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PILLBUGS

(Isopods; *Armadillidium*)

Pillbugs thrive downtown despite vulnerability to predators, parasites, pathogens, and desiccation. They have gained safety in numbers.

Figure 16.1 Pillbug, *Armadillidium nasatum,* rolled into an imperfect ball, with a gap on the right. Rolling into a ball (conglobation) protects pillbugs from desiccation and predators.[1]

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In the first volume of the *Journal of the Academy of Natural Sciences of Philadelphia,* published in 1818, Thomas Say presented "An Account of the Crustacea of the United States." Crustacea are arthropods such as lobsters, crabs, shrimp, barnacles, and fourteen-legged creatures called isopods. Terrestrial isopods include familiar garden animals known by many colloquial names, such as woodlice, sowbugs, roly-polies, and pillbugs. Say noted that one species, currently named *Armadillidium vulgare*, "is very common in moist places, under stones, in decaying wood, &c."[2] This species inhabits our garden in Center City.

Figure 16.2 Our Center City row house garden, habitat for a diverse community of exotic animals, including six species of isopods, such as pillbugs.

Introduction of pillbugs

Unlike the Chinese mantid, *A. vulgare* in North America left no obvious clues to its place of origin. A genetic study of 10,000 of these pillbugs in 157 populations in Europe and North America concluded that this species was introduced from northern Europe.[3] Root balls in imported horticultural and agricultural stock could have carried it in, or dirt used in ship ballast dumped near American ports could have transported it here.

All species of terrestrial isopods in the northeastern United States have been introduced except for the few endemics that inhabit caves or seashores, which protected them from Pleistocene glaciation and permafrost.[4] Pleistocene permafrost on the mid-Atlantic Coastal Plain, which includes Center City, extended at least as far south as southern Delaware and southern Maryland.[5]

A century after Thomas Say's report on crustaceans, Henry Fowler of the Academy of Natural Sciences of Philadelphia noted that *A. vulgare* "is of world-wide distribution, living mostly in moist places, as under stones or logs, in crevices or rocks, about greenhouses, cellars, under boards, etc." He named four neighborhoods in Philadelphia where he collected it.[6] Now, almost two centuries after Thomas Say's paper on crustaceans, those he described are still here, and new ones have arrived and established themselves.

Figure 16.3 Pillbug, *Armadillidium vulgare*, introduced from Europe and common in this region by 1818. Specimen from our garden.

Figure 16.4 Pillbug, *Armadillidium nasatum*, a more recent introduction and the most abundant isopod in our garden. Specimen from our garden.

Microbes

In 1984, Philip F. Ganter and Wilma Kane Hanton at the University of North Carolina reported that more than 80 percent of pillbugs (*A. vulgare*) in local populations were female. Referring to electron micrographs revealing bacteria in pillbug ovaries, they hypothesized that an intracellular bacterial parasite skewed sex ratios by transforming male pillbugs into females.[7] In 1991 Thierry Rigaud and colleagues in France identified the bacterium as *Wolbachia*,[8] named after the Harvard microbiologist S. Burt Wolbach, who, with Marshall Hertig, first described the bacterium in the house mosquito in 1924.[9]

Wolbachia, transmitted maternally through pillbug eggs, transforms genetic male pillbugs into functional females that produce viable eggs and offspring. By converting genetic male pillbugs into reproductive females, the microbe commandeers the reproductive machinery of the pillbug and subordinates it to the bacteria's own benefit. *Wolbachia* behaves like a selfish gene, reprogramming its host's reproduction to maximize its own.[10]

In one survey *Wolbachia* infected almost half of species of terrestrial isopods,[11] but the actual proportion is likely greater.[12] It infects about two thirds of all species of insects,[13] plus an indeterminate number of nematodes, spiders, scorpions, and mites.[14] Reproductive effects of *Wolbachia* on infected hosts differ depending on host species. In some cases, it kills developing males; in others, it creates females that reproduce asexually,[15] permanently eliminating males from propagation unless the insects are treated with antibiotics.[16]

Wolbachia's reproductive gain is not necessarily the pillbug's loss. Spread of a similar maternally transmitted infection to populations of the sweet potato whitefly increased the fly's fitness.[17] Elimination of *Wolbachia* infection from the bedbug (*Cimex lectularius*) retarded the bedbug's growth and induced sterility.[18]

Wolbachia infection may have helped pillbugs colonize our garden. Normal males are poor agents for dispersal: a solitary male that has dispersed into a new habitat cannot alone found a colony; but males that *Wolbachia* has transformed into females can mate, disperse, and then establish populations in new habitats. Radioactively labeled pillbugs tracked in the field dispersed as far as 25 meters.[19] *Wolbachia* infection, at least theoretically, helps pillbugs cope with severe fragmentation of habitat, such as that in downtown Philadelphia.

