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Social Beetles

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Synonyms

Ambrosia beetle; Bark beetle; Bess beetle; Burying beetle; Darkling beetle; Dung beetle; Fungus beetle; Rove beetle; Stag beetle

With about 400,000 species, beetles (Coleoptera) are the largest order of animals, making up almost 40% of described insect species and 25% of all known animal species. Beetles are present in virtually all habitable terrestrial environments. They can live well both on land and in fresh water and use a great variety of food sources from detritus to living fungi, plants, and other animals. Very few species live in durable structured groups, but social structures of various kinds are nonetheless diverse. These include larval and adult aggregations, prolonged uni- and biparental care, facultative eusociality, and possibly even obligate eusociality [3].

A very small number of these social systems are well studied, such as parental care in burying beetles (Silphidae) and adult aggregations in tree-killing bark beetles (Curculionidae) [5]. It is regrettable that the present database is so meagre, as beetles are an extraordinary group for the comparative study of the ecological, behavioral, and genetic drivers of social evolution. There is variation within and between lineages in proposed drivers of sociality, such as ploidy (haplodiploidy, diploidy), mating system (monogamy, polygamy, inbreeding), and ecological conditions not found in other animals [2].

Aggregation – especially of adults – is present in so many beetle taxa that it is not possible to give a number of independent evolutionary origins. Larval aggregations and subsociality (i.e., prolonged parental care) are less common but have been documented in at least nine of the 176 beetle families, Chrysomelidae, Curculionidae, Erotylidae, Lucanidae, Passalidae, Scarabaeidae, Silphidae, Staphylinidae, and Tenebrionidae, and probably Silvanidae (Table 1). Currently the greatest known number of independent origins of subsociality is in dung beetles (Scarabaeidae, eight origins), followed by weevils (Curculionidae, six origins) and leaf beetles (Chrysomelidae, five origins).

Many of the social taxa are described in just one or very few reports, so it would not be surprising if many more group-living beetles were discovered in the next period. Here we give a brief

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Social Beetles, Table 1 Overview of social beetle families and their ecology

Family	Social forms[a] (no. of origins)	Nests of most social species	Food of most social species
Chrysomelidae	LA, MC (5)	Free nesting	Phytophagous
Erotylidae	LA (3), MC (1)	Free nesting	Fungi
Silvanidae	CB, BPC? (1)	In petioles	Honeydew
Lucanidae	MC (1)	In wood	Rotting wood
Passalidae	BPC, OG, APC (1)	In wood	Rotting wood
Scarabaeidae	BPC (8)	In soil ground	Animal dung
Silphidae	BPC (1)	In soil	Carrion
Staphylinidae	MC (3)	In substrate or soil	Fungi, dung, or algae
Curculionidae	LA, CL, CB, MC (6), BPC, OG, APC, RDL (2)	In wood	Phloem, seeds, or farmed fungi
Tenebrionidae	CL, CB, BPC, OG, APC (1)	In soil	Phytophagous

[a]*LA* larval aggregations, *CL* cooperative larvae, *CB* communal breeding, *MC* maternal care, *BPC* biparental care, *OG* overlapping generations, *APC* alloparental care, *RDL* reproductive division of labor

overview of beetle families with known social taxa (except temporary adult aggregations) and briefly describe peculiarities of their ecology and social structures. See refs. [2, 3] for more detailed reviews of sociality in different families.

Chrysomelidae

Leaf beetles (Chrysomelidae) are the third largest beetle family with more than 37,000 known species. As far as is known, they are exclusively phytophagous. Relative to the number of species, sociality is rare in leaf beetles and presents only as larval gregariousness and maternal care in the subfamilies Chrysomelinae, Cassidinae, and Galerucinae [3, 4].

