The Role of Conflict in Breeding Systems: Burying Beetles as Experimental Organisms
Author(s): Stephen T. Trumbo
Source: *The American Biology Teacher*, Vol. 58, No. 2 (Feb., 1996), pp. 118-121
Published by: University of California Press on behalf of the National Association of Biology Teachers
Stable URL: http://www.jstor.org/stable/4450092
Accessed: 22/09/2010 12:29

The Role of Conflict in Breeding Systems: Burying Beetles as Experimental Organisms

Stephen T. Trumbo

A small mouse or bird corpse that is placed upon the forest floor usually disappears within one or two days due to the quiet and efficient work of insects known as burying beetles. Also known as undertaker or sexton beetles because of their talent for interring the dead, these organisms are extremely helpful in recycling nutrients and in removing the obnoxious remains of dead animals. Their underground habits, however, mask the fact that much of their social life is based on conflict over possession and use of the highly prized carrion resource.

Charles Darwin (1871) was one of the first to appreciate the significance of conflict in biological systems. Darwin realized that conflicts between two coevolving parties could select for mutually intricate adaptations and counteradaptations. Thus predators continually evolve to become more stealthy while prey evolve to become faster and ever more vigilant. Likewise, Darwin saw that conflict played an important role in mating systems. As first detailed by Darwin, males compete for breeding females in two ways. Males often engage rivals in direct combat (intrasexual selection) or males compete with other males for the attention of females by employing elaborate behavioral and morphological displays, impressively exemplified by the strutting dance of the peacock (intersexual selection, Darwin 1871). Darwin, however, did not fully understand the potential for conflicts between a breeding male and female within an established pair bond. While Darwin understood that females may be reluctant to mate with a male that has not demonstrated superior combative or seductive abilities, he little appreciated that conflicts can arise over the composition of the breeding group, how much care should be given to young, and who should provide that care. For example Darwin held the view, prevalent until the 1970s, that sexual advertisement by males serves solely to bring together mates of the same species and to show off the superior qualities of the male. More recently, sexual advertisement also has been seen as a means to bias the composition of a breeding group in favor of the advertiser.

Stephen T. Trumbo is Assistant Professor of Biology at the University of Connecticut at Waterbury, Waterbury, CT 06710.

Here, I relate how burying beetles can be used to explore conflicts between breeding individuals. Some of these conflicts would be very familiar to Darwin, while others perhaps would surprise him. Questions concerning mating systems are often difficult to address in the limited time devoted to laboratory exercises. Most such studies require extensive fieldwork, and even then, key events indicating conflict are often rare and difficult to observe. Fortunately, burying beetles will behave naturally and reliably in small enclosures in the laboratory. Additional advantages include:

1. The insects are widespread.
2. They possess distinctive black and red-orange markings on their wing covers.
3. Most locales have a fall-breeding species which is active during daylight hours and thus convenient for academic schedules.
4. It is easy to manipulate the day-night cycle of nocturnal species so they will be active during scheduled laboratories.
5. Beetles are easy to catch in small jars that can be sunk into the soil and baited with liver or a dead mouse.
6. Males and females can be differentiated rather easily (see Figure 1).
7. The only materials required to keep beetles in the laboratory are plastic shoeboxes, soil, food (chicken liver) and dead mice (for experiments).

Most importantly, burying beetles exhibit a variety of fascinating behaviors that can be observed by novice investigators. These include transporting a carcass over the soil surface, cooperative burial of a carcass, shaping a carcass into a brood ball, feeding of young, fights between same-sex individuals over possession of the resource, infanticide, a distinctive pheromone-emitting posture in males, and attempts by the female to terminate male pheromone emission.

General Experimental Procedures

Trapping

Burying beetles can be trapped from late spring until the fall whenever evening temperatures exceed 55° F. Although these beetles occupy nearly all terrestrial habitats in North America (excluding desert), they are caught more abundantly in woodlands with a well-developed canopy. Almost all areas of North America have a fall breeding species. The eastern half of the continent has a particularly distinctive fall breeder which possesses a velvety yellow pronotum (*Nicrophrous tomentosus*; photograph in Scott & Traniello 1989). Beetles can be trapped by placing chicken parts or dead mice in a clean plastic bucket, burying the bucket flush with the soil, and covering with a rain guard. Prop the rain guard up on one side to allow beetles access to the trap. Traps usually will attract beetles for a week.

