Scient. Am. 235(1976)(2):84-89

The Social Behavior of Burying Beetles

These insects, usually working as a mated pair, can quickly inter a carcass many times their size. The carcass serves them and their larvae as food, and both parents participate in caring for the young

by Lorus J. Milne and Margery Milne

An observant person who sees the carcass of a small animal lying on the ground is likely to find, if he returns to the spot the next day, that the object has disappeared. The chances are that it has been buried, either there or nearby, by a pair of *Nicrophorus* (or *Necrophorus*) beetles. They will use it as food for their young during the larval stages. The feat of these small insects in rapidly interring a carcass that is many times their size is remarkable enough, but it is only a step toward the most advanced form of parental cooperativeness known among the Coleoptera (the beetles). We have spent much time watching these burying beetles (also called carrion beetles and sexton beetles) and putting them to various tests, which demonstrate an impressive plasticity in the behavior of the insects.

The patient French naturalist Jean-Henri Fabre set out fleshy bait of several kinds to lure burying beetles to where he could watch them. He admired these little gravediggers of the animal world, describing them as being "elegantly attired" in black, with a "double, scalloped scarf of vermilion" across their shining wing covers. The observer cannot watch for long. Unlike the scarab beetle of Mediterranean countries, which walks in plain view while rolling a ball of dung to some still undiscovered place of burial, a burying beetle quickly slides out of sight below the carcass of a mouse or a bird it has found. There, lying on its back, the insect uses all six of its powerful legs as levers to shift its prize. From time to time it rights itself and bulldozes headfirst into the earth to loosen the soil and push it away. Inconspicuously, a fraction of an inch at a time, the carcass moves horizontally or disappears into the ground.

Nicrophorus beetles are by no means the only insects that sequester food for their larvae before they lay the eggs that will give rise to the larvae, but they work as a team, whereas the others (the scarab and its relatives and various solitary bees and wasps) work alone. Either a male or a female *Nicrophorus* will initiate the flexible behavior that gets the larval food into a safe place. At any time during the operation a mate is likely to arrive. The partner is accepted with no time off for courtship. The two labor together at intervals and also separately in a loose cooperation that advances the common effort. Yet either member of the pair may also creep into a more or less concealed place and appear to sleep for as much as half an hour or depart on feet or wings to some unknown destination for a comparable period, thereafter returning and resuming the work. Ordinarily copulation is deferred until the beetles are securely in possession of their carrion in a chamber of their own making, an inch or more below the surface of the ground.

At this juncture the male might be expected to perform his brief sexual duty and depart. The inseminated female would then carry on alone to the end of the sequence of behavior specified by her inheritance. Occasionally this pattern is followed, but usually both parents remain. Together they work the mass of food into a compact ball. They free it of fur or feathers, perhaps adding secretions that modify the course of decomposition.

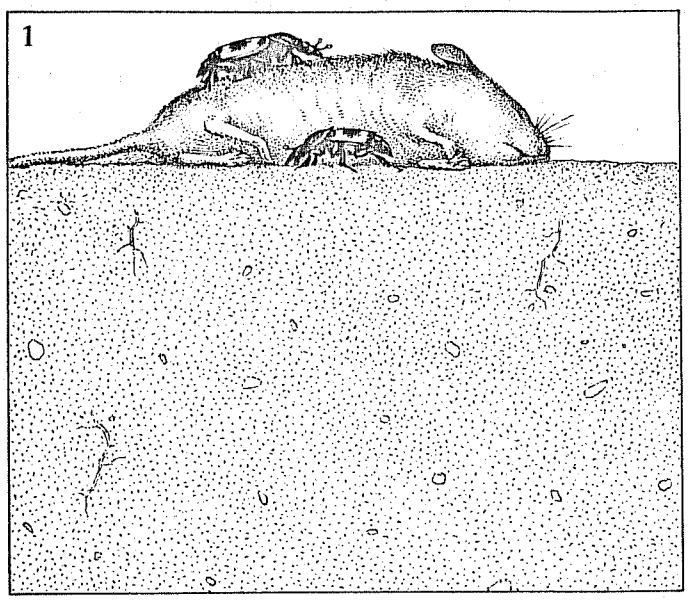
As the insects clamber around the carcass, which will provide food for them as well as for their young, the floor, the walls and the roof of the earthen chamber become firmly packed. The female constructs a short vertical extension of the chamber above the carrion and lays her eggs in the side walls of the passageway. She returns to the carcass, and by a combination of selective feeding and clawing at the upper surface prepares a conical depression. Both beetles regurgitate into the depression droplets of partly digested tissue. The fluid accumulates as a pabulum for the larvae that will soon hatch.

