416-415

Parasites That Change the Behavior of Their Host

In doing so they make the host more vulnerable to predation by their next host. Among such parasites are certain thorny-headed worms, which infest pill bugs that are later eaten by songbirds

by Janice Moore

ne of the most familiar literary devices in science fiction is alien parasites that invade a human host, forcing him to do their bidding as they multiply and spread to other hapless earthlings. Yet the notion that a parasite can alter the behavior of another organism is not mere fiction. The phenomenon is not even rare. One need only look in a lake, a field or a forest to find it.

For a long time most ecologists considering the animal component of living communities have preferred to concentrate on free-living animals and to leave the study of parasites to parasitologists. Nevertheless, it was well known that many parasites have complex life cycles, spending their early life in one animal (the intermediate host) and reaching maturity in another (the definitive host). Gradually evidence began to accumulate that some parasites do not wait passively for a chance to reach their final destination but have ways of increasing the likelihood that the first host will fall prey to the second. They may do so by simply changing the intermediate host's size or color, making it more conspicuous. In other instances, however, they change the animal's behavior in a way that makes it more vulnerable. For example, as early as 1931 Eloise B. Cram of the U.S. Department of Agriculture noted that grasshoppers infested with the larvae of the nematode Tetrameres americana might be easy prey for chickens, in which the worm lives its adult life; the larvae encyst in the grasshopper's muscles and make it less active.

Some parasites, it was later found, change the behavior of their intermediate host by invading its central nervous system. Gid, a disease that makes ruminants such as sheep stagger in circles and become separated from the herd, is caused by an invasion of the animal's brain or spinal column by the larva of the canine tapeworm Taenia multiceps.

Wolves and wild dogs, which prey on such ruminants, are the tapeworm's definitive hosts.

The lancet fluke Dicrocoelium dendriticum interferes with the behavior of its intermediate host in a more specific way. D. dendriticum matures in sheep but spends part of its early life in ants; it must thus overcome the fact that sheep do not ordinarily eat ants. When a group of immature worms invade an ant, one of them encysts in the subesophageal ganglion, the part of the nervous system that controls the insect's mouth parts and locomotion. Wilhelm Hohorst and his co-workers at Hoechst A.G. in Frankfurt, West Germany, showed that an infested ant crawls to the top of a plant and, if the temperature is low enough, becomes locked onto the plant by its mandibles. It is then likely to be eaten by a grazing sheep.

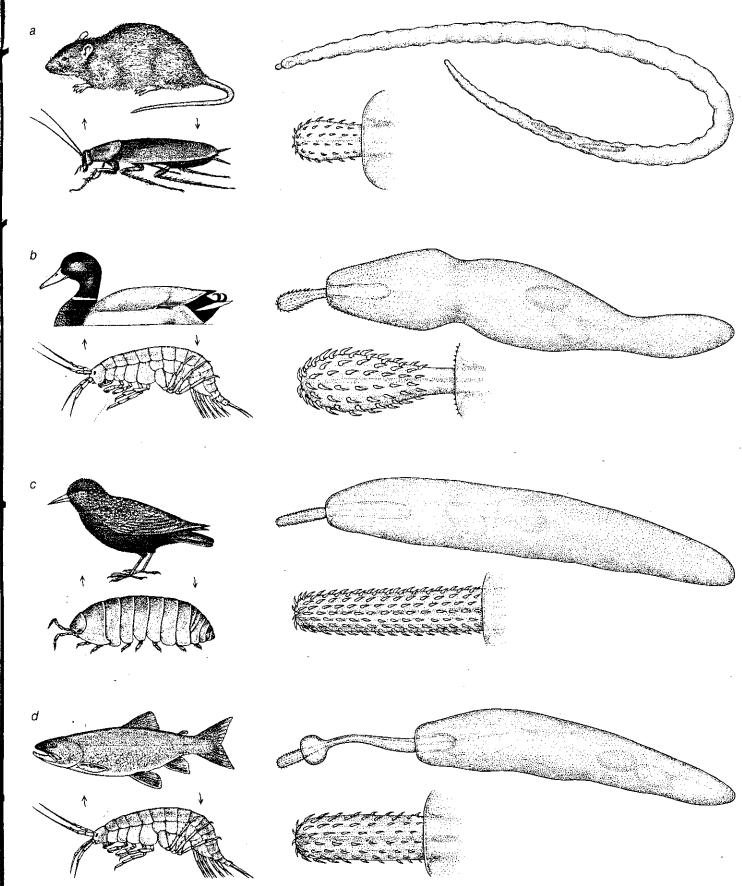
At least one group of parasites induce specific behavioral changes without damaging either the muscular or the nervous tissue of their host: the members of the phylum Acanthocephala, commonly called the thorny-headed worms. Acanthocephalans do not invade muscles or the nervous system, so that the mechanism underlying their behavioral effects is probably biochemical; little, however, is known about it. The ability of these organisms to elicit what would otherwise be normal behavior patterns from their hosts at inappropriate times has in recent years attracted the interest of a number of investigators. The resulting research, including my own, has demonstrated that this ability is present in members of all three classes of acanthocephalans. It may well be universal in the phylum.

