

DECOMPOSER INSECTS

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In any natural or semi-natural habitat, three types of organisms exist: producers, consumers and decomposers. Good functioning of the ecosystem will depend on their suitable action and interaction. Organisms capable of catching energy and synthesizing organic matter from inorganic compounds constitute the producers. Though chemosynthetic bacteria exist, most producers are plants. Green plants use solar energy and fix CO₂, producing organic compounds rich in energy. Most of this accumulated energy will get used in the ecosystem by respiratory processes and other vital functions, whereas some organisms of the community such as the consumers and decomposers will use the energy accumulated by other organisms.

The consumers are heterotrophic organisms that obtain food from producers or from other consumers, with the possibility of several levels of complexity inside an ecosystem. Primary consumers feed directly on the producers. Secondary consumers feed on primary consumers, etc. Finally, we have the decomposers, saprophytic organisms feeding on dead matter or decaying remains derived from producers and consumers. Thus, the organic matter synthesized by producers goes on to other levels of organisms across the trophic chains, though much of the energy will be used in respiratory processes at all levels.

In these trophic processes, an important element to take into account is

that the decomposers operate at all the levels. Thus, all energy not used by the consumers and producers, as well as that accumulated in excretory products, is used by the decomposers and recycled into the ecosystem. This process constitutes the energy cycle, and good functioning and subsistence of the ecosystems depends on effective energy cycling.

In a terrestrial ecosystem, more than 90% of the organic matter synthesized by the green plants remains unconsumed, and it passes to the level of decomposers as plant material decaying on soil, together with the remains of animal corpses, and the excretory products of all levels.

The process of decomposition is one of the most important events in the functioning of ecosystems. Decomposition can be defined as the process by means of which a dead organism or its remains are broken down into the parts or elements that comprise it, and at the end of the process the animal or plant remains will have gradually disintegrated until their structures cannot be recognized, and their complex organic molecules will have fragmented. This involves a complex process in which biotic and abiotic agents interact within the ecosystem. To sum up, the decomposition processes cause the liberation of energy and mineralization of chemical nutrients, turning the organic matter into inorganic elements.

In the process of decomposition, there are two phases, sometimes

difficult to distinguish, that we could call 'destruction' and 'degradation' of the organic matter. The process of destruction refers to the initial phase of the decomposition cycle and is characterized by breaking down the organic remains by mechanical means so that at the end of this process small-sized particles are obtained. During this initial phase both abiotic (rain, wind, temperature, etc.) and biotic elements (decomposer fauna) play an important role. In the second phase, degradation of the organic matter occurs, resulting in the disintegration of the small particles into molecules, producing CO₂, H₂O and mineral salts as final products.

The destruction phase also results in dispersion of the organic matter, because the small resulting particles can be taken by means of diverse mechanisms out of the initial source (dragging by wind and water, or direct action of animals such as burial, ingestion, movement, etc.). It is important to note that nutrients released by decomposers constitute a food source for numerous animal species, extending the cycle by means of incorporation of the nutrients into tissues, and eventually constituting new corpses and excrements.

The groups of arthropods involved in the processes of decomposition of animals and plants remains belong to many taxa (Fig. 1). They are considered to be mesofauna when their size ranges between 100 and 200 µm (such as mites (Acari), springtails (Collembola) and small insects), or macrofauna when they are larger, such as some beetles (e.g., Scarabaeidae, Geotrupidae or Silphidae), Diptera larvae (e.g., Muscidae, Sarcophagidae, Scatophagidae or Calliphoridae),

centipedes (Diplopoda), woodlice (Isopoda), etc. All these groups are responsible for the fragmentation of plant or animal remains, contributing to the destruction phase. They contribute both to the redistribution of the organic remains and formation of soil elements. These groups of arthropod decomposers are present in nearly all terrestrial habitats, and generally in very high numbers. In some cases, millions of individuals belonging to hundreds of species have been identified in just one square meter. Especially in temperate areas, arthropods are the major decomposers, playing a very important role in degradation of waste. Thanks to the action of the arthropods during the initial phase of fragmentation, organic remains can be degraded, and eliminated from the soil surface.

When a suitable community of decomposers exists, it prevents the appearance of potential bottlenecks in the recycling of basic elements in the ecosystem. Thus, when entomofauna capable of acting effectively on plant and animal remains does not exist in a terrestrial ecosystem, serious alterations in the ecosystem arise, with a reduction in energy flow and great loss of biodiversity.