The capacity of a normal male pillbug to inseminate many females compensates for depletion of males in populations after the males have been transformed into females,[20] but this transformation has its costs: normal males prefer real (i.e., genetic) females,[21] and they exhaust their supply of sperm after mating multiple times.[22] The pillbug may be either *Wolbachia's* beneficiary or its victim, depending on the value of the traits that *Wolbachia* transmits. This value may differ under different environmental conditions, as in the case of *Wolbachia* infection in mosquitoes.[23] Populations of pillbugs can eliminate *Wolbachia* infection,[24] possibly by evolving resistance.[25]

Parasites: spiny-headed worms

Another infection commandeers pillbugs, but unlike *Wolbachia*, its life cycle is not confined to pillbugs. The infectious agent is a parasite, a spiny-headed worm (*Plagiorhynchus cylindraceus*) in the phylum Acanthocephala, which includes over a thousand named species and is unrelated to earthworms, flatworms, or roundworms. *P. cylindraceus* has been found in birds on five continents. The only study of its prevalence in North American birds found it in 62 percent of robins, 56 percent of grackles, 42 percent of starlings, and lower frequencies in blue jays, house sparrows, and brown-headed cowbirds.[26]

The parasite was first discovered in North America in 1918 by Harley J. Van Cleave,[27] who later looked for it but did not find it in Joseph Leidy's collection of Acanthocephala preserved in the University of Pennsylvania and the Academy of Natural Sciences of Philadelphia.[28] Van Cleave reported the parasite in birds in Pennsylvania, New Jersey, Maryland, New York, and Washington, DC, and inferred that it is an exotic species introduced only recently.[29]

In 1929 D. T. Sinitsin, a Russian parasitologist who had fled the Soviet Union,[30] reported finding a 4-millimeter worm in a pillbug (*Armadillidium vulgare*) that he had collected near the Chesapeake and Ohio Canal in Washington, DC. He identified the worm as a young *P. cylindraceus*.[31] In 1964 Gerald D. Schmidt and O. Wilford Olsen at the University of Colorado harvested eggs of gravid *P. cylindraceus* worms located in the small intestine of robins. They presented the eggs of the worm first to beetles, which ate and digested them. They then presented the eggs to pillbugs, which ate the eggs but did not digest them; the eggs hatched and developed into infectious cysts inside the pillbugs. When birds consumed pillbugs containing parasitic cysts, the proboscis of the worms pierced the cysts' walls and attached to the birds' guts, where the worms developed to maturity and produced eggs. The eggs exited in the birds' feces, where they became available to pillbugs, completing the cycle.[32] The parasitic infection has been found to lower birds' metabolic rate and weight, but effects on mortality and fitness have not been studied.[33]

Reported prevalence of these worms in populations of pillbugs is paradoxically low —for example, only 1 in 1,500 individuals examined in one study.[34] How could the worm be so abundant in birds yet vanishingly rare in pillbugs? In 1982 Brent B. Nickol and Glen E. Dappen at the University of Nebraska showed that mature pillbugs were relatively resistant to infection by the parasite, which infected predominantly young individuals.[35] The next year, Janice Moore at the University of New Mexico showed that the worm changed the behavior of the pillbugs it infected such that its victims exposed themselves to predators such as robins.[36]

Like *Wolbachia*, the worm commandeers the behavior of pillbugs for its own benefit. Unlike *Wolbachia*, it offers pillbugs nothing in return. The worm's diversion of pillbugs to predators explains the paradoxical rarity of worm-infected pillbugs compared to worm-infected birds. Worm-infected pillbugs promptly become food for birds such as robins.

Pillbug aggregation: vulnerability to enemies

Pillbugs in our garden aggregate, piling up on each other beneath stones or logs. Why would they clump together and risk exposing themselves to predators and pathogens? Most aggregations of pillbugs in our garden consist of *A. nasatum*, a pillbug susceptible to infection by both *Wolbachia*[37] and spiny-headed worms[38] and probably also iridovirus.[39] This pillbug initially inhabited greenhouses in North America, but by the 1950s it had established populations outside greenhouses.[40] A genetic polymorphism produces different color forms.[41]

Aggregations of *A. nasatum* would appear to be easy targets for the European centipede (*Cryptops hortensis*) and the pillbug hunter *Dysdera crocata*, an introduced spider that specializes in preying on terrestrial isopods.[42] This spider has long fangs that it uses like pincers to seize isopods, which it secures with one pincer clamping down on the armored top and the other puncturing the soft underside,[43] which it injects with venom that can kill within seven seconds.[44] It hunts at night without use of a web to snare prey.[45]

Figure 16.5 Pillbug hunter (*Dysdera crocata*) under a log in our garden. Remains of its victims are scattered about.

Figure 16.6 Pillbug hunter. I collected this individual in our garden.

Figure 16.7 Pillbug hunter's formidably long fangs work like pincers. The top fang holds the victim and the bottom fang skewers it on the soft underside and injects the venom.