The number of acanthocephalan species is not precisely known; the highest estimate puts the total at less than 1,200. The few species for which life cycles are known all live as adults in the

small intestine of vertebrates, particularly birds and fishes. There the female releases eggs that are excreted by the vertebrate and subsequently eaten by an intermediate host: an arthropod such as an insect or a crustacean. The egg hatches in the arthropod's intestine, and the larva burrows through the intestinal wall to the body cavity, where it develops to the stage called a cystacanth, which can infest vertebrates. When an infested arthropod is eaten by an appropriate vertebrate, the cystacanth takes up residence in the small intestine and develops to a sexually mature adult.

Morphologically, acanthocephalans are marvelously adapted to their parasitic way of life. The adult body is essentially a little bag of reproductive organs attached to a proboscis that is covered with backward-curved hooks. This thorny proboscis enables the organism to attach itself to the intestinal wall of the vertebrate. Acanthocephalans themselves have no intestine or any developmental remnant of one; they can survive without a digestive tract because they live in an environment that is rich in digested nutrients, which they simply absorb through their skin. How acanthocephalans evolved these morphological characteristics, and what their closest living relatives are, remain subjects of speculation-largely because no other organism looks very much like an acanthocephalan.

Given the worm's life cycle it is reasonable to suppose it may have evolved, through natural selection, traits that increase its chances of reaching a definitive host. In the 1970's William M. Bethel and John C. Holmes, working at the University of Alberta in Edmonton, did a series of experiments designed to test specifically whether acanthocephalans change the response of their intermediate host to environmental stimuli. They examined three species of worm that have amphipods (small aquatic crusta-

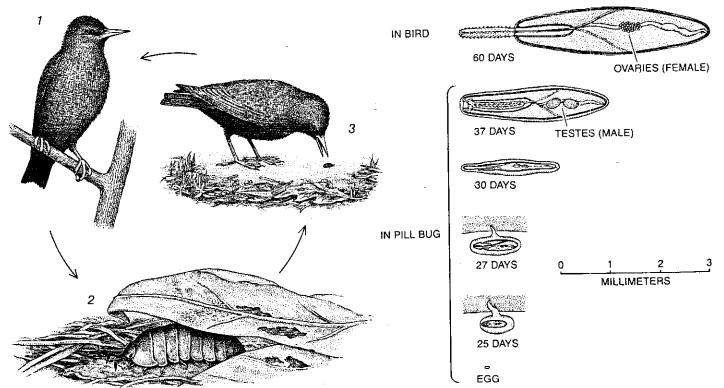


THORNY-HEADED WORMS, or acanthocephalans, are depicted along with their intermediate host (an arthropod), in which the larva develops, and their definitive host (a vertebrate), in which the parasite reaches sexual maturity. All four species depicted here have been found to change the behavior of arthropods such as crustaceans or insects. Moniliformis moniliformis (a) grows in cockroaches and then infests rats that eat the roaches. Polymorphus paradoxus (b) is transmitted from amphipods (small aquatic crustaceans) to mallards and other predators. Plagiorhynchus cylindraceus (c), whose behav-