Decomposers of plant remains

Arthropods play an important role in degradation processes of plant remains. Nevertheless, most lack the ability to develop enzymatic processes for degrading the fundamental components of any plant: lignin and cellulose. Degradation of cellulose requires the presence of the enzyme cellulase, which most arthropods lack. Many insects have solved this problem by means of mutualistic relations with micro-organisms, having bacteria or

symbiotic protozoa in the intestinal tract. Others take advantage the cellulase produced by external microflora. Among the well-known insect decomposers are termites (Isoptera) and cockroaches (Blattodea). The termites possess symbiotic bacteria and protozoa, and in their absence wood cannot be assimilated by these insects.

In many ecosystems millipedes (Diplopoda) have special importance as decomposers. These arthropods, which specialize in leaf litter consumption, sometimes are abundant, concentrated in relatively small areas, and active during a great part of the year.

Another important group in the degradation of plant remains is woodlice (Isopoda), which also possess symbiotic microorganisms in their intestine that allows them to degrade cellulose.

Not all arthropods assimilate cellulose by means of symbiotic bacteria, but they make use of woody materials that are pre-digested by extraintestinal microorganisms. Included in this group are some species of springtails such as *Tomocerus* (Collembola), ambrosia beetles (Coleoptera: Scolitydae), ants of the genera *Atta* (Hymenoptera: Formicidae) and termites (Isoptera) that cultivate fungi.

All plant remains do not always present the same difficulty of digestion for arthropods. Fruits are extensively exploited by arthropods, thanks to the existence of yeasts that enhance fruit decomposition, allowing many arthropods such as flies (*Drosophila* is probably the best known example) and wasps (Hymenoptera: Vespidae) to feed into the product resulting from the fermentation. Nevertheless, a fact that must be remembered is that the relationship between micro-organisms

(bacteria, fungi and protozoa) and plant remains is very close, and therefore, in most cases it is inevitable that the arthropods consume both resources simultaneously. In some cases, the ingested biomass of micro-organisms is more important nutritionally than the ingested plant remains.

The entomofauna of excrement and corpses

The studies of ecosystems have generally paid preferential attention to the decomposition processes of vegetative remains, due to the importance that litter has in the composition of the soil and the contribution of its nutrients. The process of decomposition of carrion and dung, though sometimes not well known and little studied in many ecosystems, is also important.

To understand the processes of degradation of corpses and excrements, and the attractiveness of this decaying matter to arthropods, we must consider that they are very rich resources of organic components that have very special microclimatic conditions. Dung and carrion represent not only a rich source of energy, but also a very specialized habitat that is exploited, in most cases, by very specific entomological fauna. This fauna obtains food either directly, such as in the case of the coprophages and carrion-eating arthropods, or indirectly, such as in the case of the predators that feed on the decomposers.

It is generally difficult to establish the limits of an arthropod community, but when we study carrion or dung we meet a perfectly defined ecological unit, limited in both space and time. Carrion (Fig. 2) and dung present many special characteristics that influence the

composition and dynamics of the set of species using them. These resources constitute isolated microhabitats inside an ecosystem in which they are deposited, forming a patchy system. These microhabitats are relatively small in size (except for corpses of large vertebrates), rich in nutrients, and with a short existence (generally not more than one insect generation). Carrion and dung are special microhabitats characterized fundamentally by their rapid ecological successions, being extremely ephemeral micro-ecosystems that are rapidly destroyed by the action of the arthropods that colonize them. Arthropod species are sometimes very abundant in these resources, and thousands of individuals belonging to a set of arthropod decomposers may be attracted to an isolated unit. For example, more than 100 species of arthropods belonging to 16 orders and 48 families have been found in just one rabbit corpse, or 16,000 dung beetles found in elephant dung.

The arthropods involved in succession vary according to geographical areas, even in places with similar climates. Also, the number of individuals and the species colonizing these microhabitats vary enormously from one patch to another, and also through time. Typically, these species are more or less aggregated in these limited resources, with interspecific differences in foraging and breeding behavior. The aggregated spatial distribution and resource partitioning allow a great number of decomposer species to coexist in an ecosystem, but great differences in numbers of individuals and species composition are generally found among similar amounts of carrion or dung. However, the broad

taxonomic categories of carrion or dung specialists are similar worldwide.

Sometimes it is difficult to discern whether the arthropod fauna involved in decomposition processes contributes directly to the recycling of organic matter or, as in leaf debris systems, they make the substrate more available to the microorganisms (bacteria and fungi) considered by some authors to be the true decomposers. The action of the larvae of flies and other insects, for example, produces liquefaction of corpse tissues, preparing the substratum for the intervention of microbial decomposers. On the other hand, the mechanical action associated with removal of excrement by beetles, and in making tunnels by both beetles and fly larvae, enhances microbial activity. The existing studies show that the action of decomposer species of arthropods and microorganisms is complementary, but not purely additive.

