. However, we failed to find even a single instance of mandibles embedded or attached to the skin. Primary attachment appeared to be exclusively by the mandibles; legs do not grasp the fur and appear to be used primarily for stabilizing the beetle in position. Mandibles grasp the hair tightly, often making the beetle very difficult to remove, and occasionally the fur may be torn from the skin when the beetles are forcibly removed.

In no instance, among the numerous hosts examined, was any damage or irritation to the

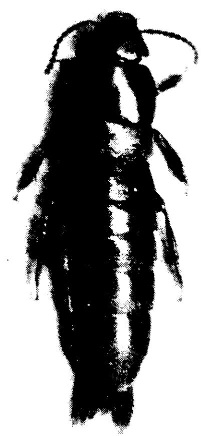

PLATE I. *Amblyopinus emarginatus* Seevers, habitus. Length of beetle = 10·0 mm. (Photograph courtesy of Barbara L. Clauson).

skin found that could be attributed to amblyopinine feeding activities or attachment. Since amblyopinines are relatively large beetles, with well developed and heavily sclerotized mandibles, it seems likely that any bites to the skin of the host would be readily visible upon close examination. In addition, individuals of *Amblyopinus* were not associated with cuticular wounds found on a few hosts and did not congregate around a wound on one captive host.

More long-term observations of captive hosts and members of both *A. emarginatus* and *A. tiptoni* confirmed that attachment directly to clumps of fur is typical and invariant. During the entire period of observation of these captive beetles, no behaviour was seen that appeared to be biting of the skin of the host.

Observations of feeding

In order to examine the relationship between amblyopinines and associated ectoparasitic arthropods, specimens of *Amblyopinus tiptoni* were confined in a petri dish with fleas taken from their host, *Peromyscus nudipes*. On 11 May, an adult female in a container with six fleas was observed to lunge at a flea which landed within 1 mm of her head. She captured the flea in her mandibles, carried it about 1 cm and began to manipulate it with her mouthparts. The beetle consumed the body fluids of the flea and discarded the remaining crushed cuticle after about 2·5

PLATE II. Four specimens of *Amblyopinus emarginatus* Seevers in the typical attachment posture and position behind the ears of an adult *Oryzomys albigularis*. (Photograph courtesy of Barbara L. Clauson).

min. This feeding behaviour did not appear to differ from that of other staphylinine staphylinids which are known to be predaceous. By 2 May, four of the five remaining fleas had been captured and eaten. In addition, on 11 May, four specimens of *Amblyopinus emarginatus* collected from *Oryzomys albigularis* were placed together in a petri dish with 15 mites of the genus *Gigantolaelaps* taken from the same individual host from which the beetles were collected. One beetle was clearly observed to capture and consume a mite later that day. Within three days, most of the mites had been eaten as evidenced by the presence of discarded mite carapaces.

Natural feeding behaviour

Data presented below clearly show that members of *Amblyopinus tiptoni* exhibit a marked diurnal activity cycle. Beetles are only on the host during the night-time hours. During daytime hours, beetles are active in the nesting material. When on the host, beetles were always observed to be attached by their mandibles in a characteristic posture (Plate II). Except when crawling on to the host or repositioning themselves to another attachment point, the beetles were not observed to move about on the host or engage in any activity which could be interpreted as hunting for food. On numerous occasions, beetles were observed to ignore potential prey (fleas) which came very near their attachment site. In contrast, beetles were very active in the nesting material and routinely observed to engage in activity which appeared to be typical staphylinid hunting behaviour. In addition, numerous remains of fleas which were similar to those known to have been consumed by amblyopinines were found in the nest.

Activity patterns

Captive beetles were observed on the host only during the time period of 18:30 to 06:30 h. From 06:30 to 18:30 h beetles were observed only within the nesting material. A plot of total number of beetles on the hosts over an eight-day period (Fig. 1) is striking evidence for a circadian cycle in the behaviour of these beetles. The invariance of this pattern across the two weeks of observations is particularly notable. These observations are consistent with the hypothesis that individuals of *Amblyopinus* are normally only present on their hosts during the hours of darkness.