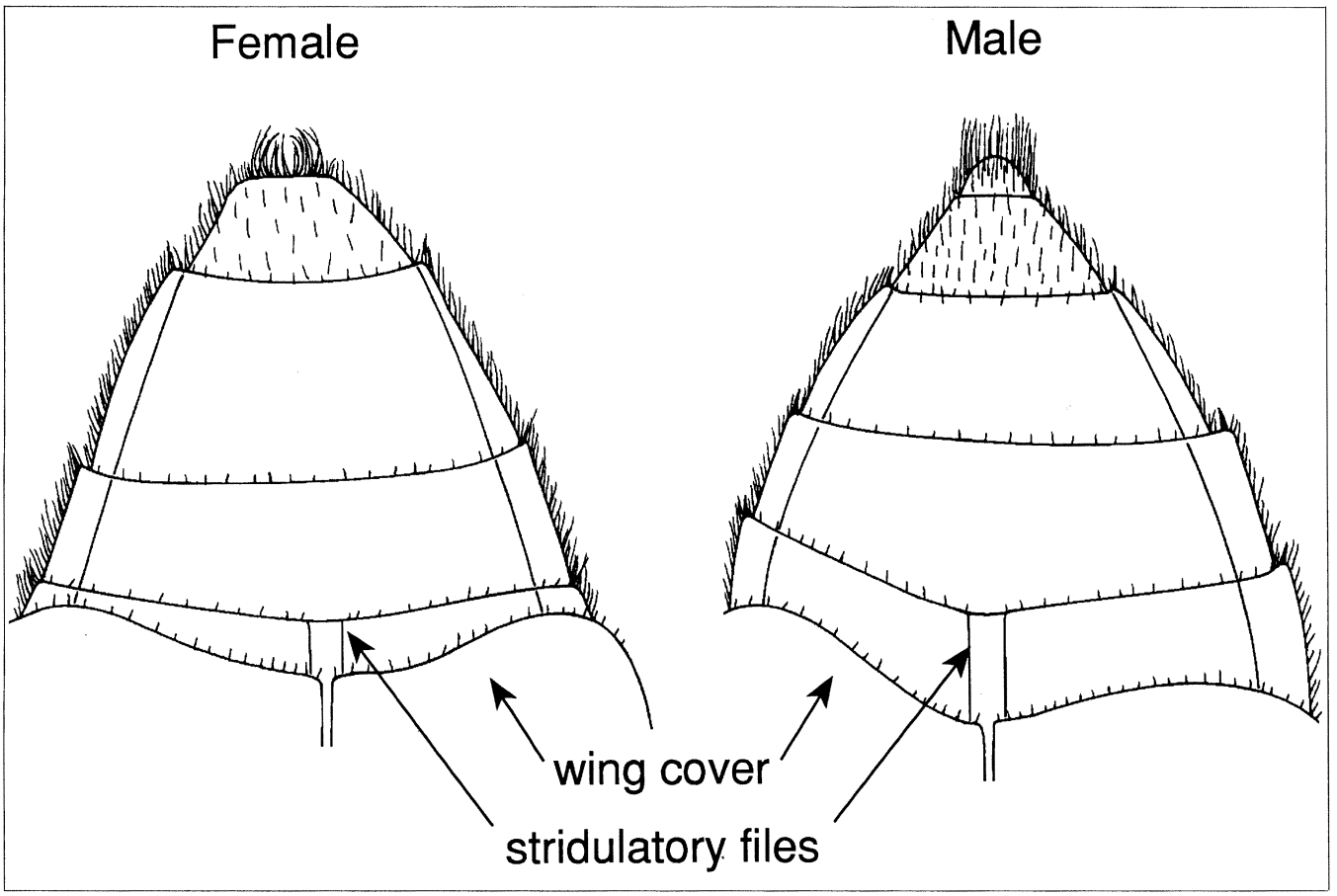

Figure 1. Burying beetles can be sexed by comparing their abdomens. Note the two parallel stridulatory files on the animal. (These can be seen where the wing covers terminate.) Females possess three exposed abdominal segments past the stridulatory file while males have four segments. To facilitate inspection, the abdomen can be gently pressed on the sides to force the last abdominal segment farther out.