Larval gregariousness begins with eggs being laid in batches, so that they require protection from natural enemies when there is no maternal care (Fig. 1). Indeed, gregariously laid leaf beetle eggs and the hatching larvae are mostly aposematic (i.e., with warning coloration), as they are well protected by unpalatable or even toxic chemicals acquired by modification and/or sequestration of compounds from the host plant. The only exceptions are the tortoise beetles, whose larvae protect themselves instead by taking cover under a fecal shield that contains toxic plant compounds.

In species with gregarious larvae, these typically feed in groups, move in procession, and may in a few cases rest in presumed defensive formations. A curious behavior in this regard is *cycloalexy*, in which disturbed larvae arrange themselves in a rosette with their heads pointing outwards in the manner of a herd of muskox or bison under threat from wolves. Gregarious leaf beetle larvae and pupae move their abdomens when disturbed, with the whole group flexing in synchrony [1]. This behavior might alert siblings and the guarding mother as well as deter enemies. The duration of the gregarious periods is variable between species and can last even to pupation.

Overall, these groups are regarded as *selfish herds*, because grouping can benefit individual survival against natural enemies (e.g., dilution effect, active defense) and probably also has nutritional benefits (e.g., overcoming of secondary plant defenses). This is corroborated by the fact that groups are not always siblings but may contain mixed broods. Leaf beetles show considerable variation in the display and duration of larval gregariousness and so could serve as a useful basis to explore the ecological and life-history conditions that facilitate these differences.

Maternal care evolved at least five times independently in at least 35 species of the leaf beetle subfamilies Chrysomelinae (>4 origins) and Cassidinae (>1 origin) [3]. All of these also

Social Beetles, Fig. 1 Adult females of the leaf beetles (Chrysomelidae) (**a**) *Acromis sparsa* with her first instar larvae and (**b**) *Acromis spinifex* with her clutch of eggs. (Photos by Caroline S. Chaboo)

have gregarious larvae. Depending on the species, mothers may care for and defend eggs, larvae, and even pupae for a few weeks or months. As for larval aggregations, the most important benefit of the mother's presence is protection against natural enemies and intraspecific competition. This has been demonstrated by the fact that larval groups suffered increased predation/parasitism when the mother was experimentally removed. Remarkably, maternal care evolved in combination with ovoviviparity or viviparity in some Chrysomelinae, which can give offspring a further head start in cases of high competition and ephemerality of the host plant. Cohesion is a secondary benefit of the mother's presence.

Erotylidae

The pleasing fungus beetles (Erotylidae) are a cosmopolitan family of about 3500 species. Most feed on fungi (Basidiomycota, Zygomycota) and a few on plants. Sociality is uncommon, with three origins of gregarious larvae and at least one case of maternal care [3]. The functions of larval gregariousness have not been studied in this family, but as in leaf beetles, group feeding may serve to overcome secondary defenses of fungi or help against predation and parasitism. Maternal care is described from one genus (*Pselaphacus*), in which larvae are also gregarious and display *cycloalexy* (see leaf beetles). Mothers protect their offspring and guide their herds of larvae beneath their body back and forth between fungal food sources, where they spend their nights and shelter to spend their days. How these groups stay together and the way mothers orient remain unstudied.

Silvanidae

Flat bark beetles (Silvanidae) are a small family of about 500 species, mostly living under tree bark and feeding on plant material, fungi, or detritus. Sociality is uncommon, but at least two remarkable species live in family groups of adults and larvae. *Coccidotrophus socialis* and *Eunausibius wheeleri* live within petiolar domiciles of ▶ ant plants, where they feed on ▶ honeydew produced by mealybugs [3]. A pair of beetles colonizes a nesting chamber not used by ants, cleans it of debris, and soon after nest foundation is joined by mealybugs. Larvae have unusually long antennae and together with adults solicit honeydew from the mealybugs by antennation – a behavior well known in ants but unique for beetles. Soon the whole colony contains offspring at all ages from larvae to adults. This is most likely a form of communal breeding, because the only observed cooperative task is the guarding of the entrance, which does not seem especially effective.