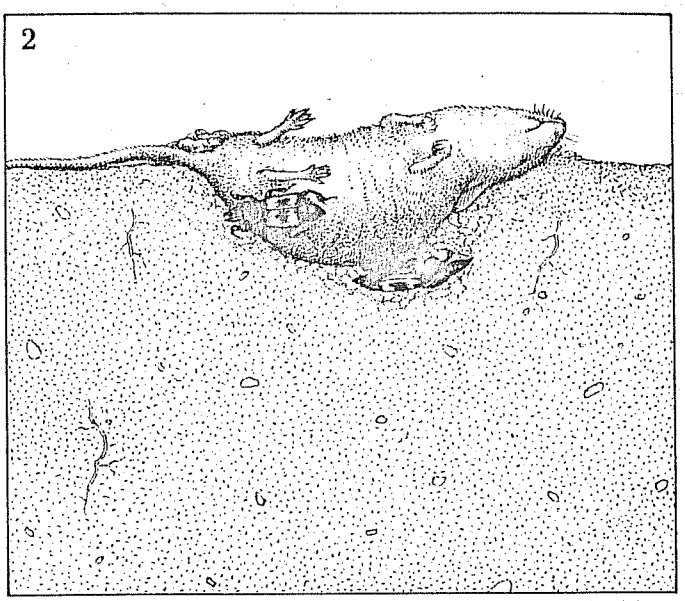
This much Fabre or any other persistent observer could discover by exhuming the beetles and their food supply at the proper time, just before the young hatch. Erna Pukowski, studying species native to her Polish countryside, managed to learn more. She made captive burying beetles so much at home, notwithstanding the unnatural condition she created by illuminating their burial chamber, that she could follow the next steps.

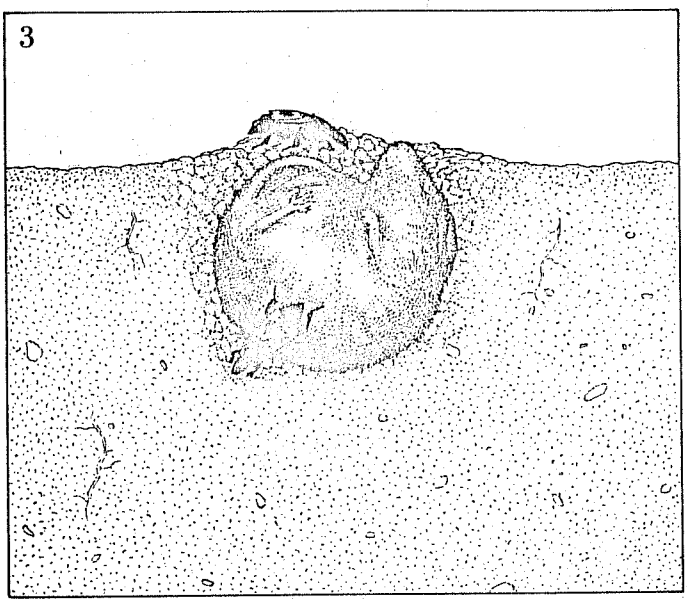
One beetle (perhaps the female, although the members of a pair are too much alike externally for an observer to distinguish sex) stood beside the pool of liquid nourishment and began to stridulate. The sound brought hatchling larvae (some two or three millimeters long and almost like maggots in appearance) to the parent's side. The parent sipped from the pool and then transferred the fluid food to one larva after another. The larvae lifted their mouth ends, the better to receive the food. Sometimes both parents shared in the feeding operation.

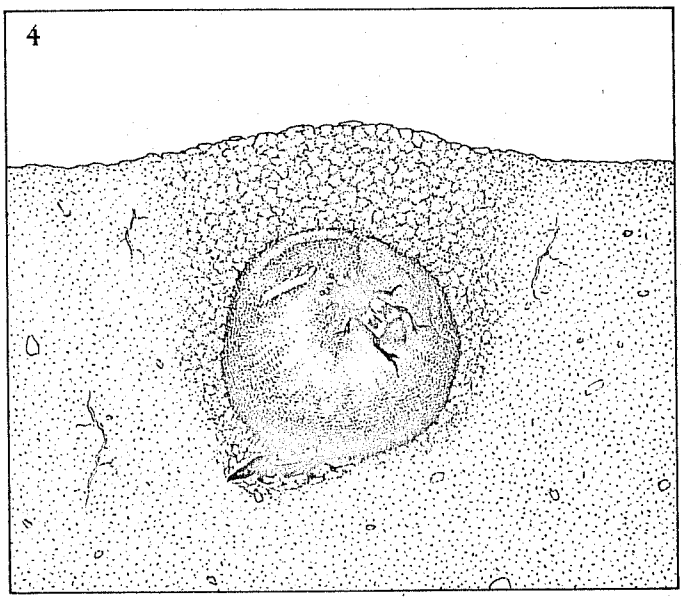
The British entomologist R. L. Morley discovered in 1902 that the sound of stridulation arises when twin plectrums on the inner surface of the cover of a beetle's wing fret against crosswise ridges on the fifth segment of the abdomen. The sound is clearly audible to human ears. Pukowski noticed it also during the three or four seconds when copulation is in progress. We have heard it when burying beetles are under stress, as they are in repelling an insect of another species or a smaller member of the same sex and in confronting an obstruction that impedes the movement of a carcass.