ioral impacts on pill bugs were studied by the author, matures in starlings and other songbirds that eat pill bugs. Pomphorhynchus laevis (d) moves from amphipods to fishes such as trout. The thorny proboscises with which adult worms attach themselves to the vertebrate intestinal wall are drawn to a common scale; in life the proboscis of Plagiorhynchus is about a millimeter long. The worms themselves vary considerably in size: Moniliformis can be as much as 30 centimeters (12 inches) long, and the other species are less than a twentieth that size. They have reproductive organs but no digestive tract.

DIFFERENT BEHAVIORAL IMPACTS on amphipods of three acanthocephalan species were demonstrated in a laboratory experiment conducted by William M. Bethel and John C. Holmes of the University of Alberta. Uninfested amphipods avoid light; when they are disturbed, they burrow into the mud at the bottom. Amphipods infested with *Polymorphus paradoxus* (a) move toward light, and when they are threatened, they tend to cling to floating vegetation

or skim along the surface; there they are eaten by dabbling ducks such as mallards. Although crustaceans infested with *Polymorphus marilis* (b) also prefer lighted areas, they do not go to the surface; they are preyed on by diving ducks such as scaups. Amphipods harboring *Corynosoma constrictum* (c) do swim to the surface, but some of them dive when they are disturbed; their predators are dabbling as well as diving ducks. The worms mature in the duck's intestine.



LIFE CYCLE OF PLAGIORHYNCHUS CYLINDRACEUS' begins in the small intestine of a starling, where the adult female lays eggs that are excreted by the bird (1). When the bird feces are eaten by a pill bug or some other suitable isopod (2), the eggs hatch within a few hours. The larva, initially no more than a tenth of a millimeter long and armed with tiny spines, burrows through the wall of the isopod's gut and eventually drops into the body cavity, remaining attached to the intestine by a stalk. In the body cavity the larva greatly increases in size and develops adult organs. From 60 to 65 days af-

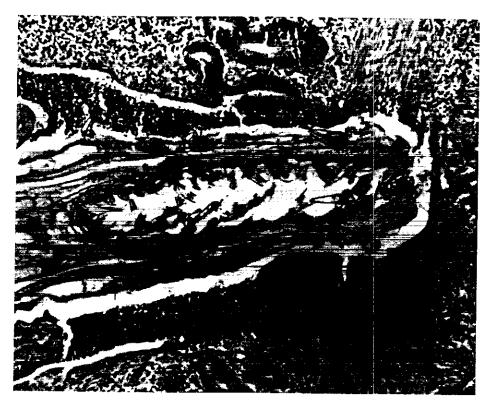
ter hatching it is about four millimeters long and can infest a bird. Through a mechanism that is not yet understood the larva changes the behavior of a pill bug; for example, infested pill bugs are less likely to seek shelter from predators under leaf litter. The thorny proboscis usually remains inverted inside the body of the worm until the pill bug is eaten by a bird (3), at which time the proboscis evaginates and attaches to the bird's intestine. The parasite continues to grow, eventually becoming as much as 15 millimeters long. *P. cylindraceus* life cycle was studied by Gerald D. Schmidt and O. Wilford Olsen.

ceans) as intermediate hosts but that reach adulthood in different vertebrates. They found each species induces different behavioral changes that increase the likelihood of the amphipod's being consumed by the appropriate type of definitive host.

Uninfested amphipods move away from light and are rarely at the surface of a pond or lake. When they are disturbed, they dive and burrow into the mud at the bottom. In contrast, Bethel and Holmes showed that amphipods infested with cystacanths of Polymorphus paradoxus, which lives as an adult in the small intestine of mallards, beavers and muskrats, move toward light. When the infested amphipods are disturbed, they skim along the surface, sometimes clinging to vegetation or other floating objects. This makes them likelier to be eaten by surface-feeding predatorssuch as mallards, beavers and muskrats. Crustaceans infested with Polymorphus marilis, on the other hand, move toward light but do not go all the way to the surface; the definitive hosts for this parasite are diving ducks such as the lesser scaups. Finally, amphipods harboring Corvnosoma constrictum move toward light, but more than half of them-dive when they are disturbed. C. constrictum matures in both diving and surface-feeding ducks.