Vertebrates are often considered to be important scavengers, and many species feed on carrion. Vertebrates may not distinguish between freshly killed prey and a freshly dead animal, and many predators eat both of them. It is not easy to know how much organic matter is recycled in this manner, but depending on the period of the year, many of the small animal corpses can be totally destroyed by scavengers. However, during summer and autumn in temperate regions, and in the rainy period in tropical areas, corpses are rapidly colonized by arthropods. As a result, rapid decay is observed, with the vast majority of carrion being consumed by various arthropod species, principally fly larvae.

The process of decomposition among excrement and corpse systems varies as a result of the particular

composition of the remains, which attracts its own specialist community of arthropod decomposers. Likewise, differences between the entomological fauna of excrement are found, especially between the excrement of carnivores and those of herbivores. This occurs because the composition of nutrients is totally different between carnivore and herbivore excrement. While the excrement of herbivores contains a great number of vegetative components that are little changed from the plants ingested (80-75% of the ingested weight), the digestive system of carnivores is much more efficient and the excrements contain less organic matter suitable for exploitation by arthropod species. The fauna feeding on the carnivore excrement is generally depauperate, and decay often results exclusively from the actions of microorganisms.

Decomposers of corpses

Arthropod species attracted to corpses change according to the ecosystem and environmental conditions. The importance of necrophagous arthropods is not only the ingestion of carrion, but also in making the carrion available to microorganisms. Many insects, principally fly larvae, secrete enzymes directly into the carrion, producing liquefaction of the tissues. Likewise, adult and larval beetles, and fly larvae, make tunnels through the carrion, increasing aeration and microbial activity. The dominant groups, both in number of individuals and diversity, are dipterous and coleopterous species. Also, in geographic areas where ants are abundant, the corpses are removed rapidly by these insects, specially the corpses of invertebrates. Nevertheless,

the arthropods involved in this processes, and the intensity of the action of these animals, vary according to the spatial location of the corpse, type of soil and depth of burial. The number of insects living in carrion diminishes with depth of burial.

The arthropods colonizing corpses form a sequential succession of groups and species that depends on the size of the carrion, and on the climatic and edaphic conditions of the area where they live. Very few species are widespread throughout the world, and each geographical area and ecosystem has its specialist species feeding on carrion.

The colonization of a corpse is a sequence of arthropods arriving as successive waves at the carrion. The form, nature and timing of the succession depend on the geographic area, the surrounding non-biological environment, and the size of the carrion. The first waves involve blow flies (Diptera: Calliphoridae) and house flies (Diptera: Muscidae) arriving for a few hours to oviposit or drop live larvae. Later, there is a second wave of sarcophagid flies (Diptera: Sarcophagidae) that together with species of calliphorid and muscid flies, deposit their eggs or live larvae on the corpse. The larvae of these flies are, in turn, consumed by larvae and adults of predatory beetles living in corpses. Staphylinids (Coleoptera: Staphylinidae), histerids (Coleoptera: Histeridae) and silphids (Coleoptera: Silphidae), all are predators of flies, though they also feed on carrion. When the viscera decompose and the fat of the corpse turns rancid, a third wave of insects starts, with some species of phorids (Diptera: Phoridae), drosophilids (Diptera: Drosophilidae) and hover flies

of the subfamily Eristalinae (Diptera: Syrphidae) arriving. The fourth wave consists of cheese skipper species (Diptera: Piophilidae) and related families of flies. Finally, a fifth wave occurs, the larvae and adults from some groups of beetles such as dermestids (Coleoptera: Dermestidae), trogids (Coleoptera: Scarabaeoidea: Trogidae) and clerids (Coleoptera: Cleridae) and tineid caterpillars (Lepidoptera: Tineidae) that eat keratin and feed on the remaining hair and feathers.

Diptera are among the most important decomposers, especially some of the Calliphoridae (e.g., *Lucilia*, *Calliphora*, *Chrysomyia*, etc.), followed by some Muscidae (e.g., *Fannia*), and Sarcophagidae (e.g., *Sarcophaga*). Though the adults feed on the fluids of the corpse, the larvae are the true decomposer organisms, secreting enzymes directly into the carrion and helping with the liquefaction of the corpse tissues while assisting the increase of microbial activity. These families of Diptera are more abundant from early summer to mid autumn in temperate regions, and also in the rainy season in tropical areas.

