The Mystery of the Gracious Hosts

Insect guests don't get under the skin of some accommodating rodents

by Robert M. Timm and James S. Ashe

Most of the 40,000 species in the rove beetle family are indeed rovers, being free-living predators. But 40 of those 40,000—known to scientists as amblyopinines—travel by clinging to the fur of small mammals. Most amblyopinines live in cool temperate forests and cloud forests throughout Central and South America. We have studied them and their associated hosts, native rats and mice, in Central America for three years and have found this mammal–insect relationship to be a most unusual one.

A European professional collector, C. Jelski, discovered adult beetles on Peruvian rice rats in 1875 and was the first to report on the amblyopinines. Jelski offered circumstantial evidence that the beetles were parasitic, stating that they were "frequently attached very firmly to the living mice—almost as tenaciously as ticks and lice." He also reported that the rodents' hair was damaged and the skin swollen at the base of the tail, where the beetles were ensconced. In 1900 the French entomologist Albert Fauvel published similar observations of amblyopinines found on tuco-tucos, endemic South American burrowing rodents. These early observations became the basis of a rich, but highly speculative, literature on the unusual habits of amblyopinines, which were labeled "obligate" ectoparasites, external parasites unable to live or reproduce if separated from their hosts. After an experiment in the 1960s revealed mammalian blood in the gut of one species, the view of these beetles as blood feeders was widely accepted. This conferred a unique status on amblyopinines: while some other beetles are parasitic, none is known or even suspected to feed on blood.

But many facets of the rodent–rove beetle relationship remained puzzling. Most inexplicable were observations made in Colombia in 1952 by Philip Hershkovitz, a mammalogist from the Field Museum of Natural History in Chicago, on the behavior of one amblyopinine species on captive rice rats. He noted that hosts took no notice of the beetles even when they ran across their eyes and whiskers—far from the usual reaction of a host to a blood-sucking parasite, especially one that is one-tenth of the host's own length. An amblyopinine two-fifths of an inch long would presumably be a nasty encumbrance for a rodent only four to five inches long. Interestingly, Hershkovitz was not able to find any skin damage caused by the beetles. His anecdotal observations suggested a more benign association of insect and rodent.

Furthermore, although amblyopinines share some physical traits with other insects that live in mammalian fur—they are wingless, for example—many of their attributes are inconsistent with a parasitic mode of life. Their mouthparts are not very different from those of the free-living rove beetles; their tarsi are not modified for grasping hair (as is often found in parasitic arthropods); and the body is not flattened to the degree normally seen in parasitic insects.

The more we read, the more we realized that the conclusion that amblyopinines are blood-feeding parasites was based on surprisingly little objective data. With this problem in mind, we began to study these insects intensively in the cool temperate and cloud forests of the Talamancan and Tilaran highlands of Costa Rica, where amblyopinines live on small and medium-sized rodents. Our basic approach was to livetrap the rodents, examine them for amblyopinines and any skin damage that could be attributed to beetles, then mark and release them.

By retrapping marked mice over several successive days, we were able to confirm host relationships and track changes