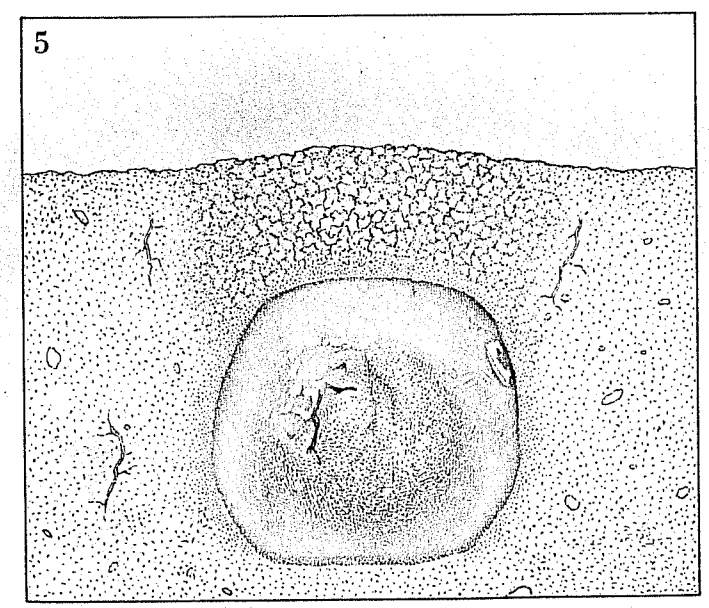
In 1972 Carsten Niemitz of Justus

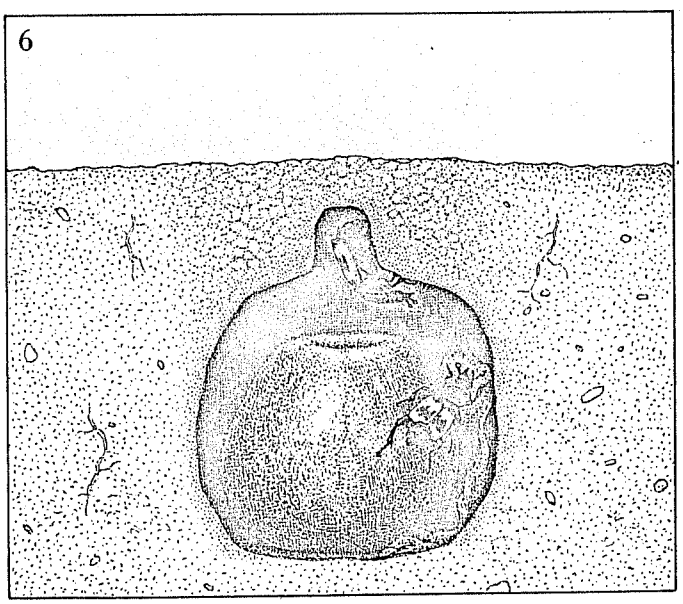




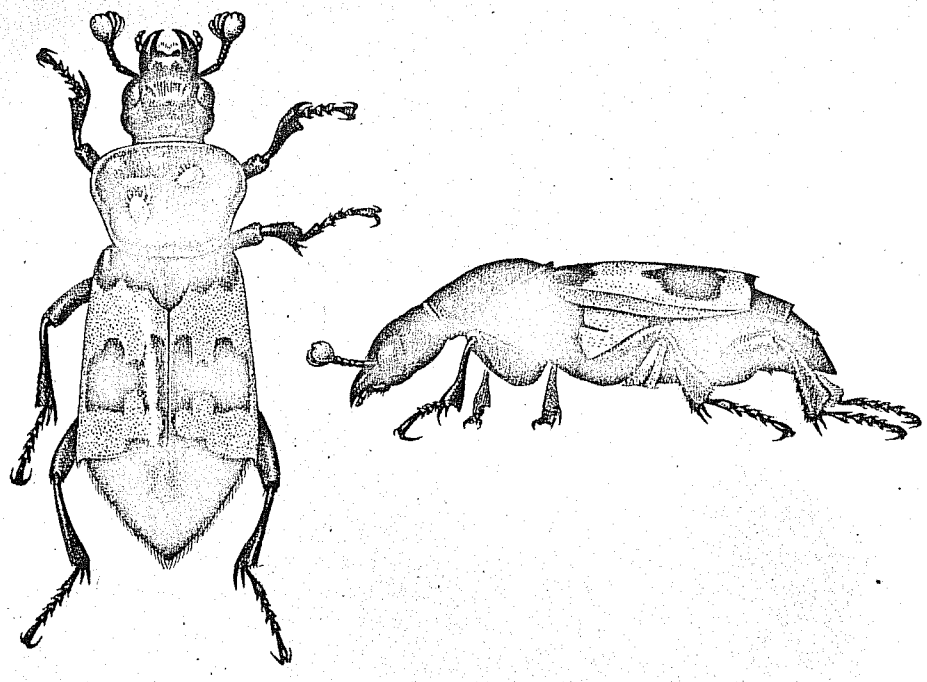




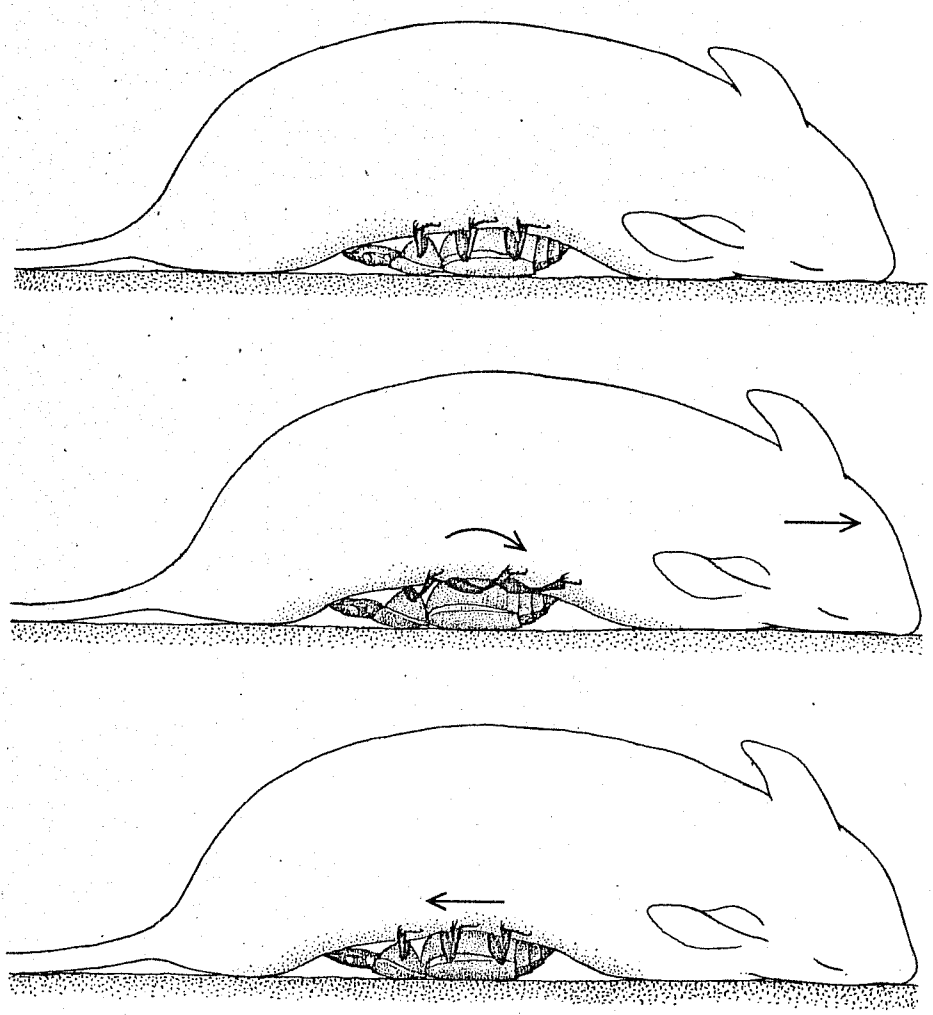




BURIAL OF MOUSE by a pair of *Nicrophorus* beetles is depicted. Usually a carcass is discovered by one beetle, which is soon joined by a mate. Here a male and a female, indistinguishable externally, are shown as they inter the carcass of a mouse in a burial chamber they prepare by moving earth and packing it radially and upward. The scale is about two-thirds life size. At the end of the process (6) the carcass is about an inch below the surface of the ground. The beetles have shaped it into a ball and have removed the skin and tail. They create a pool of liquid food for their larvae in the top of the ball, and the female then lays her eggs in a small chamber above the pool.



BURYING BEETLE of the species *N. marginatus* is portrayed in top and side views. The beetle employs all six of its powerful legs in moving and burying a carcass. A beetle is likely to carry at all times a cargo of mites of the genus *Poecilochirus*, which evidently live in some kind of symbiotic arrangement with the beetles. Two such mites appear in the top view of the beetle.



TRANSPORT OF CARCASS is a technique that *Nicrophorus* beetles employ when the ground where they find the body is too hard. The beetle lies on its back and uses its legs as levers to shift the carcass. If a pair of beetles are present, they work together at times and also separately in a loose cooperation. They will transport a carcass several meters if necessary.