Lucanidae

Stag beetles (Lucanidae) comprise about 1200 described species of which only one is known to exhibit parental care. Similar to bess beetles, stag beetle larvae usually live inside rotting wood on which they feed until pupation. Adult beetles, on the other hand, either never feed or drink sap from flowers or trees. Although larvae and parents in many species spend their time together inside the wood, parental care and nestmate recognition are reported only for *Figulus binodulus* [6]. In this species, larval growth benefits from the presence of adults, and, although infanticide seems to be common, own offspring are killed significantly less than unrelated larvae. Adults might preprocess wood for the larvae and protect them from infanticide and natural enemies, as in bess beetles.

Additionally, recent studies suggest that some stag beetles possess fungus-spore-carrying organs, which contain xylose fermenting yeasts. The application of these yeasts onto the wood where the larvae feed might thus represent an indirect form of parental care, since only larvae feed on the rotting wood (adults are carnivorous). Sociality in stag beetles is very little studied so far.

Passalidae

Bess beetles (Passalidae) are a family of large (14–80 mm long) and invariably subsocial beetles with 680 known species distributed over the tropical and subtropical regions. They are named after the various stridulating calls both adults and larvae can produce, which likely serve in communication within the family group, although functions remain poorly studied [3].

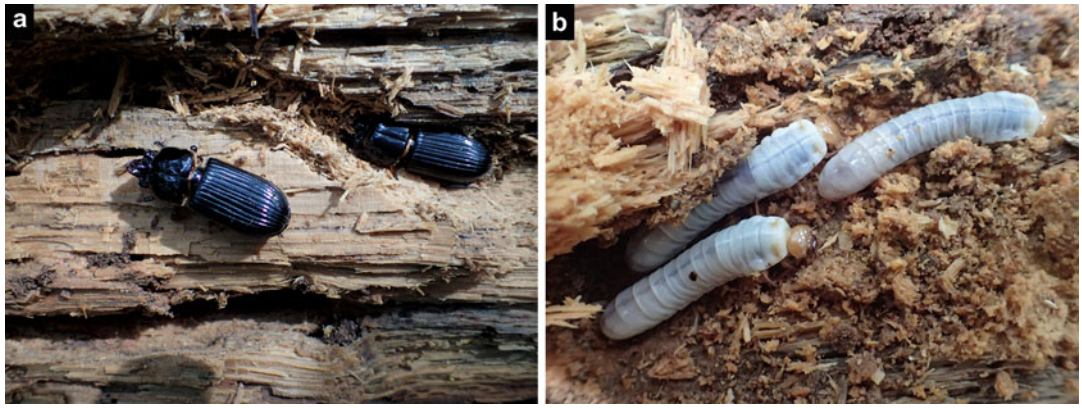
The beetles' primary habitat and food source is moderately rotten wood (>2 years dead), but there are also species living in detritus chambers of ► fungus-farming ants. Wood-living species dig tunnel systems within the wood that either a male or a female initiates. He/she is later joined by a mate to form a monogamous breeding pair. In mature nests the pair lives together with eggs, larvae, pupae, and often several teneral adult offspring (Fig. 2). The developmental period from egg to teneral adult is relatively short for these large, wood-feeding beetles (about 10 weeks), but delayed dispersal periods of the sexually immature adults in the natal nest are exceptionally long (several weeks to months).

The fitness benefits of such delayed dispersal are unclear, but they certainly engage in cooperative brood care, both actively and passively [9]. Together with their parents, they (i) construct and repair pupal cases for their larval siblings, a behavior elicited by chemical and probably acoustic larval signals; (ii) defend immature siblings against predators, including other cannibalizing passalids; and (iii) actively inhibit the spread of fungal pathogens (e.g., by grooming eggs and burying infected and diseased individuals). In addition, their presence passively supports larval siblings' nutrition, because larvae solely feed on shredded and pre-chewed wood as well as feces of the adults (frass). This frass has been termed an "external rumen," as it lines the tunnel systems and is rich in microorganisms that degrade the resistant plant material. Although detailed investigations of the microbiome and nutrient content of adult frass are lacking, it can safely be assumed that it is more nutritious than the wood itself. This is corroborated by the observation that other non-social, wood-feeding beetles in rotten wood (e.g., lucanids) develop much more slowly and have larval periods of 1 or more years.