The biology of all the Diptera species is similar. Females of blow flies and house flies lay eggs or drop live larvae on to the surface of the fresh corpses, generally at the base of the hairs or near to the natural holes. Such natural openings facilitate the penetration of larvae into the inner regions of the corpse. The ovoviparous females of sarcophagids are less fecund than blow flies and house flies, and do not deposit all their larvae in the same carrion, rather distributing them evenly among several corpses. Development of fly larvae is normally very fast (3 to 6 days during the favorable periods of the

year) and pupation takes place away from the corpse, in the soil surrounding it. Sometimes the mature larvae may migrate more than one meter from the carrion. Ten to 30 days after pupation, the new adults emerge and fly off to search for new corpses, starting a new life cycle.

Among Coleoptera, a principal group in many temperate ecosystems is Silphidae (e.g., *Nicrophorus*, *Silpha*). It is a group specifically adapted to living in carrion and its action is comparable to that of the Diptera. The adults of *Nicrophorus* species show a very special biology. When a species of this genus arrives at the fresh corpse, the male and female bury the carrion underground (Fig. 3), thereby reducing the risk of colonization by other insects. Once the carrion is safe in the burial chamber, and the beetles have copulated, they make the corpse into a ball. The eggs are deposited into a short chamber above the carrion ball. The female makes a conical depression on the top of the ball, and defecates and regurgitates droplets of partially digested food, and stridulates, attracting the larvae to the depression in the carrion. The female, and sometimes the male, give parental care and provide food by regurgitating into this depression. Thus, they ensure the survival of the offspring and avoid predation and competition.

In tropical forests, many species of Scarabaeinae are attracted to both carrion and dung. Availability of resources for dung beetles in most Neotropical forests is low because of the low density of large mammals and the low availability of any particular type of dung. This absence can probably be attributed to the absence of suitable numbers of large herbivores in the

forests of Central and South America, and the few natural pastures of this region (except where cattle have been introduced). In African forests, where large herbivores are present in relatively large numbers, many dung beetles specialized in the use of excrement may be found.

Forensic entomology

Knowledge of the succession of species taking place in a corpse following death has been used in studies of forensic entomology. This rather consistent succession has been used for medical legal analyses to estimate the time elapsed since death of an animal. The study of arthropod species from a cadaver gives us information about the location, time, and conditions to which the corpse was exposed before being found. The generalized sequence of fly colonization is most frequently used. The first colonizing species are the bigger flies belonging to the blow fly family (Calliphoridae) followed by sarcophagids (Sarcophagidae) and house flies (Muscidae). The adults of the lesser-sized families such as Psychodidae, Scatopsidae, Sciaridae, Phoridae, Sepsidae and Sphaeroceridae come to the corpse in the last phase of decomposition, after the corpse has been abandoned by the larvae of the first colonizing flies. Their larvae leave the corpse to pupate away from the larval site, normally in the ground or substrate below carrion. The development of larvae is temperature dependent, and knowledge of the larval cycle and its relationships at different temperatures, can be used to estimate of age a cadaver. Forensic entomology is an important instrument in criminal investigation; however, we must take

into account that each succession will consist of different species in different geographical regions. This is true even in sites with similar climatic conditions, because few species are widespread in distribution, and each area may have its own carrion-feeding species.

Nevertheless, the broad taxonomic levels of decomposers of carrion are constant worldwide. Also, some differences may be found as a result of variation in ambient temperatures that may speed the process (sunlight and high temperatures) or retard it (shelter and cold conditions), variation in exposure of the carrion, possible burial of the corpse, cause of death, etc.

Some carrion-feeding flies can cause myiasis, an infestation of live vertebrates by larvae of Diptera, particularly blow flies of the genera *Lucilia*, *Chrysomyia*, *Cochlyomyia*, etc., that feed on live or dead tissues of the host. This infestation causes problems in some farming areas, and may be of considerable economic importance. Probably one of the best known examples of myiasis is with *Cochliomyia hominivorax* (Diptera: Calliphoridae), a species living in neotropical regions. Larvae of *C. hominivorax* develop on wounded animals and humans, and can provoke the death of the host.

Decomposers of excrement

The excrement of vertebrates generally is a rich source of nutrients, and insects play an important role in the rapid recycling processes of feces. However, carnivorous excrement contains little material useable by insects because of their efficient digestive process. In contrast, the digestive system of herbivores is less efficient, and the dung produced is quite similar to the original leaf material. More

than half the food consumed by herbivorous animals is returned to the ground in the form of unassimilated material, i.e., dung. Because it is abundant in organic matter and moist, herbivore dung is an ideal medium for establishment of a specific, rich entomofauna involved in the process of decomposition and elimination of feces. Quantitatively, large herbivore dung pats are the most important resource for dung beetles in most regions, and this fauna is especially abundant in historic grazing areas.