In tests conducted with mallards and muskrats in a laboratory tank Bethel and Holmes confirmed that the observed changes in behavior affect feeding patterns. Compared with uninfested control animals the surface-feeding mallards ate a large number of amphipods containing P. paradoxus, a smaller but still significant number of amphipods infested with C. constrictum and no amphipods containing P. marilis, whose intermediate hosts avoid the surface. Muskrats ate a significant number of amphipods containing P. paradoxus and none containing P. marilis. The investigators also found that the changes in amphipod behavior only occur once the acanthocephalan has reached the cystacanth stage, when it can infest vertebrates. If the amphipod were eaten at an earlier stage, the immature parasite would not survive.

By 1979 seven species of acanthocephalans, all in the class Palaeacanthocephala, had been shown to alter the behavior of five species of aquatic crustaceans, both amphipods and isopods. Laboratory predation tests on six of these parasites had in every case confirmed that infested crustaceans were likelier to be eaten than uninfested controls. I wanted to extend this work to a terrestrial palaeacanthocephalan and for the first time to examine a parasite's effects on predation in the field as well as in the laboratory. In addition, by look-



THORNY PROBOSCIS of *P. cylindraceus* is seen embedded in the intestinal tissue of a starling in this photomicrograph. The damage caused by the parasite is generally local, confined to within 90 micrometers of the proboscis, which in life is about one-quarter millimeter wide.

ing at an acanthocephalan thought to cause disease in its definitive host (none of the species studied previously were known pathogens) I hoped to determine whether the host might develop a way of avoiding the parasite.

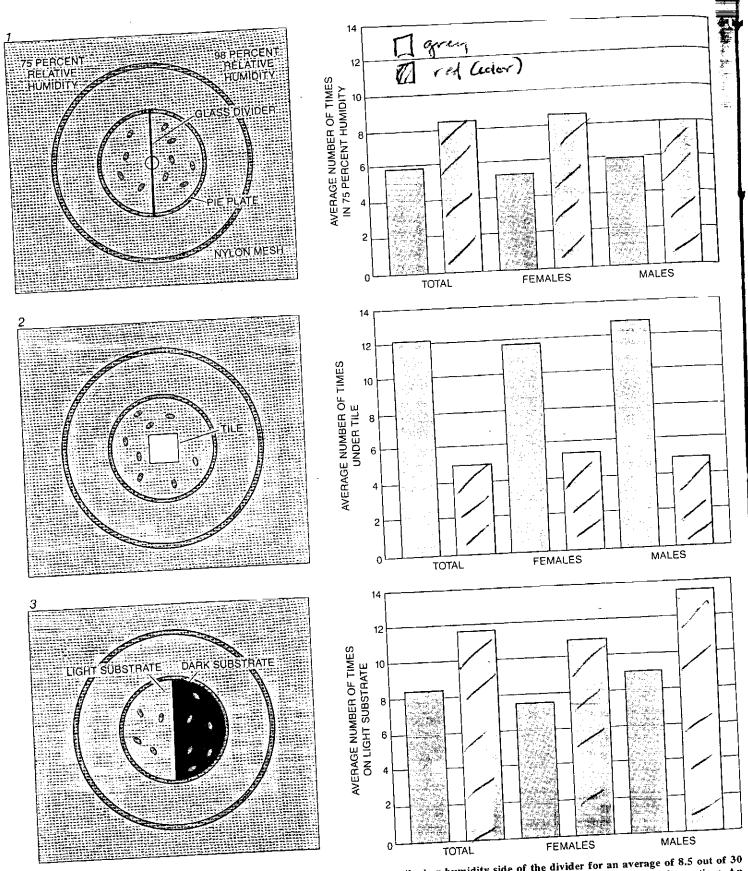
Plagiorhynchus cylindraceus, cited in anecdotal reports and some textbooks as being highly pathogenic for songbirds, seemed to be the worm I was looking for. As an adult it often lives in starlings, and its intermediate hosts are terrestrial isopods such as the common pill bug. There was good reason to believe P. cylindraceus might alter pill bug behavior: in an eight-millimeter pill bug its cystacanth may grow to almost three millimeters in length and one millimeter in width. Moreover, Gerald D. Schmidt of the University of Northern Colorado had reported that female pill bugs infested with this parasite do not develop ovaries. Finally, field surveys had shown that more than 40 percent of birds were infested with P. cylindraceus in areas where the worm's prevalence in isopods was less than I percent. Since isopods are not known to be a significant part of a bird's diet, these results were hard to explain without assuming that the acanthocephalan had some way of making isopods more attractive to birds.

