

Guardians of the Underworld

Burying beetles are faithful parents, a rarity among insects

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One parent circles the nest, repairing and cleaning it. The other hunches over a cluster of young in the center of the nest while the ever-hungry offspring scramble over her legs, jockeying for position to beg for food. They stretch upward and reach their mouths eagerly toward their mother's. At first, this may evoke an arboreal scene with a family of warblers, but this nest is several inches underground. And the conscientious parents are not birds; they are beetles that have fashioned a nest from a dead mouse that they buried.

The behavior of these beetles, of the genus *Nicrophorus*, is well described by their various common names: grave-diggers, undertaker beetles, or more commonly, burying beetles. Jean Henri Fabre, a nineteenth-century French naturalist, was so intrigued with the ability of these beetles to move and bury small vertebrate carcasses that he set out dead moles and mice in his garden in order to study the phenomenon more closely. Each time, he devised a problem for the beetles to solve by tethering or suspending the carcasses and watching as the insects freed their booty and got it underground. His experiments convinced Fabre that burying beetles were capable of conscious planning. Although we, too, are impressed by the beetles' ability to move and bury a carcass a hundred times their size, we find the lengthy care provided by both male and female parents far more remarkable.

Extended parental care is rare in invertebrates, with the notable exception of social insects such as ants, bees, wasps, and termites, which live in complex societies and cooperate extensively in brood care. Most insect females make little provision for their eggs other than laying them in a protected place or near a suitable food supply. Some, however, continue to supply food to young maturing in a nest or brood cell. Male insects, typically, have no involvement with offspring, leaving their mark on posterity by putting their efforts into finding additional females to mate with.

Exceptions do exist, however. For example, the male giant water bug provides all the care for eggs glued to his back by the female, fanning water over the eggs

A burying beetle holds one of its young while feeding it regurgitated food.



A pair of beetles, right, bury a mouse. Right, below: Burying beetles are also master embalmers. After stripping the mouse of its fur, they shape it into a ball and preserve it with secretions.



for days to keep them aerated. Wood roaches form long-term family associations; they are monogamous and cooperate in the defense and rearing of a single brood, which takes three to five years. Wood roaches live in a burrow system that is hard to excavate, but once done, it provides a stable, protected environment. Two parents are needed to guard the entrance, and males would have no success if they wandered off in search of additional mates because the females would already be mated. Burying beetles provide considerable parental care in response to somewhat different environmental conditions. They use an ephemeral, unpredictable food source for their developing offspring. This "bonanza" resource is so valuable to the prospective parents that to protect it from competitors, which range from flies to weasels, they bury it.

The antennae of male and female burying beetles have highly sensitive chemical receptors to detect the odors of decomposition, and the insects are quickly attracted to vertebrate carcasses such as a dead mouse or pheasant chick. Even a large garter snake is fair game although it may present considerable problems of transportation and burial, especially when two beetles start work at opposite ends. Carcasses that are too big for burial are rejected, but not until they have provided a quick meal.

As soon as a carcass is located, the beetles walk around and under it, assessing its suitability, and make short trips to nearby terrain to find the right spot for burial. Females generally get right to work, but if a single male locates a carcass, he may take time out to attract a female. He climbs to a high spot, such as a rock, and assumes a characteristic posture in which the segments of his abdomen are extended and raised high, presumably releasing a pheromone that serves as a sex attractant. If two or more males or females arrive simultaneously at the carcass, they confront each other, fighting until only one male and one female remain. Eavesdropping on the battles, one can hear the agitated squeaking made by both males and females as the stridulatory organ on their abdomens is moved against the wing cov-



ers. Combatants can lose legs and antennae as they push and grapple, but usually the smaller insect is quickly intimidated and retreats.

The victorious male and female burying beetles have simply won the same prize and appear to be oblivious to each other's qualities as mates. During competition on the carcass, neither males nor females appear to defend or assist one another; by not doing so, they insure that the largest and best male and female will mate. The two of them make remarkably quick work of interring the carcass. They crawl upside down beneath it, and with their legs pushing up against the carcass and their backs resting on the ground, the beetles "walk" the body forward, sometimes a foot or more, to a suitable burial spot. (When we put out a dead lab mouse for an experiment, we tie about two feet of dental floss to one of its legs to make sure we can locate it the next morning.) Once the carcass is buried about four inches below the surface, the beetles construct a brood chamber. Then they begin to remove fur or feathers, and the carcass, with its skin intact, is gradually shaped into a ball and covered with secretions from the beetles' hindgut that act as a preservative.