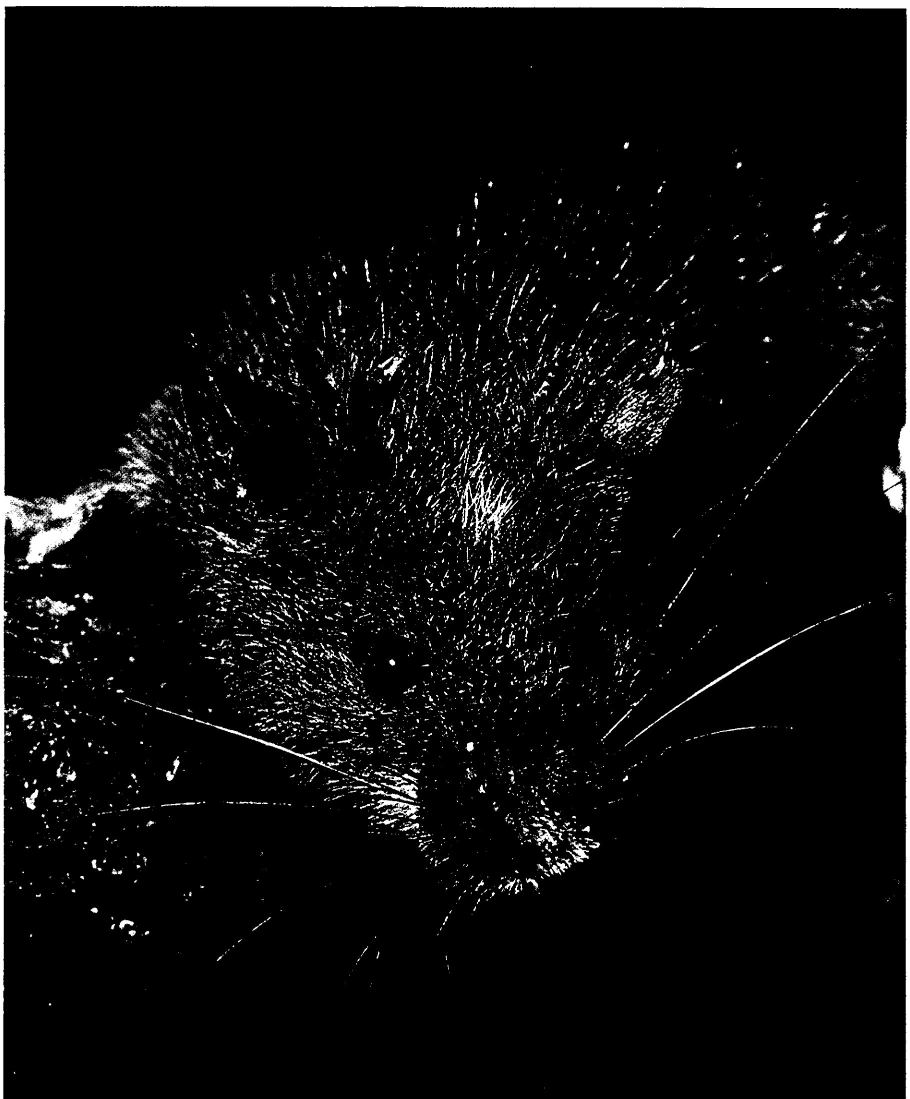
Photographs by Barbara L. Clauson

High-elevation forest, like that of the continental divide at Monteverde in Costa Rica, is prime habitat for amblyopinine rove beetles.

in beetle activity for individual mice. In supplemental laboratory experiments that year and the following year, we maintained the mice and beetles in captivity and observed them day and night. We also examined the reaction of amblyopinines to other parasites that they were likely to encounter, either on the host or in the host's nest.

During our first trip we examined 326 wild-caught rodents (many snared several days in succession) for beetles and other external parasites. In all, 254 beetles were found on 69 hosts. The number of beetles on each host varied from 1 to 13, with an average of 3.7. Amblyopinines in our study area were most commonly attached to the base of the host's ears, nape of its neck, or elsewhere on the head. The sight of ten or more of these large beetles on the head of a small mouse is unnerving. Yet, as Hershkovitz reported more than three decades earlier, the hosts seem unconcerned and even oblivious to the presence of the beetles.

Amblyopinine beetles, like most parasites, show a marked host specificity. Host specificity is the restriction of a parasite to a single species or closely related group of hosts. Although we captured ten species of rodents that could conceivably serve as hosts for the beetles, amblyopinines were found only on three species. One species of *Amblyopinus* was found almost exclusively on the naked-footed deer mouse (with the exception of a few individuals that were found on the Chiriquí harvest mouse). A second species of *Amblyopinus*, which we discovered for the first time in Costa Rica, was restricted to Tome's Neotropical rice rat. Captive beetles provided with a choice of host species consistently choose the host on which they are normally found in the wild. On the surface, this host specificity appears to confirm the beetles' parasitic habits.



With heads buried and abdomens raised, five amblyopinine beetles adhere to the fur of a young Tome's Neotropical rice rat.

We were, however, unable to substantiate many of the observations in the earliest literature. Given the amblyopinines' size and armored mandibles, we expected that their bites would be readily visible upon close examination of the host's skin. But we consistently found that rather than embedding their formidable jaws in the rodent's skin, the beetles used their mandibles to grasp clumps of hair. Because attachment is tight and very near the skin, and because hair is often torn out as the beetle is forcibly removed, casual observations could easily have led to the conclusion that the mandibles actually pierced the skin. We found not a single instance of beetles pinching or biting the skin of the rodents nor could we discern any damage caused by the beetles, even on heavily infested hosts. Instead, infested hosts were in excellent condition: their fur was rich and luxuriant, and their skin healthy. The same was true of the infested captive rodents. After several weeks of observing them, we found no evidence that amblyopinines feed on the rodents' blood, skin, or secretions.