To examine pill bug behavior in the laboratory I made a simple chamber out of two pie plates. The bottom plate, containing a saturated salt solution that generated the desired relative humidity, was covered with a nylon mesh on

which the pill bugs could move around. The inverted top plate closed the chamber, and the junction was sealed with weather stripping. All the experiments were done at the same temperature of 24 to 25 degrees Celsius (75 to 77 degrees Fahrenheit).

I then fed the pill bugs pieces of carrot covered with P. cylindraceus eggs. After waiting three months for cystacanths to develop I mixed infested animals with uninfested controls. The experiments were conducted blind: infestation does not change the isopods' dark color, and so I did not know which animals contained P. cylindraceus until I dissected them after observing their behavior in the experimental apparatus. In order to keep track of more than one pill bug at a time I marked the pill bugs with paint of different colors. In a series of experiments I then examined the impact of P. cylindraceus infestation on four types of behavior that may be important in determining whether a pill bug falls prey to a bird: the isopod's reactions to humidity, shelter, light and color of substrate (the surface on which it rests).

First I gave the pill bugs a choice between relative humidities of 98 percent and 75 percent, which I generated on opposite sides of a divided chamber with different salt solutions. The pill bugs could move freely under the glass divider because it did not quite touch the nylon mesh. At one-minute intervals over a period of about half an hour I



CHANGES IN PILL BUG BEHAVIOR were observed by the author when she compared pill bugs infested with *P. cylindraceus* (color) with uninfested controls (gray) in a series of laboratory experiments. The "behavioral chamber" consisted of a pie plate with a nylon mesh stretched over it and a second plate inverted on top of the first. After an acclimation period groups of 10 individually marked pill bugs were allowed to move about freely on the nylon mesh for half an hour, and each isopod's location was recorded at intervals of one minute. Pill bugs were first allowed to choose between relative humidities of 98 percent and 75 percent (1). Infested isopods were on

the low-humidity side of the divider for an average of 8.5 out of 30 observations, uninfested controls for fewer than six observations. An even more striking difference was found in the isopods' response to a raised tile that simulated a shelter (2): uninfested pill bugs were under the tile, which covered 9.5 percent of the mesh, for more than 12 out of 30 observations, whereas infested pill bugs were under the shelter only slightly more often than one would expect from random motion. Finally, infested isopods were found more often on light substrate (3), where they were notably conspicuous. Pill bugs moving in open areas or on light substrate are more likely to be eaten by birds.

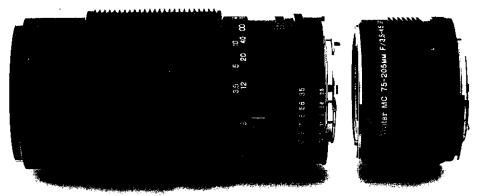
checked the location of each isopod. Infested pill bugs were found on the lowhumidity side much oftener than the uninfested controls.

Ordinarily pill bugs will desiccate and eventually die when the relative humidity is less than 98 percent. Since infested pill bugs display less aversion to lower humidity, P. cylindraceus may either increase their ability to withstand dryness or impair their ability to perceive humidity, or both. The mechanism by which terrestrial isopods perceive moisture is not known, so that it is impossible to say how the parasite might alter it. Conceivably P. cylindraceus could enable an isopod to withstand drier environments by somehow decreasing the permeability of its skin, thereby reducing its water loss, but the results of experiments I did to test this hypothesis were inconclusive. One conclusion, however, seems reasonable: pill bugs that frequent dry areas might spend more time in exposed locations, where they would run a greater risk of being preyed on by birds.