The beetles mate as they construct the brood chamber, and within two days the female lays thirty or more eggs in a side tunnel leading from the burial chamber. Three or four days later, the eggs hatch into larvae, which crawl to the top of the "mouse ball," where, like a nestful of young birds, they cluster in a hollow that has been prepared by the parents. Both parents regurgitate food to begging larvae. Observations by our colleague Isabelle Fetherston showed that the frequency of feeding increases over the next few days. The larvae grow tenfold each day and are soon able to feed themselves. In addition, both parents circle the carcass, clipping it with their mandibles to keep it clear of fungi and dragging their abdomens to spread secretions that inhibit bacteria. Usually the original brood of thirty or more is too large to be raised on a small carcass, so both male and female will cannibalize their young while they are still very small, reducing the larvae to a number that can be successfully reared on the available food.

When the young are three or four days old, one parent, usually the male, leaves. By the time the young are eight or nine days old, they have polished off the car-

Protecting his brood, right, the father flips an intruding male on its back. Right, below: The loser of a fight is typically eaten. Here, only wings and their hard covers remain.

cass, leaving only the largest bones. The larvae disperse to pupate in the soil nearby, and the female's work is then done. A month later, the young emerge as adults, in time to fatten up on insect prey and the occasional large carrion before they become inactive for the winter.

When we began our research on burying beetles four years ago, we knew that both male and female burying beetles helped to rear their brood and this unusual behavior raised many questions. How long did the male and female provide parental care? Did longer care result in more offspring surviving? What exactly were they doing that made it worth such a big investment in time on each brood?

In general, both males and females of any species face a simple trade-off between greater survival odds for their current brood if they stay and the chance of additional matings and offspring if they leave. If either parent is to benefit by staying, it is usually the female, because the number of offspring she can produce in her lifetime is usually limited by the resources she needs to produce eggs. Because males have lower physiological costs in sperm production, they usually leave the most offspring by putting their energy into searching for receptive females. The male's chances for many mates increase if females, or the resources they need, can be easily defended by a single male and if the females are not completely synchronized in their willingness to mate. Birds are the only group in which two parents are generally more successful than one at rearing young, and because females are often all receptive at the same time, a deserting father would have a slim chance of finding an unmated female. Biparental care and monogamy is therefore the general condition for birds. We knew when we started that both male and female burying beetles remained with the brood for quite a while, and this suggested that some unusual ecological circumstances have contributed to the evolution of this behavior.

To understand the ecology of burying beetles and the costs and benefits of their parental care, we work in the field in southern New Hampshire where four spe-



cies of *Nicrophorus* are abundant. The many abandoned logging roads are convenient sites in which to set out dead mice to attract beetles. Mice are placed above one-quart jars of soil sunk into the forest floor. Taking the path of least resistance, the beetles usually bury their prey in the jar, which we then pull up and return to our field station. The jar is placed inside a larger, covered container. Deserting parents, and later their offspring, are captured as they leave the brood chamber, allowing us to measure how long males and females remain with each brood and their resultant reproductive success.

By making carcasses available from spring to fall, we found that the four common species of burying beetles in southern New Hampshire each have a distinctive seasonal breeding pattern. Only one species, *N. sayi*, is active in April and May and therefore has exclusive access to small carcasses. However, reproductive adults of this species are seldom seen after other species appear when the nights get warm. The large, dominant species *N. orbicollis* is the quintessential burying beetle reproductively active in the summer, burying carcasses deeply, and providing lengthy parental care. The smaller *N.*

defodiens also reproduces in the summer, but only shuffles the mouse under the litter or rolls it down an existing hole and departs well before the larvae mature. *N. defodiens*, however, is able to produce more young on the same size mouse and is more tolerant of chilly nights, which tend to discourage the hard work of burying. *N. tomentosus* successfully dominates the small vertebrate carcass supply in August and continues to bury carcasses and lay eggs into the fall because its young overwinter as larvae, completing their development the following summer.