Observations

Two basic setups can be used for making behavioral observations, a soil-filled plastic shoebox or an "ant farm" arrangement. For an ant farm observation chamber, two panes of glass are oriented vertically about 1½" apart (slightly more widely spaced than a typical ant farm) sandwiching a slice of topsoil. To use a shoebox, the container is filled with soil three-fourths to the top and covered. Observations of the discovery and early stages of burial of a carcass can be made with either setup. I prefer the ant farm arrangement if observations of the latter stages of burial and carcass preparation are going to be made (see below). Otherwise, the shoebox arrangement is more than adequate for making observations of the burial and parental care, and requires less of an initial investment. If the species of burying beetle that is being employed is not active during the time of day when laboratories are scheduled, the activity period can be changed easily. For example, if your species normally is active immediately after sunset, the beetles can be put on a day-night cycle in which "sunset" occurs just prior to the laboratory period (allow the beetle one week to adjust to this new day-night cycle).

For either experimental setup, I introduce beetles into the container by placing them in a depression in the soil and quickly covering them with loose dirt. These individuals will emerge from under the soil and begin wandering at the start of their next activity period. A frozen mouse can be thawed ahead of time and placed on top of the soil. Initially, I place a glass plate or wire screening on top of the observation chamber to prevent beetles from escaping. After beetles begin work on the carcass, I can remove the cover during observations. I have found that students who remember not to breathe on beetles, jostle containers, or shine lights on experimental subjects see the greatest variety of natural behaviors. I observe beetles under low light, supplemented if needed, by red light. Individual beetles can be marked on their wing covers with Liquid Paper™ for quick identification.

An introduced female or male-female pair will locate the carcass, push it over the soil, and inter it by digging directly underneath. Milne and Milne (1976) provide extensive descriptions of the burial and detail many fascinating interment behaviors. When I want to induce the beetles to move the carcass across the soil prior to burial, I initially place the carcass on a small slab of plywood covered only by a thin layer of soil. Beetles will locate deeper soil off the plywood, and then transport the carcass in that direction by crawling beneath and pushing the carcass while lying on their backs.

If I introduce only a male into the setup, he will usually stay with the carcass for a short while and then leave and search for a perch from