Scarabaeidae

Most of the more than 12,000 species of scarab beetles (Scarabaeidae) described so far are non-social plant feeders. However, all 70 species of the dung beetle subfamily Scarabaeinae show varying degrees of parental care, with at least 8 independent origins [2, 3]. The high prevalence of sociality in this taxon is probably a result of feeding mostly on large-mammal excrement. Competition with other insects, nematodes, and fungi for feces is very high, as it is a highly unpredictable resource that dries out quickly, rendering it useless to the beetles.

Therefore, beetles have evolved three different strategies: (i) Males of "burrower" species



Social Beetles, Fig. 2 (**a**) Adults of the bess beetle *Odontotaenius disjunctus* (Passalidae) in rotting wood, where they live and what they feed on. (**b**) Larvae *O. disjunctus* feeding on woody frass that has been shredded and pre-chewed by adults. (Photos by Michael D. Ulyshen)

undermine the dung pat with chambers that they fill with dung, their own feces, and selective antimicrobials and where microbes decompose the fecal matter (the "cake") before it is formed into balls that each nourish one larva. At this stage, brood are mainly threatened by cleptoparasites, and the presence of the parents increases their survival. (ii) "Rollers" relocate a ball of the fecal mass by rolling it to a safer place and burying it in a chamber underground. Dung balls are heavy, and thus pre-ovipository cooperation of both sexes increases the speed and distance for relocation as well as the depth of the burrow. After burrowing, similar challenges to those of burrower species apply, except that competition is less severe.

A noteworthy case of dung beetles with biparental care is the compost-feeding genus *Cephalodesmius*, of which *C. armiger* is best described. A male progressively provisions a female in her burrow with decomposing leaves and fruits that he collects. A fungus, which is probably transmitted from the natal gallery of the female, is inoculated onto the rumen mass and slowly decomposes it until it has the consistency of fresh dung. The female forms the usual balls out of this mass, and, once the larvae are developing inside it, the female constantly adds more of the artificially produced "dung" to the balls. (iii) "Dwellers" form a nest in the dung pat itself or on the border between soil and dung. Male cooperation is thus greatly reduced or is lacking, since little burrowing and no relocation of dung are required. Females still prepare the cake and form dung balls.

Silphidae

Carrion beetles (Silphidae) are a small family of about 180 species worldwide that feed both as adults and larvae on either large (Silphinae) or small animal carcasses (Nicrophorinae). Parental care is absent in the first group but highly prevalent in the second group, the burying beetles with roughly 70 species [2, 8]. About a dozen species in the genus *Nicrophorus* have been investigated in some detail. The lifestyle of burying beetles resembles that of dung beetles, in which a rare but highly attractive food source – in this case a small animal's freshly dead corpse – needs to be quickly detected, moved, and buried to minimize the negative effects of intra- and interspecific competition as well as predation.

Thus, irrespective of which sex first detects a corpse, relocation, burial, and efforts to transform the meat into a more durable mass (analogous to the dung cake formed by dung beetles) start immediately. Throughout this process, competing conspecifics of the same sex and other carrion beetles as well as dipteran carrion feeders are fought off. Antimicrobial secretions as well as

defensive microbes are applied, so that carcasses do not rot as long as adults are present. If a male arrives first at the carcass, he attracts a female via sex pheromones and exhibits prolonged subsocial care.

Once the carcass is well buried and a stable nest is built around it, the female lays eggs, and larvae are fed by the parents via regurgitation. Interestingly, whenever a female finds the carcass first or when the carcass is very small, uniparental care by the mother prevails. In lab studies, male participation does not increase the size nor the number of offspring in the absence of competition or predation. On large carcasses there can be strong sexual conflict, because males try to attract more females via pheromones, whereas females try to avoid competition with other females (e.g., by biting or mounting, reducing male pheromone production). Therefore, the main benefit to males from staying and helping in brood care is to fight off intruders and possibly to remate with the female if further clutches are to be produced. Co-breeding of multiple females on the same carrion can then result in care of larvae by non-related parents.