Excrement is a very special habitat for coprophagous species, and the spatial distribution of dung increases the tendency of these insects to concentrate in a limited space. The process of colonization of excrement typically consists of three waves of insects. The first wave of colonizers involves certain flies arriving within hours to lay eggs or larviposit on the dung before a crust is formed on the pat. The second wave is several families of beetles. Lastly, mites become abundant.

The main groups of flies are Muscidae and Scatophagidae, followed by Fanniidae and Calliphoridae. Most adults and larvae of flies are coprophagous, but feeding also on the micro-organisms present in the dung. Others are facultative or obligate predator species. Many species are attracted to any decaying matter, but others only feed and breed in dung. Throughout the world, muscid coprophages such as *Musca domestica*, *Musca vetustissima* and *Haematobia irritans* are pests of cattle. But some muscids are facultative predators (e.g., *Muscina* spp.) and obligate predatory larvae (e.g., *Mydaea* spp.). The best-known species of Scatophagidae is

probably *Scatophaga stercoraria*, a species frequently found visiting dung anywhere in the Northern Hemisphere, and also in northern and southern Africa. *Scatophaga stercoraria* has coprophagous larvae, but adults are primarily predators or nectar feeding, only occasionally feeding on liquefied dung.

Females of flies may lay eggs in batches of about 150, which hatch in from 8 to 10 hours, to three days, depending on the environmental conditions and the species involved. Muscid larvae may complete their development within two days in favorable environmental periods, or delay several weeks in the colder temperatures.

Among beetles that use dung resources, the dung beetles belonging to the Scarabaeidae (Scarabaeinae, Geotrupinae and Aphodiinae) are the most important and numerous. Not all scarab larvae are strictly coprophagous, and some ingest soil organic matter or feed on roots of plants. However, many are coprophages, and often exceedingly abundant. Thousands of individuals from many species may be found colonizing single dung pats in temperate and tropical grazing ecosystems. Most Aphodiinae are saprophagous and within the Geotrupinae coprophagy is the rule for the Geotrupini. Only Scarabaeinae has coprophagy as a characteristic of most of its species. In this case, most of the nutrients eaten by the adults are derived from eating microbes or colloids suspended in dung. The larvae feed on the dung supplied by their parents in a nest chamber.

Various other groups of beetles visit dung but they are primarily predators. Coleoptera of the families Hydrophilidae, Staphylinidae, and

Histeridae are associated with carrion as predators of larvae of flies and dung-beetles. However, the two former families also include coprophagous species. In the temperate region, the hydrophilids *Cercyon* and *Sphaeridium* (Coleoptera Hydrophilidae) are coprophagous, arriving within the early hours after deposition of dung.

The behavior of dung beetles (Coleoptera: Scarabaeidae) is specialized and diversified in response to exploitation of excrement by adults and larvae (Fig. 4). The Scarabaeidae consist of approximately 7,000 species (5,000 Scarabaeinae, 1,900 Aphodiinae and 150 Geotrupinae). Many species of Scarabaeinae and Geotrupinae have developed special feeding and breeding strategies that allow them to remove dung rapidly the soil surfaces by digging burrows below the dung pad to store fragments of dung in tunnels. They also may form dung into balls and roll them away from the pad for burial far from the food source. The importance of these habits is the protection of food for adult or larvae, avoiding competitors, predators and unfavorable climatic conditions. Only Aphodiidae do not make a nest. Aphodiidae eat directly into the dung and many species deposit their eggs directly in dung pads without nest chamber or in the surrounding soil. Geotrupinae and many tribes of Scarabaeinae are tunnelers. These species dig a tunnel below the dung pad and accumulate dung in the bottom of the burrow; this food can be used either for adult or for larval feeding. Finally, some species of Scarabaeinae are rollers, making a ball of dung that is rolled away from the pad for a variable distance before burying.

One of the most important aspects of the biology of Scarabaeinae

and Geotrupini is their nesting behavior. Geotrupini nests are the most primitive and consist of simple burrows filled with 'sausages' of dung, usually containing one egg each.

The reproductive biology of Scarabaeinae has several distinct patterns, which have been reviewed and compiled in comprehensive and wonderful books by Halffter and Matthews (1966) and Halffter and Edmonds (1982). The process of nesting involves the creation of a place in the soil where a supply of dung is accumulated for development of larvae.