Liebig University in West Germany discovered that very young larvae will orient themselves to the sound of an adult's stridulation recorded on tape. This response disappears, however, after the larvae have molted for the first time. Even so, older larvae renew their solicitation of regurgitated food for a few hours after each molt by approaching any adult that is close to the pool of food and pressing their mouthparts against its jaws or palps. This action stimulates regurgitation as before. Otherwise the growing larvae feed directly from the pool or pull fragments from the surface of the carrion.

The larvae receive parental care all through their period of feeding growth. The parents may even prepare a horizontal passageway into which the fully grown larvae can crawl to pupate. Only then, when the adults can contribute nothing more to their brood, do they force their way upward through the soil and fly away.

We have not yet marked and followed the departing parents to see whether they do the same thing all over again. They probably do, since adult beetles live from three to 15 months, depending on the species. They search widely for the odor of recent death and are remarkably efficient at finding carrion. Frantisek Petruska, a Czechoslovak ethologist, has found, by capturing beetles with carrion bait, marking them and releasing them at various distances, that they will return to the carrion within 24 hours from as much as four kilometers away.

During one period of four hours, beginning just 35 minutes after we had laid out a newly dead mouse on birch-leaf litter, nine burying beetles arrived. Each beetle followed the guidance of the olfactory organs in its antennae. It dropped to the ground within three meters of the mouse, quickly folded its flying wings under its wing covers and came crashing through the litter to the carcass. There, after only a moment's hesitation, the beetle turned over onto its back, slid under the body and lifted the mouse slightly from the ground, apparently to test whether the body was movable. Emerging on the other side of the mouse and righting itself, the beetle began testing the soil.

We had placed our bait on hard ground. Each beetle rejected the site for burial and began to explore, seemingly at random, for softer earth. This was our cue to remove the active beetle and wait for the next one. Each one of the nine beetles followed essentially the same routine, even though four of them were members of one species and five were members of another.

Competition for small carcasses is frequently intense. Ants and flies (par-

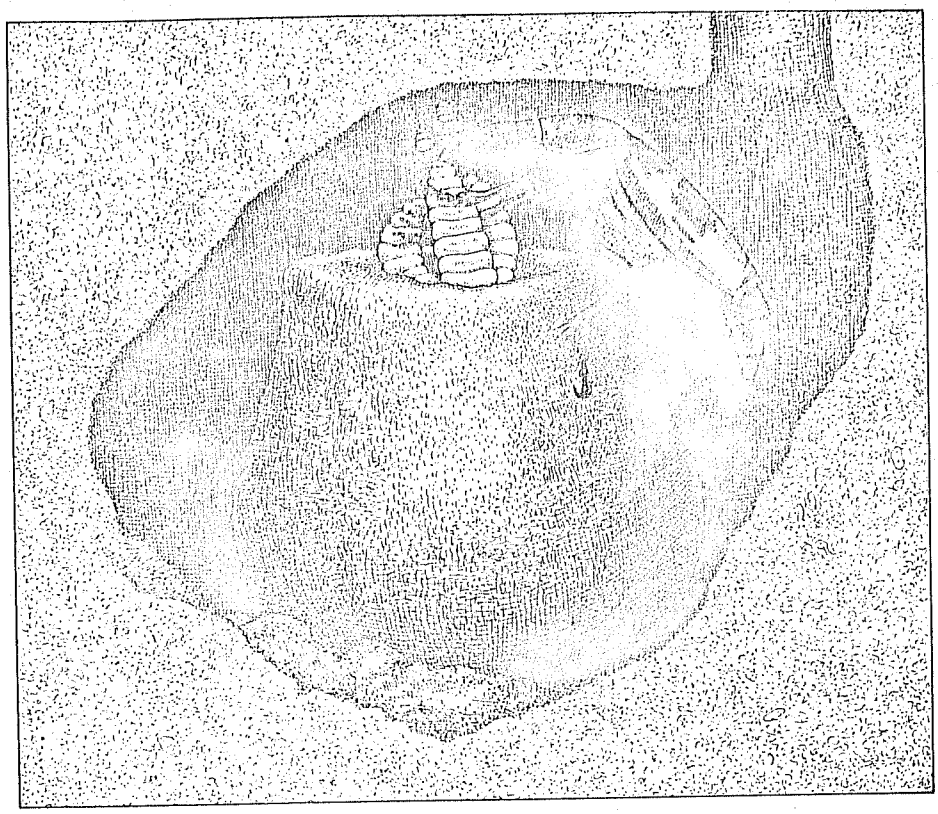
ticularly blowflies, which deposit active maggots) tend to take over during the day. Burying beetles of the species that are most active by day succeed only if they can inter a body quickly. For species that are active at night the competition is mainly from other species. The largest beetle generally repels all the others except a mate. That is probably why one more often finds a large male cooperating with a small female (or a large female cooperating with a small male) than one finds two beetles of the same size cooperating.