Next I decided to test directly the isopods' response to shelter. I placed a tile on four pebbles in the center of the nylon mesh and recorded the location of each animal, again at one-minute intervals. The tile covered 9.5 percent of the area of the nylon mesh, so that one would expect a randomly moving pill bug to be under the shelter during approximately three of 30 observations. Uninfested pill bugs were under the tile much more often, suggesting they somehow perceived and favored the shelter, but infested animals were not, suggesting they were ignoring the tile. Again the physiological mechanism underlying the change is not known. Strangely enough, it does not seem to be caused by a different response to light; when in a separate experiment I darkened half of the chamber and allowed the pill bugs to move around, I found no difference between the behavior of infested animals and that of uninfested ones. Whatever the mechanism, a random response to shelter is clearly no way for an animal to avoid predators.

Finally, I tested the pill bugs' reaction to substrates of different colors. Unlike some of their aquatic relatives, parasitized terrestrial isopods have normal pigmentation, but a change in their choice of substrate could make them just as conspicuous as a change in their own color. A dark pill bug is much more visible on a sidewalk, for example, than it is on dark soil. I re-created this choice in the laboratory with aquarium gravel, black on one side of the pie plate and white on the other. The results were quite clear: infested isopods were on the white gravel far more often than uninfested ones. Since a dry substrate is often lighter than a wet one, the changes in

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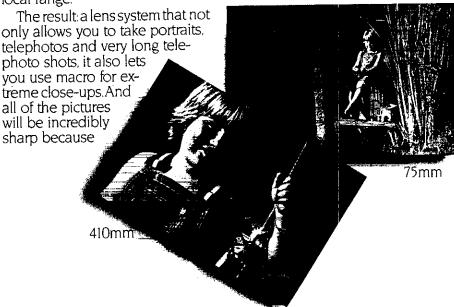
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humidity response and choice of substrate may even be mutually enhancing.

The laboratory experiments thus showed that *P. cylindraceus* alters the behavior of pill bugs in ways that make them likelier to encounter birds. An infested isopod spends more time away from shelter and on a light substrate. The next step was to find out whether these behavioral changes improve the parasite's chances of being transmitted to a starling.

with the assistance of Danny Bell and Mike Freehling I conducted field studies showing that they do. It would have been difficult to answer the question by observing individual adult starlings in the wild and then trapping and dissecting them. Instead I chose a more docile group of experimental subjects: nestlings. I provided nest boxes for starlings on the University of New Mexico campus. During the breeding season I tied pipe cleaners around the young starlings' neck for periods of no more than two hours, tight enough to keep them from swallowing prey but not tight enough to choke them. By collecting the

prey I could estimate the rate at which parents were delivering pill bugs to their young (about one every 10 hours) and also could make sure that the nestlings were not acquiring any *P. cylindraceus* worms from prey other than pill bugs. At the same time I collected 250 pill bugs from the vicinity of the nest boxes, where the adult starlings foraged. From this sample I determined that approximately .4 percent of the pill bug population in the area were harboring *P. cylindraceus* larvae.

When I dissected 22 of the nestlings, however, I found at least one P. cylindraceus in seven of them, or 32 percent. Given the prevalence of the parasite in the pill bug population, the rate of pill bug delivery and the fact that none of the nestlings was more than 18 days old, only about half that number of nestlings should have contained worms if the parents were foraging randomly, that is, if the behavioral changes were not making the infested pill bugs more attractive prey. Moreover, the pill bug delivery rate was in most cases less than one every 10 hours, and most of the nestlings were less than 18 days old. If I had

used averages for these factors rather than maximums, the parasite transmission rate estimated for random foraging would have been even lower. The actual transmission rate would have been higher if I had not counted as single infestations instances in which a nestling harbored more than one worm. Thus the above estimate of the difference between the observed transmission rate and the rate attributable to random foraging is conservative, and the evidence that *P. cylindraceus* influences pill bug predation by starlings is probably stronger than I have suggested.