Staphylinidae

Rove beetles (Staphylinidae) are the second largest family of beetles with about 63,000 known species at present. These are mainly predatory, but several specialist groups feed on fungi, dung, or algae, and it is in these that sociality has been found [3]. Maternal care has at least one origin each in the fungus-tunneling genus *Gyrophaena*, the dung-dwelling genus *Platystethus*, and the intertidal sand-boring genus *Bledius*. In *Gyrophaena* species, females bore chambers in persistent fruiting bodies of mushrooms, where they lay their eggs and protect their offspring throughout development against competitors, predators, and especially from fungus overgrowing the brood.

This resembles the maternal care of *Platystethus*, except that these species tunnel their chambers in cow dung and protect the offspring against microorganism in addition to competitors and predators. *Bledius*, on the other hand, bore tunnel systems into the sandy ground in the intertidal zone, and there maternal care evolved mainly to protect the brood from suffocation during high tide when the burrow entrance is under water by trapping air bubbles. These beetles also provision the offspring with algae that they collect outside of the burrow and protect them against natural enemies, in particular parasitoids. Although *Bledius* species occur worldwide on sandy beaches sometimes in millions, all the studies looking at their behaviors are more than 50 years old.

Curculionidae

Weevils (Curculionidae) are the largest of all beetle families with about 83,000 species worldwide, almost all feeding on plants. They are also called snout beetles on account of their usually distinctive proboscis, although this is absent in the wood-boring weevils, which are the main focus of this section. Sociality in weevils evolved almost exclusively in the wood-boring bark beetles (Scolytinae) and the pinhole borers (Platypodinae). Maternal care is ancestral in the bark beetles (about 6000 spp.) and pinhole borers (about 1400 spp.), likely because boring in woody plant tissues facilitates staying with the offspring [2, 5]. Wood or seeds exploited by these beetles are unequally distributed in the environment, relatively long-lived (relative to the life of these insects), hard to penetrate, and defendable. That means, after the discovery of a breeding substrate and its successful colonization, the excavated nest (the gallery) is a defendable resource that can provide food for a whole brood and sometimes even multiple generations of offspring. Therefore, it is rather typical for mothers in wood-boring weevils to continue laying eggs within the same gallery over relatively long periods and protecting it against intraspecific competitors and enemies. In many cases, this care is biparental, and the male also stays with the female (or females) throughout their lives within the same gallery. However,

males seem to play only a minor role for offspring fitness, and the main fitness benefit comes from the mother's presence.

Feeding habits in bark beetles and pinhole borers can be classified into three main categories: seed feeding, plant-tissue feeding, and ambrosia-fungus feeding [5]. The latter, called ambrosia beetles, are most remarkable because they feed on fungi that they cultivate within galleries in the xylem of (usually dead) trees. All species of shot-hole borers and at least ten independently evolved lineages in the Scolytinae subfamily farm their own fungal food. These ~3000 ambrosia beetle species exhibit the highest levels of sociality in beetles, likely because fungus farming benefits from division of labor between adults and larvae.

Despite their mother's presence at egg hatching, larvae in seed- and plant-tissue feeding Scolytinae typically feed solitarily, boring their own tunnels starting from the mother's egg tunnel. Larvae feeding gregariously in communal galleries, however, are found in some plant-feeding species of the genera *Dendroctonus* and *Coccotrypes* as well as in many Cryphalini. Gregarious feeding on fungi in communal galleries is also typical for most ambrosia beetle lineages. Cooperative larval behaviors, like allogrooming, cleaning the nest of frass, and protective tunnel blocking, have been observed in several inbreeding Scolytinae and several monogynous Platypodinae species. Especially in some ambrosia beetles in the tribe Xyleborini, larvae play an essential role in individual and nest hygiene as well as gallery excavation and have therefore been termed larval workers (e.g., in *Xyleborinus saxesenii*) (Fig. 3) [5].