Scarabaeinae nesting frequently involves bisexual cooperation of a pair of beetles, for either short or long periods of time, and parental care sometimes exists. The adults make brood balls in the protected nest, each of which contains the amount of food required for larvae to enable them to complete larval development. Nesting behavior is considered as an adaptation to isolate immature larvae from each other and from adults, increasing the survival of offspring. Obviously this is a process that requires the investment of considerable time and energy on the part of the parents. Nesting derives from feeding behavior and basically corresponds to food relocation: tunneling and ball rolling.

The tunneling scarabs take food from the dung pad and bring it into a previously excavated gallery. Various types of nesting have been described for tunnelers, and it is sometimes difficult to ascribe a particular type of nesting to a species.

The most primitive and simplest nest behavior is observed in some genera of Dichotomini, Oniticellini, Onitini, and also Onthophagini. A female digs a simple burrow, fills it with food,

forms a brood mass and provides a single egg. In this case, there is no bisexual cooperation or maternal care, and the species involved show relatively high fecundity.

Other groups of dung beetles make nests containing several or many brood masses such as those observed in some species of Dichotomini, Onitini, Onthophagini and Oniticellini. The brood masses are constructed in series, in the same tunnel or separated in individual side branches. In this type of nesting, bisexual cooperation may exist, but the role of the male is restricted to introducing food into the tunnel. These species have relatively high fecundity, and there is no maternal care.

Coprini and several Dichotomini, Onitini and Oniticellini species construct nests that contain several spherical brood masses arranged in a single or branched tunnel with or without separation.

Some scarabs produce a nest containing only a few brood balls in a chamber, and physically separated from other chambers. This nesting behavior is present in species with low fecundity: Phanaeni (without maternal care), several Dichotomini (with or without maternal care), and several Coprini (with maternal care).

Finally, the species of *Oniticellus* (Oniticellini) show endocoprid nesting behavior: digging burrows and making brood chambers in the dung pat, where nesting takes place. The species of this genus present moderate to extensive maternal care.

The roller habit of food relocation is only present in some tribes of Scarabaeinae: Scarabaeini, Chantonini, Gymnopleurini and Sisyphini. Species of these groups make a brood ball that is rolled away from the pat. The weight of

the ball can be up to more than fifty times the weight of the beetle. The process is initiated by one partner and the ball acts as a sexual display to the other sex. The brood ball also may be rolled by two partners, but sometimes the female is transported on the ball. Combat is common between members of the same species when rolling balls. Generally, sexual cooperation finishes when copulation takes place in the burrow, after which the male leaves the female. Females prepare 4 to 5 pyriform brood balls and lay eggs in a narrow cavity at the upper end of each pair. The female may abandon the nest after oviposition, such as in Scarabaeini, Canthonini, Gymnopleurini and Sisyphini, or they can remain in the nest until the offspring emerge, as has been described for the African genus *Kheper*.

Finally, there are some species of dung beetles that demonstrate special feeding and nesting biology. They are species using part of the food resources accumulated by other dung beetle species in burrows or a breeding chamber. These species are called kleptoparasites, and examples are found in Aphodiidae and Scarabaeidae. These species live as parasites in the nest prepared by either roller or tunneler dung beetles.

Beneficial actions of decomposer insects in ecosystems

The viability of every ecosystem is based on the normal functioning of its nutrient cycle. This is a very complex ecological process with a great number of components, including decomposer organisms. The activity of decomposers benefits humus formation in the soil, and the availability of nutrients for plants. This feature is especially evident in pasture ecosystems, where an

indispensable condition for correct functioning is that the cattle dung is rapidly used and transformed. If this does not occur, dung deposited on the soil may eventually cause serious damage because it deteriorates the pastureland by preventing plant growth.

When pats are not removed, they cover the pasture, inhibiting the growth of grass. The effect is a loss of available surface for cattle. Several authors have reported several estimates of the loss of pasture. In the U.S.A., for example, Fincher (1981) reported that cattle continuously covered more than 300 hectares of pasture with dung each year.

Dung pats remaining on pasture have a noxious effect because cattle do not graze on the rank growth around these cowpats. Refusal by cattle to graze on pasture grass growing near dung is a response to the offensive properties of the dung itself. Furthermore, most of the valuable nutrients of the unburied pats are lost. For example, 80% of the nitrogen content in a pat may be lost, but when adequate numbers of dung beetles are present and efficient burial by dung beetles exist, the nitrogen loss is reduced by 15%, with the nitrogen held by soil colloids. Another potential benefit of dung beetle activity is the increase in pasture by the incorporation of organic matter into the soil and increases in soil aeration and water content.