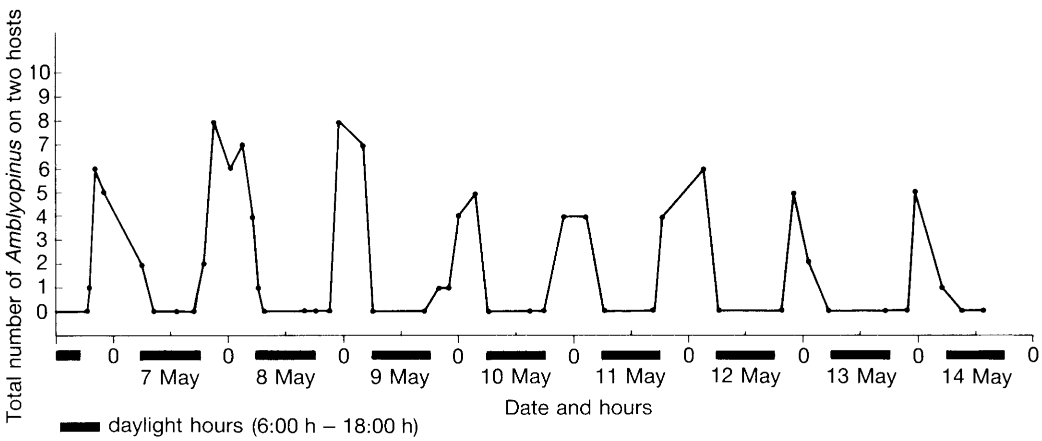

FIG. 1. Total number of *Amblyopinus tiptoni* Barrera on two captive *Peromyscus nudipes* at each observation within 24-hour periods for a total of eight days.

Though presence of beetles on the host during hours of darkness is invariant, this does not appear to be directly correlated to absence of light. Presence of artificial light in the room after sunset appeared to have some influence on beetle activity, but was not sufficient to prevent the beetles from moving on to the host. On at least one instance (7 May), presence of artificial light in the room since sunset did not prevent two beetles from crawling on to the host by 19:15 h. In contrast, in at least two instances, 10 and 14 May, the presence of artificial light in the room seems to have delayed beetle attachment to the host. In addition, on 5 May, beetles were observed to have left a mouse after lights were turned on in the room. Later, after several hours of darkness, the beetles were re-attached.

We also observed similar activity patterns of *A. emarginatus* on both wild and captive *Oryzomys albigularis*. These observations were fully consistent with the circadian cycle indicated by data for *A. tiptoni* reported above.

Collaborating the experimental data are observations from field work. All amblyopinines were found on hosts captured at night. Though the majority of potential hosts were captured at night, a significant number also were taken during daylight hours.

Discussion

Our detailed observations on large numbers of *Amblyopinus tiptoni* and *A. emarginatus* and their associated hosts failed to confirm many of the earlier reports of amblyopinine behaviour found in the literature. In particular, we found no support for Jelski's observations that amblyopinines were 'firmly attached to the skin of living mice' resulting in eroded hair and swollen skin at the point of attachment (Seevers, 1955:212). Additionally, we found no larvae on the hosts in contrast to the report by Fauvel (1900) that Philippi had observed adults and larvae of *Edrabius philippianus* around the anus of *Ctenomys*. However, Seevers (1955) noted that Fauvel did not actually receive larval specimens of this species from Philippi. It is interesting that the numerous subsequent reports of amblyopinines have not mentioned larvae, and presumably they were not present on the hosts. Equally unsupported is Zikán's (1939) report that beetles embed their mandibles into the skin of the host and probably feed on body fluids. Seevers (1955), however, noted that Zikán provided no direct evidence for this and had based most of his conclusions on presumed adaptations of the mouthparts for parasitism. Seevers further noted that the mouthparts of amblyopinines are not as unique as was implied by Zikán, and, in fact, are not greatly different from those of related predaceous staphylinids.