Burying beetles have other ways of reducing competition. Each species has a preferred combination of temperature range and relative humidity. This pattern, as Jean Théodoridès of the University of Paris showed in his laboratory, keeps certain beetles in woodland and others in open fields. Burying beetles that are active in the spring belong to species that go through the winter as adults, whereas the beetles found competing in the summer are likely to represent species that spend the cold months dormant as pupae or full-grown larvae.

Animals that eat insects are likely to constitute a hazard for burying beetles that are active by day. At least one diurnal species of burying beetle in Europe and one in North America may escape being eaten as a result of their resemblance to a small bumblebee. Unlike most burying beetles, these species have golden hair over some of their hard black surfaces. Color, sound and style of flight combine so convincingly that the British biologists Charles Lane and Miriam Rothschild have suggested that this is an example of mimicry, at least with respect to sound. Even a superficial resemblance might have survival value for the beetles.

The most spectacular feature of the activity of burying beetles is the way they transport a carcass from hard ground to soft, in one steady direction, a fraction of an inch at a time. A beetle that has yet to acquire a mate may identify a suitable burial site several meters away from the carrion. The beetle will alternate between loosening the earth at the burial site and rushing back to the carcass. There it performs its lifting feat, starting under the body at the end closest to the burial site. The dead weight is progressively shifted until the beetle emerges from under the opposite end. The insect may run around the carcass and repeat the process time after time. If a mate arrives, the progress is more nearly continuous.

A measure of the success of this way of life can be seen in the fact that the genus *Nicrophorus* includes almost 100 species, with some overlap in distribution. About half of the species are Asiatic. Almost the only areas where burying beetles have not been found are the West Indies, Africa south of the great deserts, Australia and New Zealand.



FEEDING OF LARVAE by a burying beetle of the species *N. vespillo* is shown on the basis of photographs made by the Polish naturalist Erna Pukowski. The parent beetle sips from the pool of fluid food in the top of the buried carcass and then transfers the material to one larva after another. The larvae rear up instinctively, much the way nestling birds do when feeding.

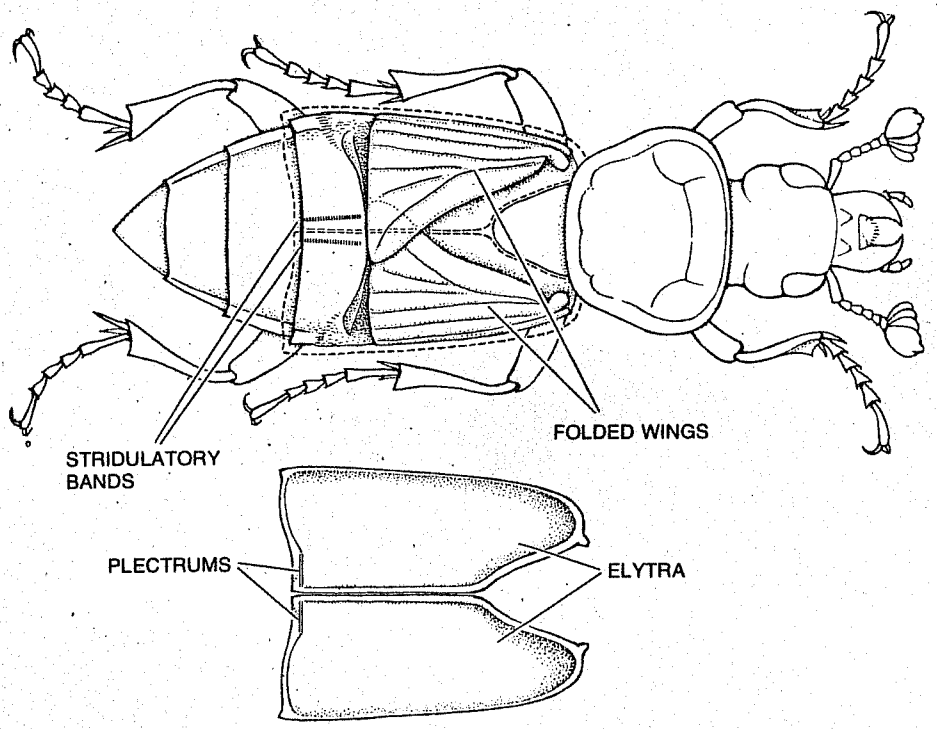
Adult burying beetles range in length from 10 to 35 millimeters, with considerable variation within a species. All of them appear able to transport the compact body of a bird or a mammal weighing up to 100 grams—up to the size of a rat or a big robin. Anything heavier is usually abandoned unless it is only slightly overweight and can be interred where it is found. A dead snake, however, can weigh more and still be buried expeditiously. Its carcass is subdivided into two or more zones of operation. One pair of beetles attends to each zone.