All of our observations were consistent with those of Hershkovitz. Hosts made no response to movements of the beetles through the fur and around the very sensitive eyes and whiskers, or to prolonged attachment at the base of the ears or elsewhere on the head. Was it possible that the mice were not aware of the beetles? We tested this by transferring beetles to other species of similarly sized rodents that also had long, soft fur. One test species, Alston's brown mouse, is a common forest rodent in areas where amblyopinines live; however, beetles are not naturally found on it. The beetles burrowed into the fur of Alston's brown mice seemingly exactly as they did on their usual hosts. The brown mice, however, were very irritated by both the movements and the attachment of the beetles and vigorously attempted to dislodge them. When this succeeded, they immediately killed the beetle. Otherwise, the mice persisted in biting and scratching at the pest until we removed it. The beetles refused to attach to other species of mice, such as spiny pocket mice, that have stiff, bristly fur.

If the beetles did not feed directly on the host or any product of the host, and the rodents tolerated their presence, just what was the animals' relationship? To answer this question, we began to observe the beetles and their hosts continuously over several days and nights. Since amblyopinines had previously been collected only from the fur of their hosts, the assumption had been that they spend most, if not all, of their time either feeding on the host or attached to it. And as most of the hosts are nocturnal, collecting was done at night, with the rodents and their accompanying beetles gathered from traps at first light. What we found, however, was that the beetles occupy the host only at night. At sunrise, they disembark and spend all day, every day, in the host's nest. The beetles' very different daytime activity proved to be one of the keys to understanding their biology.

Our next step was to find out what the beetles were actually feeding on. If they were not feeding on the rodents, then where did the blood, which had been reported from the gut of one species, come from? We decided to test the reaction of amblyopinines to parasites with which they were likely to come into contact. We placed several beetles of the blood-containing species and fleas taken from the same host into a petri dish. To our surprise, we immediately witnessed a beetle grabbing a flea in its mandibles and eating it! All the fleas in the petri dish were soon consumed. The beetles reacted to these fleas exactly as free-living predatory rove beetles do toward their prey, impaling the victim on their mandibles and, after manipulating it with their other mouthparts, crushing and devouring the soft portions and discarding the remaining hard parts. We later found that another species of amblyopinine feeds in a similar way on large parasitic mites that are common on their host. When we finally found consumed fleas in the bedding material of captive mice, we knew that amblyopinines are not parasites at all but, like other rove beetles, predators. The mammalian blood previously reported in an amblyopinine gut had come from a flea, tick, or other parasite feeding on the rodent's blood and had been secondarily ingested when the beetle, in turn, preyed upon the parasite.

The pieces of the puzzle were now available to us. Amblyopinines are not the blood-sucking parasites they were long thought to be; instead, they are specialists that prey on the ectoparasites of their host. They spend fully half of their time, daylight, hunting in the host's nesting material. At night, before the rodent leaves the nest on its nocturnal rounds, the beetles climb on board and hold snugly to its fur. On the host, they are remarkably stationary, moving only from one attachment point to another. We saw no activity that could be interpreted as hunting on the host and can only conclude that the beetles do not feed while in the fur.

If most of the feeding occurs in the nest, why should beetles attach themselves to the host at night? Host behavior patterns must have been important in the evolution of this aspect of beetle activity. The host rodents sleep during the day and forage actively outside of the nest at night. The physical and behavioral modifications—for example, winglessness—that make amblyopinines unusual among rove beetles, but similar to many true parasites, appear to be directly related to maintaining their position in their host's fur and being transported to any number of nests used by the host. We don't yet know for sure, but we suspect that these rodents use a variety of nests in a pattern unpredictable to the beetles. Thus, it is to the beetles' advantage to travel with the host during its nocturnal foraging bouts.

Both members of this association benefit, thereby making the relationship truly mutualistic. The beetles have evolved ways of tracking host behavior, allowing them access to a specialized food supply. The host tolerates the beetles because they greatly reduce its parasite load. Such a mutualism between a macroscopic invertebrate and a vertebrate is rare. Although some are known among aquatic systems—for example, cleaner shrimp and some tropical reef fish—we have not found another example among land animals. An analogous example of such mutualism between two vertebrate partners is the removal and consumption of ticks by oxpecker birds from large African mammals such as rhinos, elephants, and giraffes. Perhaps amblyopinine rove beetles can be viewed as the oxpeckers of the mouse world.

Although many of the puzzles about the amblyopinine–rodent relationship have been clarified, much remains a mystery. For example, what is it about the nesting biology of the rodents that has led to the evolution of this system? We have studied only two of forty amblyopinine species. Do the others also have mutualistic associations with their hosts or have other species made the evolutionary transition to true parasitism? Where do immature beetles live, and why have they never been encountered on the rodent hosts? Finally, if amblyopinines are primarily predators rather than parasites, why are they so strictly matched to certain rodent hosts and not others? These broader questions will form the basis of our continued study of the ecology and patterns of evolution of the night-riding rove beetles.

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