Several authors have mentioned the possible role of dung beetles in reducing infestation of livestock by worm parasites. Feces remaining on the soil could be an incubator for parasite worm larvae. If dung beetles bury these feces before parasites reach the infectious stage, the parasitism of cattle can be minimized. Dung beetles are also useful

agents in the control of flies breeding in dung. The scarabs compete with fly larvae for food, reducing the amount of breeding by depriving the flies of food.

Some authors have calculated the economic value of the role recovered by dung beetles in pastures. Fincher (1981) estimated that the agricultural sector in the U.S.A. would have potential benefits of more than 2000 million dollars a year if suitable fauna were present for rapid burial of cattle dung. The value of dung beetles in pasture ecosystems was first observed in Australia, where dung beetles were introduced to help solve the problems of loss of pasture surface and increase of flies breeding in dung. The Australian pasture was profoundly disturbed by domestic animals brought by the first European settlers who arrived 200 years ago. The native dung beetles were adapted to the dung pellets of kangaroos and other marsupials, not to the large grazing and browsing herbivores. The large, voluminous accumulated dung of horses, cattle, and sheep generated a pollution problem as a result of its unattractiveness for the native beetle fauna. In Australia, a program of dung beetle species introduction was proposed by Bornemissza about 1960 and several species of scarabs from South Africa, France and Spain, adapted to use the dung of domestic cattle in open pastures, were established successfully. These beetles were introduced to help solve the problems of pasture degeneration and increase of populations of fly pests breeding in dung.

See also, FORENSIC ENTOMOLOGY.

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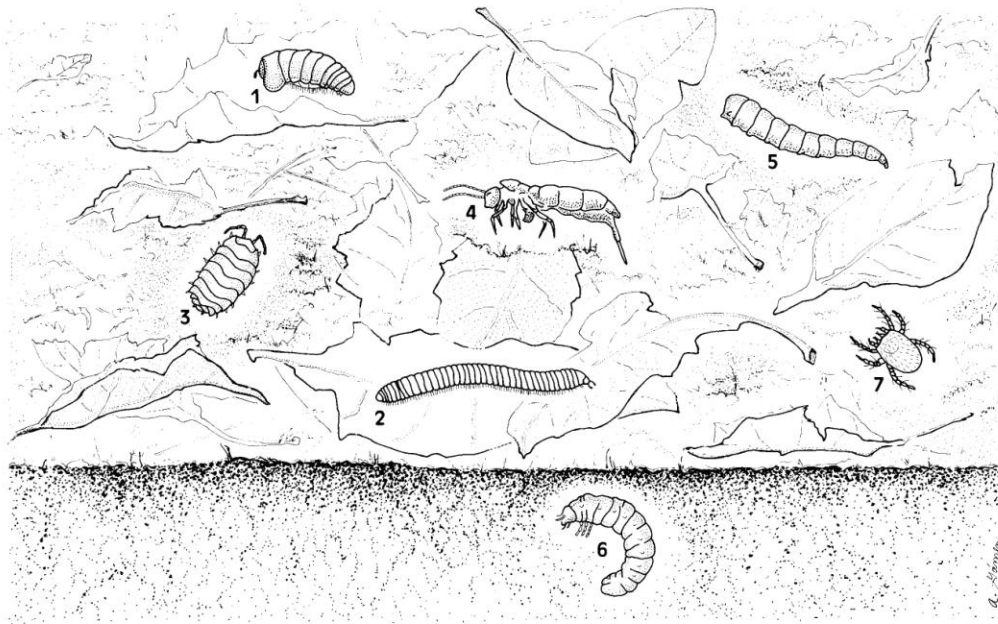


Figure 1. The arthropods involved in the process of decomposition of animal and plant remains belong to such taxa as Diplopoda (1 and 2), Isopoda (3), Collembola (4), Diptera larvae (5), Coleoptera (6), Acari (7).