Similar results were obtained in three subsequent field studies in which I dissected a total of 96 nestlings and 3,000 pill bugs. To buttress this evidence and to observe more directly the starling's response to the changed behavior of infested pill bugs I also did a laboratory predation test. I covered half of the bottom of a container with moist black sand and the other half with drier white sand. Then I put equal numbers of infested and uninfested pill bugs in the container. After allowing the pill bugs to wander around overnight I presented

	INTERMEDIATE HOST	BEHAVIOR CHANGE	DEFINITIVE HOST
PARASITE SPECIES	INTERMEDIATE HOST		
ARCHIACANTHOCEPHALA		HYPERACTIVE;	RAT
MONILIFORMIS MONILIFORMIS	PERIPLANETA AMERICANA (COCKROACH)	MOVES TOWARD LIGHT.	
PALAEACANTHOCEPHALA		TOWN DO LIGHT.	SURFACE FEEDERS:
POLYMORPHUS PARADOXUS	(AMPHIPOD)	MOVES TOWARD LIGHT; CLINGS TO VEGETATION AT SURFACE EVEN WHEN DISTURBED.	MALLARD, MUSKRAT, BEAVER
POLYMORPHUS MARILIS	GAMMARUS LACUSTRIS	PREFERS LIGHTED AREAS BUT DOES NOT GO TO SURFACE.	DIVING DUCKS: SCAUP
CORYNOSOMA CONSTRICTUM	HYALELLA AZTECA (AMPHIPOD)	MOVES TOWARD LIGHT AND GOES TO SURFACE; SOME ANIMALS DO NOT DIVE WHEN DISTURBED.	SURFACE FEEDERS AND DIVING DUCKS: MALLARD AND SCAUP
	GAMMARUS LACUSTRIS	MOVES TOWARD LIGHT.	SURFACE-FEEDING DUCKS
POLYMORPHUS MINUTUS		SPENDS MORE TIME	SONGBIRDS
PLAGIORHYNCHUS CYLINDRACEUS	ARMADILLIDIUM VULGARE (PILL BUG)	IN LOWER HUMIDITY, AWAY FROM SHELTER AND ON LIGHTER SUBSTRATE.	
POMPHORHYNCHUS LAEVIS	GAMMARUS PULEX (AMPHIPOD)	SPENDS MORE TIME IN OPEN WATER; MOVES TOWARD LIGHT AND RESTS ON SURFACE VEGETATION; SWIMS IN A SPIRAL.	
ACANTHOCEPHALUS DIRUS	ASELLUS INTERMEDIUS	MORE ACTIVE.	FISH: CREEK CHUB
ACANTHOCEPHALOS DITTO	(AQUATIC ISOPOD)	MORE ACTIVE;	FISH
ACANTHOCEPHALUS JACKSONI	LIRCEUS LINEATUS (AQUATIC ISOPOD)	CRAWLS OVER RATHER THAN UNDER OBSTACLES.	
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EOACANTHOCEPHALA	PHYSOCYPRIA PUSTULOSA G	GOES TO SURFACE.	FISH: MOSQUITO FISH
NEOECHINORHYNCHUS CYLINDRATUS	(OSTRACOD)	GOES TO SURFACE;	FISH
OCTOSPINIFEROIDES CHANDLERI	CYPRIDOPSIS VIDUA AND PHYSOCYPRIA PUSTULOSA (OSTRACODS)	PREFERS LIGHTED AREAS.	osts. In every case the change ap

ELEVEN SPECIES OF ACANTHOCEPHALAN, including members of all three classes of the phylum, have been found to alter the

behavior of their intermediate hosts. In every case the change appears to make the intermediate host easier prey for the definitive host.

the container to a captive starling and watched until it had eaten approximately half of them. The black pill bugs were very conspicuous against the white sand, and in repeated experiments the birds consistently took most of their prey from that area. In doing so they ate significantly more infested pill bugs than uninfested ones.