As Fabre observed, burying beetles show considerable plasticity in behavior. Noting the number of obstacles a typical environment is likely to present to beetles trying to move or bury a body, he wrote that the insect therefore "cannot employ fixed methods in performing its task. Exposed to fortuitous hazards, it must be able to modify its tactics within the limits of its modest discernment. To saw, to break, to disentangle, to lift, to shake, to displace— these are so many means that are indispensable to the gravedigger in a predicament. Deprived of these resources, reduced to uniformity of procedure, the insect would be incapable of pursuing its calling."

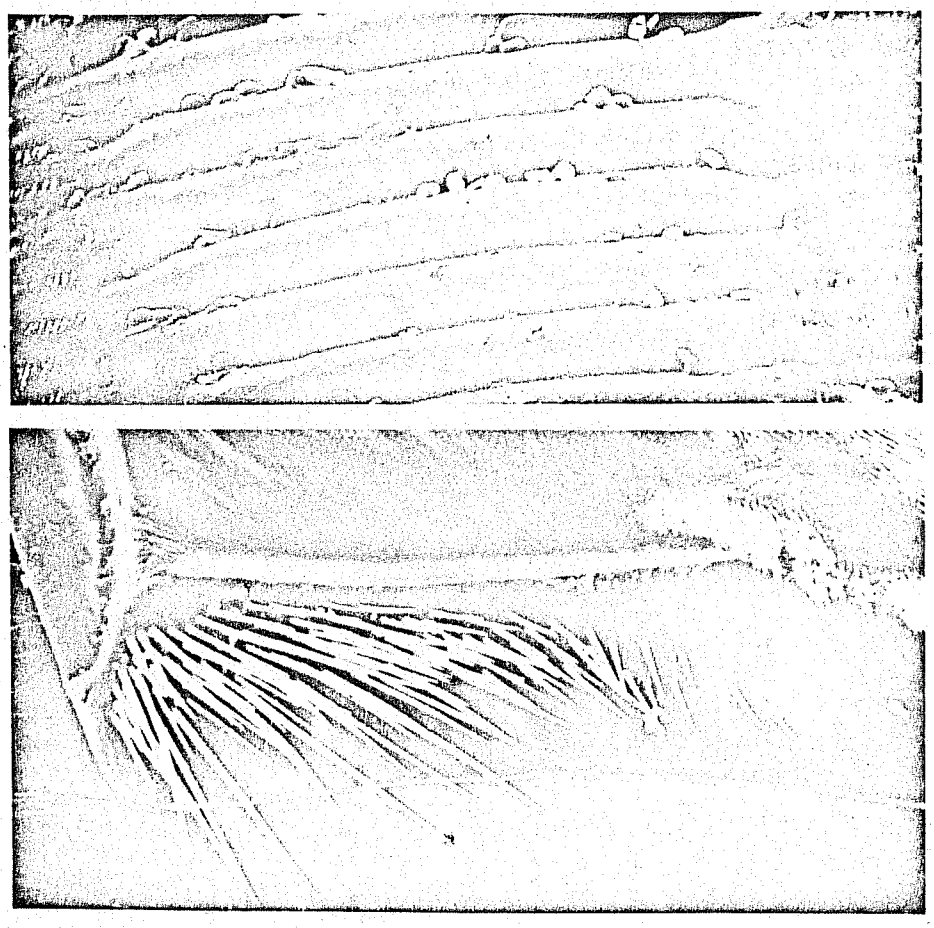
Fabre's evaluation rested on watching the beetles at work rather than on experiments. He was reluctant to disturb the carrying and burying operations because so few *Nicrophorus* beetles came to his bait. Our studies have centered in countryside (New Hampshire and Ontario) where richer woodlands and more varied fields support a larger population of beetles. Simple tests confirm the versatility encompassed within the insects' programmed patterns of behavior.

To create a reasonable facsimile of the type of obstacle a burying beetle might encounter naturally, we place a dead mouse close to a clover plant and then tie the carcass down by arching the stalk of a leaf over the torso and fastening the stalk to the ground with a hairpin. The first burying beetle to arrive discovers that the front and rear ends of the carcass can be raised but that the middle cannot. The beetle promptly climbs over the mouse, discovers the tight leaf stalk, forces its head under the stalk and pushes forward. The stalk does not break, but it stretches enough to release the carcass for transport and burial. Repetitions of the experiment with other beetles all have the same result.

Once we drove a good-sized stake into the ground at a 45-degree angle and tied a strong cotton string around its upper end. We tied the dangling end of the string around a hind leg of a dead mouse lying on soft ground. A pair of *Nicropho-*



STRIDULATING MECHANISM is employed by a *Nicrophorus* beetle to call larvae to food and also in times of stress. Here the elytra, or wing covers, are shown (*below*) removed from the beetle's back and turned over, so that the plectrum at the bottom of each elytron is visible. The sound is made when the plectrums are rubbed against ridges on a segment of the abdomen.