In all four species, we found that females stay with the brood longer than males. In the case of *N. orbicollis*, the main focus of our field studies, females remain an average of seven days longer than males, and the longer they stay, the larger their offspring. Although the number of individuals in the brood is determined by the size of the carcass, females seem to recognize a good opportunity and tend to provide longer care on larger carcasses. Our greatest surprise came when we discovered that male assistance could have a negative effect. We reared young in boxes of soil and either removed the male after twenty-four hours or left him

there until larval development was complete. Even though they were reared on the same size carcasses, broods that had been reared by two parents were smaller. We were tempted to conclude that males made inept parents, but further investigation showed that single males did just as well as single females; the detrimental effect was caused by the presence of two parents rather than the male per se. It is still unclear to us why two parents reduce the size of the brood. The two of them may cannibalize too many young in reducing the brood to a size that can be reared successfully on a small mouse. Perhaps because both parents remain in the brood chamber and must live off the carcass themselves, less food is available to biparental broods.

The smaller broods from two-parent "families" created a whole new mystery since we had logically assumed that male assistance enabled the pair to rear more young. If male burying beetles are not helping the female rear more young, why do they spend eight or nine days with their brood instead of looking for an additional carcass and another mate?

We theorized that the males' importance lay in the defense of their broods. To test this hypothesis, we introduced an insect predator, a staphylinid beetle, to broods from which both parents had been removed and found that the intruder made a quick meal of the small larvae. But if we left the mothers with their broods, they successfully defended them alone. Male assistance in brood defense against insect predators seemed unimportant.

Could other burying beetles of the same species be a greater threat to the brood than the staphylinid beetles? Even though the nest may be several inches underground, it may be discovered and usurped by other burying beetles as long as the carcass is not completely consumed. To test this possibility we marked beetles with dots of paint and put them with dead mice on the forest floor at dusk. Both pairs and single, previously inseminated females were allowed to set up brood chambers. We could then discover what the male defensive role was by comparing the fates of broods reared under the usual

circumstances by a pair and those reared by single females. (The latter group recreated the situation of broods raised by females deserted immediately after insemination.) Eight days later we dug them up. In a few cases, either the male or female of biparental broods had been replaced by an intruder. But when single females guarded broods, unknown *N. orbicollis* males were more successful at locating and taking possession of the carcass. The intruders killed the original brood, reinseminated the female, and remained to guard the new young.

We were still puzzled by the female's tolerance of male help, when it appeared to reduce the number of her offspring. Apparently, intruders were infrequent and even if a male intruder killed her first brood, she would have a second. This second brood, raised on the slightly depleted carcass, might be smaller and run the risk of being discovered and killed by a third male. Nonetheless, the female still appeared to have less to lose than males when the original male deserted early.

We set up pairs and single females again, this time eliminating the random nature of the intruders in the first study. On the third night after a carcass was buried, we introduced a marked intruder of known size and sex and kept the brood protected from all other intruders by placing a flowerpot over each brood chamber. Since beetle size determines the outcome of competition on the carcass before burial, we thought it would be important now, too.

The results were dramatic. With only a single female to protect a brood, large and small male intruders killed the brood two-thirds of the time. Intruder females, if larger, were also successful at driving off the resident female about two-thirds of the time. The two-parent broods usually fared well no matter what the sex or size of the intruder. Male and female appeared to cooperate in the defense of their brood, whereas earlier, when competing for the carcass, they appeared to be indifferent to the affairs of the opposite sex. The battles were now ferocious and frequently lethal, especially on the larger mouse carcasses. In one notable example, two larger intrud-

*Having killed the brood's father, an intruding male, below, plucks up two larvae, crushing one in his mandibles. After eating the entire brood, he will inseminate the resident female and raise his own family. A burying beetle, *Nicrophorus tomentosus*, right, crawls on a dead squirrel; too big to bury, it will make a good meal. All other photographs are of *N. orbicollis*.*



ers lay dead at the entrance of the brood chamber and the parents were missing most of their legs and antennae. Neither could walk, but the carcass was still theirs and their offspring were alive.

Although males do provide care to the young by helping to preserve and clean the carcass and feed the young, their principal role seems to be defense against others of their species; they remain with the brood until the carcass is depleted to the point that intruders will no longer be interested in fighting over it. If a male were to leave the female right after inseminating her, he would stand a good chance of losing his offspring. Although females can manage to rear young on their own and can defend them against smaller female intruders, they too can lose their opportunity to reproduce; without male assistance, larger female intruders can displace them and kill the young.

Parental care has not evolved in most groups of invertebrates because in most species individuals can guarantee their reproductive success by putting less investment into a large number of offspring. Burying beetles are an exception because they must find an unpredictable but very valuable resource in order to reproduce. Once they have a carcass buried, however, it provides a secure and nutritious supply of food, raising the probability that many offspring will survive. □