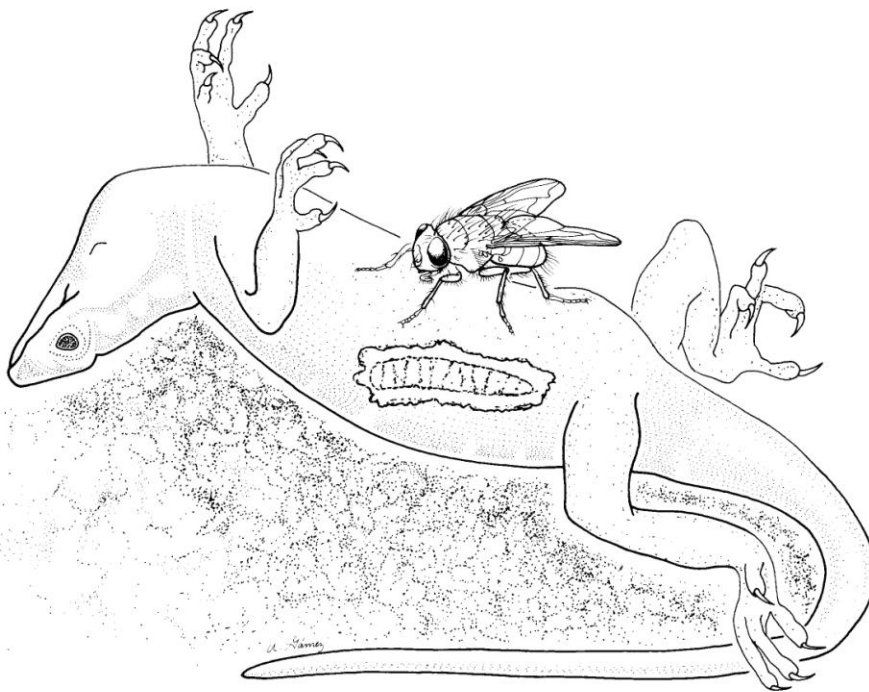


Figure 2. Adult and larva of a blow fly (Diptera: Calliphoridae) on a lizard cadaver. Blow flies constitute the first wave of insects colonizing corpses.



Figure 3. Male and female *Nicrophorus* (Coleoptera: Silphidae) burying a mouse corpse underground. These insects are specifically adapted for living in carrion.

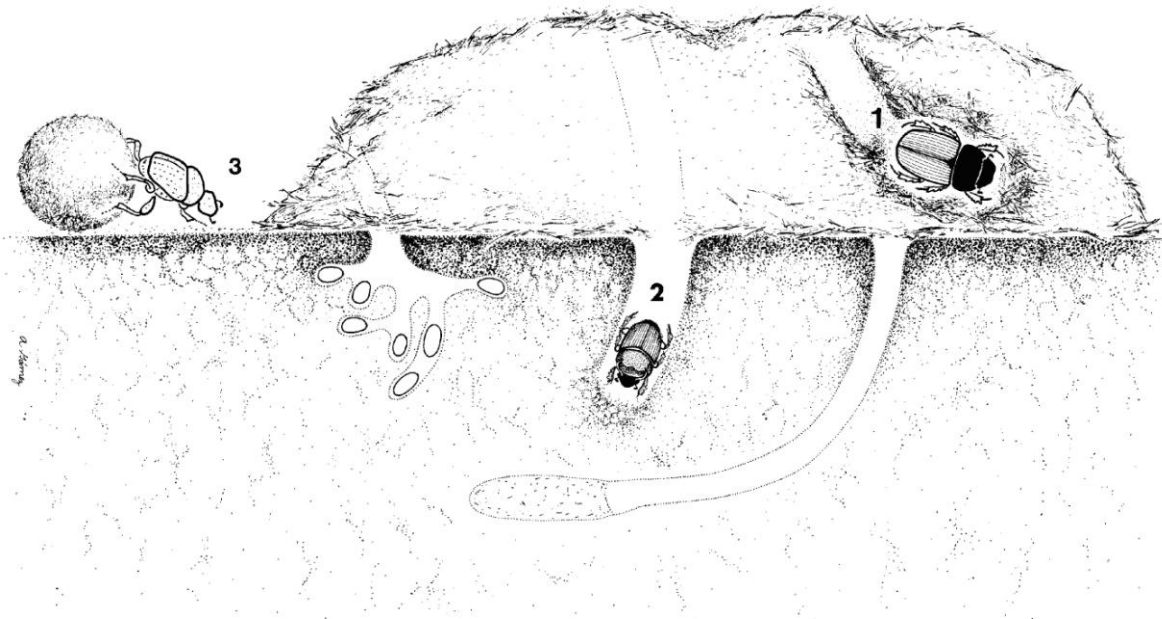


Figure 4. Behavior of dung beetles (Coleoptera: Scarabaeidae) is both specialized and diversified to allow exploitation of excrement. Aphodiinae do not make nests, and dwell within the dung (1). Geotrupinae and many tribes of Scarabaeinae are tunnelers (2). Some tribes of Scarabaeinae are rollers (3), making a ball of dung that they roll away from the dung pat.