STRIDULATORY APPARATUS of the *Nicrophorus* beetle consists of the *pars stridens* (*top*), which has the crosswise abdominal ridges the plectrums rub against, and of the plectrums, one of which is shown at bottom. The plectrum is the ridged white structure that is in a form approximating a right angle; the bottom part does the striking and the part at the left serves as a guide. In these scanning electron micrographs, made by Rolf Schumacher of the University of Bonn, the *pars stridens* is enlarged about 445 diameters and the plectrum 120.

rus beetles pushed away the soil below the body until the mouse hung from the tethered leg over a cup-shaped depression. The insects cleared a space the thickness of their bodies between the mouse and the soil and then kept swiveling the carcass in wide arcs. The tail of the mouse dragged on the rim of the depression until one of the beetles chewed it off.

That did not solve the problem, and so both beetles explored the surface of the carcass. Only about six hours after they had begun to work did one of them discover the tether. In less than a minute the insect settled down to gnaw through the cotton fibers. By dawn the carcass had been liberated and buried.

To test the strength of *Nicrophorus* beetles we rested one end of a flat rock on the body of a 50-gram mole. The rock applied about half a kilogram of unyielding weight to the body. Two beetles were nonetheless able to work the body free. First they took up positions side by side with their back against the rock and their legs against the body. They shifted the body about a centimeter in relation to the rock and then repeated the performance with respect to the hard soil below the body. Alternating between these two areas of contact, they freed the carcass in less than half an hour, whereupon they transported it to soft ground and quickly buried it.

In tests of the memory of burying beetles we have found that if a beetle has had 15 or 20 minutes of experience with a suitable carcass, it can be removed and held captive for at least 16 hours without losing its readiness to return to the body within minutes of being released. After 24 hours of separation from its trophy the beetle is more likely to fly off. Two beetles of the species *Nicrophorus orbicollis* that had shifted a mouse about six inches were picked up and put in separate boxes with moist earth. Two hours later, while two smaller beetles of the species *N. tomentosus* were working on the mouse, we released the male *orbicollis* six inches to the east of the body and the female six inches to the north. They both feigned death for a few seconds and then set out almost directly for the body of the mouse. They repelled the *tomentosus* beetles and resumed their normal activities.

In this test the female was the larger *orbicollis*. If the disparity had been the other way, the behavior probably would have been different. We find that females are much more aggressive than males in ousting rivals from carrion. A male is more likely to allow other *Nicrophorus* beetles, particularly those of other species, to work for a while before repelling them. In the end each manageable carcass serves as food for the adults and larvae of only one pair of *Nicrophorus* beetles—the ones that bury it.

Beetles need both memory and some special sense (probably olfaction) to recognize a particular trophy. If we move a carcass a meter or less to one side while the beetles of a pair are momentarily away from it, they immediately begin exploring on their return to the vacant site. In a few minutes, aided no doubt by scent, they find the carcass and resume work as though nothing had happened.

Possibly burying beetles mark a carcass with a chemical secretion, which would explain what happens when the beetles return to a site where they have been working on a carcass only to find a different carcass there. They examine the substitute and then go off exploring. If they find the original carcass within a meter or less, they resume work on it. If they fail to locate their prize, they are as likely to fly away as they are to accept the substitute. A volatile substance that conferred a distinctive odor on a carcass, as a message to be read later by the same insect or its mate, might serve also as a pheromone. Pukowski noticed that a lone *Nicrophorus* beetle, after laboring for a long time without being joined by a mate, would climb on top of a plant or a stone, elevate its abdomen obliquely and extend it as though emitting a secretion.

The social behavior of burying beetles fits between extremes in the behavior of other insects. In the most primitive insect social behavior the parent or parents attend only to their own offspring. The most advanced social insects have a female at least providing care for the offspring of other females, often as a sterile surrogate parent. Burying beetles often show some altruistic behavior in that small members of the same species or a different one may contribute significantly to the rapid burial of a carcass and then leave, taking no part in reproduction. The dominant, mated pair take over the food supply. The female, at least, remains to care for the larvae, but she will not tend the larvae of any other female.

Parental interactions that promote the survival of further generations have evolved independently in more than two dozen families of insects. Among the beetles, which are the most varied order of animals, *Nicrophorus* is unique in extending maternal care so far and in having the aid of the male so often until the larvae are ready to pupate. No other members of the same superfamily show social behavior of any kind. Indeed, entomologists regard the superfamily (Staphylinoidea) and the family (Silphidae) to which the *Nicrophorus* beetle belongs as being made up of rather unspecialized beetles. It is odd that behavior of such plasticity should have arisen at all and then should have succeeded so widely.