In contrast to these reports, Hershkovitz, who was the first actually to observe amblyopinine behaviour on their hosts in captivity, was not able to determine the substance of the host consumed by the beetles. In addition, he could find no marks on the host attributable to beetle activity (quoted by Seevers, 1955).

The strongest support for parasitism by amblyopinines was provided by Barrera (1966:287) who found a positive benzidine test for occult blood in the gut contents of 'some specimens of the large series of *Amblyopinus tiptoni*'. However, he did not find it commonly enough to suggest that amblyopinines feed primarily on blood. Instead, he suggested that amblyopinines feed on skin exudates or other cuticular structures that do not contain haemoglobin. While our data failed to confirm the attachment of amblyopinines to the skin, we provide the context for understanding how these results may have been obtained by Barrera. If amblyopinines feed primarily on blood-sucking ectoparasites, it is inevitable that they will sometimes secondarily imbibe blood of their mammalian host from the guts of their prey. Thus, Barrera's positive test for occult blood need not be taken as evidence that amblyopinines feed directly on the blood of their host.

Our data are most consistent with the observations of Hershkovitz (quoted in Seevers, 1955) in that we found no evidence for the attachment of amblyopinines to the skin of the host. In contrast, we found beetles to be only attached by the mandibles to clumps of hair. Additionally, we could find no evidence that skin had been penetrated or otherwise irritated by the beetles. Nor could we find evidence that these amblyopinines feed on or near naturally occurring wounds. Instead, we clearly observed predation upon obligate, blood-feeding ectoparasites.

Our findings also provide an explanation for one of the most baffling aspects of amblyopinine biology which had been previously reported. Hershkovitz (in Seevers, 1955) observed, to his surprise, that hosts routinely ignored these large beetles during their movement through the fur, even when around such sensitive areas as the eyes. Our numerous observations of *A. emarginatus* and *A. tiptoni* completely concur with Hershkovitz's findings. The host takes no notice of the activities of the beetles, and even beetle activity around the very sensitive vibrissae does not elicit a reaction from the host!

These observations are difficult to understand if these amblyopinines regularly embed their large and well sclerotized mandibles into the flesh of their host. They are, however, easily understood if the host does not recognize the beetles as a source of irritation.

Clearly, the beetles exhibit a strong diurnal rhythm. Beetles are present on the host at night and active in the nest during the day. In the nest, beetles frequently were observed in what appeared to be an active hunting behaviour. On the host, beetles were observed only in the typical stationary, attachment posture, most often behind the ears or elsewhere on the head. While on the host they were never observed to be in any behavioural mode which could be interpreted as hunting.

This circumstantial evidence suggests that most, if not all, feeding activity takes place within the nest rather than on the host. The extreme morphological and behavioural adaptations exhibited by amblyopinines (Seevers, 1944, 1955) are similar to those observed in known ectoparasitic arthropods, including: extreme reduction of eyes, loss of wings, and other structural and behavioural modifications which appear to be associated with maintaining their position in the fur of the host. If feeding does not take place on the host, these structural and behavioural adaptations are enigmatic.

All available evidence is consistent with the hypothesis that the beetles use the host primarily as a vehicle for tracking their prey. Our studies, as well as those of others, have demonstrated that members of *Peromyscus* are almost exclusively nocturnal (Falls, 1968). Since beetles were observed on the host only at night, individual beetles appear to be directly tracking this behavioural pattern of the mice. Thus, under normal circumstances, the attachment behaviour of the beetles results in their being transported by the host during its period of normal activity. If the host uses more than one nest site, the nocturnal attachment behaviour of the beetle would result in their being transported to the nest actively used by the host. By maintaining direct contact with the host, the beetles concurrently maintain direct association with the parasites of the host which make up their potential food source. The hypothesis most consistent with these facts is that the beetles have evolved an activity pattern which tracks the host behaviour, thereby enabling them to maintain contact with their specialized food supply. This has resulted in structural adaptations which are convergent with those observed in true ectoparasitic arthropods.

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