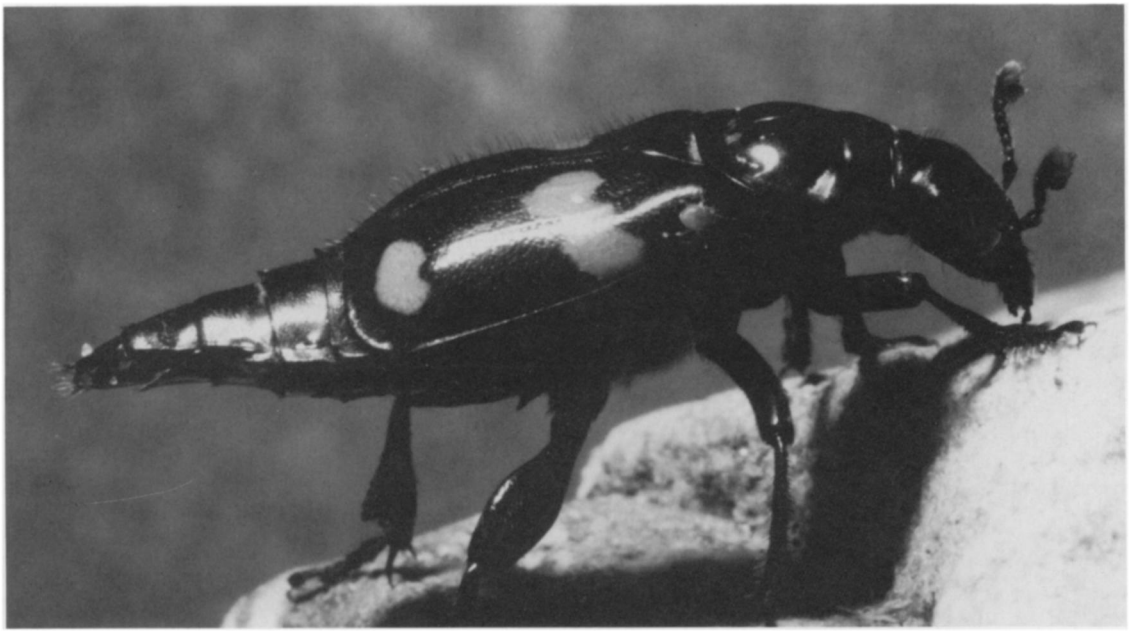

Figure 2. A male in the "handstand" pheromone releasing posture. Note the large lighter shaded markings (orange-red) on the black wing covers.

which to advertise for a female. He does so by climbing a rock or small stick (which can be provided), getting into a handstand posture and releasing pheromone from the tip of his abdomen (see Figure 2). Presumably the male seeks higher elevation so that the signal can be broadcast over a wider area.

Once a male-female pair buries the carcass, the beetles remove the hair, round the carcass into a ball, and deposit anal secretions that help to control the decomposition. Fortunately these secretions reduce somewhat the intensity of odor from the decaying corpse, making observations less unpleasant. After about a day, the female will lay 20–40 oval white eggs in the soil surrounding the carcass (a few can usually be seen through the sides of the container). By day 5, the larvae hatch out and make their way to the nest.

A new set of behaviors can be observed once larvae are on the carcass. When I use the ant farm arrangement, I often find it necessary to clean the glass that makes up the side of the nest. A thin paintbrush can be inserted down the inside of the glass pane and can be used to brush soil to the side. When I employ the shoebox setup, I exhume the carcass carefully and bring it to the soil surface after larvae appear. The adults are reluctant to re-bury a carcass if larvae are present, and if low lighting is maintained. At this time, I can observe adults feeding young (regurgitating liquefied carrion), direct feeding from the carcass by young, and adults attempting to re-cover the carcass (pushing soil back towards the nest) (May 1993). Adults that are feeding offspring make soft audible stridulations which attract their young. These rasping sounds are produced by rubbing the edge of the wing covers over files on the dorsal side of the abdomen (Milne & Milne 1976). During the first 24 hours that young are on a smaller carcass (mouse size usually works), I also witness parents reducing the size of the brood by killing some of their own young. In this way, adequate food reserves remain for surviving offspring. The male parent will almost always leave the carcass before the female (two to four days after larvae arrive; see Figure 3 for a chronology of the reproductive cycle). If I remove the female shortly after larvae arrive on the carcass, however, the male will stay with the larvae until the larvae are ready to leave the resource. This represents a subtle conflict of interest over which parent should be providing care. More overt conflicts are detailed below.

Conflicts of Interest

Conflict over Ownership of the Resource

Intrasexual conflict can be observed during the initial stages of burial. To do so, I first allow a male-female pair to get a one-hour head start in burying a carcass. During the lab period students can introduce a second male and/or female. Allow this "intruder" to crawl out of a small plastic cup (containing some soil) directly onto the carcass. Be sure not to touch the animal directly. (It is wise to have a

DAY	Events of the Reproductive Cycle
1	Discovery of carcass; transport and burial of carcass; intrasexual contests; frequent matings; male emits pheromone if female not present.
2	Removal of hair from carcass; rounding carcass into a ball; anal secretions to control the decomposition; egg-laying in soil near nest.
3–4	Continued nest-making.
5	First stage larvae crawl to the carcass; regurgitations to larvae; parents reduce the number of young if necessary.
6	Second stage larvae; parents continue to feed young; nest repair if necessary.
7	Third stage larvae; larvae depend less on parents and increase feeding directly from carcass.
8	Parental care limited to protection; male parent may leave the nest.
11	Carcass falls apart; larvae disperse.
12	Female parent leaves larvae, flies off, and searches for another carcass.