Pillbug aggregation: avoidance of dessication

In 1931 Warder Clyde Allee published *Animal Aggregations: A Study in General Sociology*. Citing his own research,[46] he suggests why isopods bunch:

> Land isopods (Allee, 1926) tend to collect in aggregations in the hot, dry summer and in the cold, and often physiologically dry, winter. These aggregations are frequently such as might result when shelter is limited, provided there is a tolerance for the presence of other similar animals; but at times these animals collect in much closer units than can be entirely explained on this basis. That is to say, the isopods do not occupy all the available and apparently equally desirable space, but clump together in one part of this.
>
> When a drop of water was introduced on a dry background, the isopods tended to occupy all of that favorable location regardless of whether or not they were in contact. The bunching in close physical contact came later, and might take place as a thigmotropic reaction, perhaps modified by chemical stimuli, or might have been conditioned by the drying of the small moistened region.[47]

Fifty years later Naokuni Takeda at Toho University in Japan showed that the pillbug (*A. vulgare*) produces a pheromone that promotes aggregation, which in turn reduces desiccation and increases growth. In other species of isopod, aggregation pheromone was shown to prolong survival.[48] Mark Hassall and his colleagues at the University of East Anglia in England concluded that aggregation can protect isopods from climate warming,[49] which might apply to our garden, located as it is in an urban heat island. Cédric Devigne and his colleagues in France have shown experimentally that changes in temperature and humidity alone do not fully explain why isopods aggregate; they concluded that unidentified social benefits favor aggregation.[50]

Pillbug aggregation: Avoidance of pillbug hunters

In 1971 William D. Hamilton published his iconoclastic "Geometry of the Selfish Herd," presenting the evolution of aggregation behavior as a selfish response to predators. He refers to birds, fish, frogs, ungulates, and insects—but not isopods:

> This paper presents an antithesis to the view that gregarious behavior is evolved through benefits to the population or species…Gregarious behaviour is considered as a form of cover-seeking in which each animal tries to reduce its chance of being caught by a predator. It is easy to see how pruning of marginal individuals can maintain centripetal instincts in already gregarious species...Besides this, simply defined models are used to show that even in non-gregarious species selection is likely to favour individuals who stay close to others.[51]

Pillbug aggregations—like those of ungulates, birds, and fish—buffer members in the inside from attack by predators on the outside. Pillbug hunters hide under logs and stones, as do pillbugs. I have not found the hunters within aggregations of pillbugs. Pillbug hunters could, in theory, exploit pillbug aggregations by grouping inside these aggregations, much as bridge spiders exploit concentrations of prey at electric lights along the Schuylkill River; but, unlike bridge spiders, pillbug hunters are solitary, and they dwell outside aggregations of pillbugs. The pillbugs most vulnerable to pillbug hunters would be expected to be those on the periphery of aggregations or outside them—as Hamilton's theory predicts. Protection against predators may be the primary benefit of pillbug aggregation, or it may be secondary, after protection against desiccation.

Figure 16.8 Bunching of pillbugs (*Armadillidium nasatum*) on the underside of a paving stone in our garden. Aggregation protects individuals from desiccation and predators. A genetic polymorphism contributes to differences in color among individuals.

Hamilton contended that even nongregarious species gain safety in numbers. In our garden his conclusion sheds light on pillbugs that happen to live outside of aggregations. Typical of territorial spiders[52] pillbug hunters in our garden space themselves apart and keep their population densities low. Searching in pillbug hunters' favorite shelters such as under logs, I usually find no pillbug hunters. When I do find one, it is solitary. In our garden, low densities of pillbug hunters and high densities of pillbugs keep ratios of pillbug hunters to pillbugs low; these low ratios also keep the odds of an attack on any individual pillbug, even those outside aggregations, low.

Abundance of any one kind of isopod in our garden would be expected to contribute to the protection of others. Pillbug hunters specialize in all kinds of isopods, not just pillbugs. Our garden has six species of isopods, all introduced. Two are pillbugs (*A. vulgare* and *A. nasatum*), which defend themselves by rolling into a ball, and the rest are runners that defend themselves by fleeing.*

Slugs

Like isopods, slugs aggregate, or "huddle," a behavior that also protects them from desiccation.[53] All three species of slugs in our garden have been reported to huddle,[54] but I have observed huddling in only the most common, the threeband gardenslug (*Lehmannia valentiana*).[55] For this slug, high population densities facilitate huddling and protection from desiccation—another instance of safety in numbers.†

Figure 16.9 Threeband gardenslugs (*Lehmannia valentiana*), huddling under a paving stone. Huddling protects slugs from desiccation. (A recent synonym for its scientific name is *Ambigolimax valentianus*.)

Impact of exotic animals on our garden's ecology

Daniel Simberloff coined the phrase invasional meltdown for destruction of native ecosystems by introduced species. The term meltdown, an allusion to nuclear power plants, refers to positively reinforcing interactions among the immigrants.[56]

Safety in numbers of slugs and isopods in our garden exemplifies positively reinforcing interactions— but not an invasional meltdown. These animals have enriched an urban habitat stripped long ago of most native plants and animals. They decompose organic debris, amend the soil, and obviate my need to dispose of leaf litter. They are members of a community of diverse animals including native species, such as the common eastern firefly, *Photinus pyralis*, and the American robin.

* In our garden the four isopods that are runners are: common pygmy woodlouse (*Trichoniscus pusillus*), common striped woodlouse (*Philoscia muscorum*), *Porcellionides pruinosus,* and *Hylonisclus riparius*.

† The two other slugs are the giant garden slug (*Limax maximus*) and the grey field slug (*Deroceras reticulatum*).