The fact that P. cylindraceus is good at $oldsymbol{L}$ increasing the probability that it will get transmitted from a pill bug to a bird raises an interesting question: Given that the parasite is supposed to be pathogenic, why does a starling eat infested pill bugs and feed them to its young? It may be that the bird cannot distinguish infested pill bugs from uninfested ones. (The two look alike to human beings.) But then one might ask why a starling does not totally avoid pill bugs, which are ordinarily an insignificant part of its diet. The answer, I believe, is that although P. cylindraceus may have adverse effects on some birds, it is not usually, contrary to anecdotal reports, a pathogen.

Weight loss is a general indication of ill health, but I found no relation between weight and the presence or number of P. cylindraceus worms, either in the nestlings I examined or in 103 adult starlings I trapped. Furthermore, when infested bird tissue is examined under the microscope, there is no sign of damage more than 90 micrometers from the acanthocephalan's proboscis. If the parasite causes disease only rarely, or if its adverse effects are usually minimal, it may not be worthwhile to a starling to forgo eating pill bugs. Along with the fact that deviant behavior makes infested pill bugs easier prey, that would explain why P. cylindraceus is present in

so many starlings.

The pill bug, of course, pays a higher price for harboring P. cylindraceus. Not only is it likelier to be eaten but also, if it is female, it develops no ovaries and therefore does not reproduce. The low incidence of the parasite in natural pill bug populations may mean that the isopods are avoiding the parasite, or it may simply reflect the fact that infested pill bugs are being eaten. To determine whether pill bugs, particularly females, make any effort to avoid consuming acanthocephalan eggs, I dried and weighed bird feces and gave two pieces to each of 26 females. One piece was covered with an aqueous suspension of P. cylindraceus eggs, the other was simply rehydrated. After a week I dried and weighed the remaining pieces. The pill bugs showed a tendency to shun the "infested" feces, but the result was not statistically significant, and in any case the tendency did not seem dramatic given the penalties involved. Perhaps pill bugs, as omnivores, are not capable of

being very discriminating. It may even be that the benefits of eating nutrientrich bird feces outweigh the risk of being eaten by birds.

The ability to alter host behavior is not limited to palaeacanthocephalans such as *P. cylindraceus* but extends to the other two classes of acanthocephalans. David J. DeMont and Kenneth C. Corkum of Louisiana State University recently found the ability in two eoacanthocephalans, both of which mature in fishes and have as intermediate hosts ostracods (another type of aquatic crustacean). The two parasites probably make ostracods more vulnerable by increasing their attraction to light.

Cockroaches infested with Moniliformis moniliformis, a member of the third class of acanthocephalans (Archiacanthocephala), are also attracted to light. Furthermore, they are hyperactive, as I discovered when I placed infested animals in activity wheels connected to devices that record the frequency of motion. Hyperactive cockroaches that move toward light are less likely to remain hidden and so are probably more likely to be caught by rats, which are the definitive hosts for M. moniliformis.

The effects these acanthocephalans and others have on their hosts are not as magical as they might sound. For one thing, the parasites do not induce novel behavior patterns but merely elicit existing patterns at disastrously inappropriate times. Nevertheless, this is quite a feat, and a general physiological explanation of how an acanthocephalan accomplishes it while floating in the body cavity of the host has yet to be found.

The realization that parasites can change host behavior has intriguing implications. Biologists observing certain animals in the field must now take into account the possibility that the observed behavior may have been "rigged." A parasite may even influence the evolution of its host, as many predators influence the evolution of their prey. Although this phenomenon is not evident in the case of P. cylindraceus, a truly pathogenic parasite might cause the host to evolve ways of avoiding the parasite or of resisting its pathogenic effects; any animal with these abilities would have an advantage over other members of its species. William D. Hamilton and Marlene Zuk of the University of Michigan have recently suggested that resistance to parasitic disease is expressed in the physical appearance and courtship display of songbirds and may affect the choice of a mate. More information is needed to confirm such a connection, but it is clear from this and similar research that biologists are beginning to understand the extent to which parasites can influence the behavior of other organisms.

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