Figure 3. Chronology of the reproductive cycle. The duration of the cycle and timing of events will vary slightly according to laboratory temperatures and species employed.

backup in case the animal decides to hide in the dirt.) Students should observe biting, chasing and stridulations (much louder than those produced during feeding of young). The larger individual normally prevails and is then able to pair with the opposite-sex beetle.

Conflict over resource ownership also can be observed during the first 48 hours larvae are on the carcass. At this time the carcass is still in good shape and represents an attractive resource to an intruder. The intruder should be introduced by covering it with soil about 6–18 hours before the start of its active period. In this way the intruder will emerge at the start of the active period and quickly locate the carcass. If the intruder is considerably larger than the residents, repeated fights will often ensue. Whereas fights during the burial are intrasexual, fights when larvae are on the carcass can be intersexual as well. The reason is that a successful intruder will take over the carcass and kill all the young, thus saving the resource for its own progeny. Obviously, this represents a threat to both the resident male and female parent.

Conflicts Between Males & Females over Composition of the Breeding Group

A male and female that discover a mouse carcass attempt to hide the resource as quickly as possible from competitors. A larger carcass, however, can support the brood of more than one female. It pays the male, therefore, to attempt to attract additional mates. While a male produces more offspring if he can attract a second or third mate to a large carcass, the first female produces fewer offspring when he is successful in doing so. This represents a clear conflict of interest between the male and first female (Trumbo & Eggert 1994). To examine this conflict, a single male and female can be introduced into an observation chamber, as described earlier, and provided with a large carcass (a small laboratory rat, 40–60 g, will usually do). The male and female initially will interact, copulate, and bury the carcass. A large proportion of males, however, will begin to climb perches and emit pheromone, despite the fact that they already have a mate (such behavior is never seen on a small carcass). Interestingly, females will then locate pheromone-emitting males and attempt to prevent sexual advertisement by pushing, grappling with, and walking on the dorsal side of the male (physically preventing him from getting into the handstand posture necessary for pheromone emission).

Conclusions

The importance of conflict as an evolutionary force has been appreciated ever since Darwin. Although addressing conflict within a breeding system is typically difficult in the laboratory, burying beetles can be successfully employed as model organisms for such a task. Burying beetles can be used to explore intrasexual contests for possession of a critical resource, and intersexual conflicts over the composition of the breeding group, who should provide care, and who should defend the brood against infanticidal intruders.

Burying beetles exhibit a number of additional features that can be brought to the attention of students. These beetles are strikingly outfitted in red and black which is thought to warn possible predators of the beetles' distastefulness. Burying beetles also carry large mutualistic mites which can easily be seen with the naked eye. These mites disembark quickly after a carcass is discovered and benefit their host by destroying carrion fly eggs. The mites, in turn, use the beetles as transportation between carrion resources. Although the beetles can be quite aggressive, same-sex individuals often will cooperate in nest-making when the task is difficult, such as when exploiting a large carcass. Cooperation is developed to the extent that individuals will feed each others' young. Burying beetles thus are a rich biological system for exploring many prominent issues in modern evolutionary biology.

References

Darwin, C. (1871). *The descent of man, and selection in relation to sex.* Princeton, NJ: Princeton University Press.

May, M. (1993). Coleopteran child care. *American Scientist, 81,* 20–22.

Milne, L.J. & Milne, M. (1976). The social behavior of burying beetles. *Scientific American, 235,* 84–89.

Scott, M.P. & Traniello, J.F.A. (1989, June). Guardians of the underworld. *Natural History,* 32–36.

Trumbo, S.T. & Eggert, A.K. (1994). Beyond monogamy: Territory quality influences sexual advertisement in male burying beetles. *Animal Behavior, 48,* 1043–1047.