Mothers in wood-boring weevils typically continue to lay eggs over several weeks, which means that in species with gregariously feeding larvae, offspring of various developmental stages are present together. In ambrosia beetles as well as in a few seed-feeding Cryphalini and *Coccotrypes* species, adult female offspring may delay dispersal from such nests and engage in alloparental brood care of younger siblings at the natal nest. Similar to larval workers, these adult offspring display cooperative behaviors such as allogrooming, nest maintenance, control of weedy fungi, and nest protection. Some family groups possibly transition from cooperative to communal breeding (daughters inbreed with brothers and co-breed with their mother in the genus *Ambrosiodmus*), but in a few ambrosia beetle species, there is clear evidence for reproductive division of labor. The scolytine ambrosia beetle *Xyleborinus saxesenii*, for example, is such a facultatively ▶ eusocial species, as sib-mated daughters can flexibly decide whether to disperse and breed independently, help in the natal nest, and/or co-breed with the mother, although most do not exercise the last option. In the platypodine *Austroplatypus incompertus*, there is even evidence of obligate eusociality, because these family groups contain unmated adult daughters that are unable to disperse because they have lost their tarsi and that appear to engage in alloparental care.

Facultative eusociality thus evolved only in fungus-farming lineages, as far as we know. It did so at least twice, but it seems likely that study of further ambrosia beetle species will uncover further instances. Facultative eusociality is only found in inbreeding Xyleborini, and the putatively obligately eusocial *A. incompertus* is strictly monogynous. Wood-boring weevils vary widely in their ecology (fungus-farmers, phloem/seed feeders), mating systems (monogyny, harem-polygyny, inbreeding), and ploidy (diploidy, haplodiploidy), but understanding how these factors influence social evolution will require comparative investigations of many more species.

Apart from the bark beetles and shot-hole borers, there are at least four independent origins of parental care in the wood-boring Cossoninae and one group of wood-boring Brenthidae [5]. Also, there are a few examples of gregariously feeding larvae in the gall weevils (genus *Strongylorrhinus*) and the neotropical genus *Phelypera.* Parental behavior similar to that of scarab beetles is also found in a dung-burying weevil of the genus *Tentegia* [3].

Social Beetles, Fig. 3 Fully and not-fully sclerotized adult females and larvae of the ambrosia beetle *Xyleborinus saxesenii* (Curculionidae: Scolytinae) in its brood chamber bored into freshly dead wood

Tenebrionidae

Darkling beetles (Tenebrionidae) are a cosmopolitan family of over 20,000 species living in a diversity of habitats. They are best known for the strong chemical defenses that some species deploy, most notably the famous bombardier beetle, which defends itself by squirting explosively decomposing hydrogen peroxide. Much less explored are the social systems that are some of the most complex found among beetles. *Parastizopus armaticeps* found in the Kalahari and Namib deserts of southern Africa is the best described species [7]. These beetles feed almost exclusively on fallen foliage and twigs of a shrubby legume. The demanding desert environment forces them to form colonies around these plants, where they often aggregate in shared burrows of up to 20 individuals during the dry season. During the night, males dig burrows, while females gather food that is deposited next to the burrows. Either males or older larvae help pull down these food items and provide them to their younger siblings. Such division of labor between adults and larvae is very rare in social insects and in beetles only found in some ambrosia beetles. Not-fully sclerotized beetles take part in alloparental brood care by foraging. Other tenebrionid species, like *Blaps sulcata*, form aggregations of up to 300 individuals and probably share many social characteristics with *P. armaticeps*.

Cross-References

- ▶ Ant Plants
- ▶ Eusocial
- ▶ Eusociality
- ▶ Fungus-Farming Ants
- ▶ Haplodiploidy
- ▶ Honeydew

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