THE ECOLOGY AND BEHAVIOR OF BURYING BEETLES

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ABSTRACT

Burying beetles conceal small vertebrate carcasses underground and prepare them for consumption by their young. This review places their complex social behavior in an ecological context that focuses on the evolution of biparental care and communal breeding. Both males and females provide extensive parental care, and the major benefit of male assistance is to help defend the brood and carcass from competitors. As intensity and type of competition vary, so do the effectiveness and duration of male care. In many species, a single brood may be reared on large carcasses by more than one male and/or female. Limited reproductive opportunities, the greater effectiveness of groups in preventing the probability of brood failure (especially that caused by competing flies), and the superabundance of food on large carcasses have contributed to the evolution of this cooperative behavior.

INTRODUCTION

For those who take an evolutionary perspective of behavior, burying beetles (Silphidae: *Nicrophorus*) pose many interesting questions about cooperation and conflict among unrelated individuals. This genus exhibits striking examples of extended biparental care of young and of reproductive cooperation between and within the sexes. Yet within cooperative associations there is often conflict. Frequently the interests of cooperating individuals differ as each seeks to maximize its own fitness. The costs and benefits of cooperation are shaped by the environment, for example, by the competitors the beetles face and the

595

nature of their resource. These may affect participants differently, for example, by changing the effectiveness of cooperation, which shifts the balance between cooperation and conflict. Thus, although all species of burying beetles share the suite of behaviors for their unique reproductive biology, considerable variation exists among and sometimes within species. Some variation, for example, differences in habitat use and temporal activity, can be attributed to resource partitioning by sympatric species; other differences, such as in the duration of parental care or propensity to breed communally, may be influenced by the particular competitive environment each population faces.

Burying beetles use small vertebrate carcasses that they bury and prepare as food for their young. This resource is necessary for reproduction, is unpredictable in space and time, and is valuable to many other taxa. Consequently, burying beetles treat each reproductive event as if it were their only opportunity to breed, and they behave to maximize their lifetime fitness with their current brood alone (27, 66).

Beetles discover a carcass with their sensitive chemosensors (15), move it if necessary to a suitable spot for burial, and dig beneath it (29, 40, 52). As they do so, they remove the hair or feathers and shape the carcass into a ball. They walk around the carcass cleaning it and depositing anal secretions, which help delay decomposition. When it is fully prepared, it lies in a burial chamber that may be in a depression under leaf litter or as much as 60 cm underground (32, 52, 97). Eggs are laid in the soil nearby. These hatch into altricial (defenseless) larvae that are usually fed by one or both parents.

Early naturalists were so impressed by this complex behavior that they thought these beetles were capable of reason (23, p. 62). Fabre (23) was the first to conduct experiments that demonstrated the purely instinctual nature of the behavior. Since then, much interest has focused first on providing a detailed account of the natural history of these beetles, beginning with Pukowski's remarkable observations (52), and recently on examining the ecological context and evolution of their behavior. This review focuses on the recent progress in understanding the social reproductive behavior of parental care and communal breeding. First I present a detailed description of the burying beetle communities to give the context for variation in behavior we see between and within species.

COMPOSITION OF BURYING BEETLE COMMUNITIES

Nicrophorus is a northern hemisphere genus of about 75 species (32, 48, 51). Both population densities and species diversity are higher in northern localities where habitat generalists and habitat specialists occur in sympatry (1, 80). Reasons for burying beetles' lack of success in southern locales include increased

competition with ants, flies, and perhaps vertebrates, as well as increased rates of carcass decomposition (50, 69, 80). Those endemic species that are found in Latin America (50) or Southeast Asia (30) are all montane rather than lowland species.

Resource Partitioning

Recent studies on the ecology and behavior of burying beetles have concentrated on communities in the northeastern United States/southeastern Canada (especially Michigan and New Hampshire) and northern Europe (especially Germany), although some work has been done in Mexico as well. The European and North American species differ, but the communities of species that co-occur are remarkably similar. The "small carrion" niche (34, 59) is somewhat differentiated by spatial and temporal patterns of activity and somewhat by body size of beetles, which dictates preference in carcass size. In each location there is a guild of four to six species of burying beetles that has a similar pattern of seasonal and temporal activity and habitat use (Table 1). In each exists a very large species (*Nicrophorus germanicus* and *Nicrophorus americanus*, respectively) that, though once common, is now rare (2, 37, 52).

SEASONAL AND TEMPORAL PATTERNS In burying beetle communities, seasonal patterns of reproductive activity vary in several ways; emergence times may differ and patterns of sexual maturity differ, causing some species to be

Table 1 Ecological characteristics of major species of burying beetle (*Nicrophorus*) communities of northern Europe and northeastern North America

Species	Body size	Reproductive period[a]	Habitat
Europe			
N. humator	Large	April–early July	Hardwood forest
N. vespilloides	Medium-small	Late April–Sept.[*]	Forest
N. vespillo	Medium	May–July	Field
N. investigator	Medium-large	July–Oct.[**]	All types
N. germanicus	Very large	May–July	Field
North America			
N. sayi	Large	Late April–June	Coniferous forest
N. orbicollis	Large	June–Aug.	Hardwood forest
N. defodiens	Small	June–Aug.[**]	Forest
N. tomentosus	Medium-small	Aug.–Oct.[*]	Forest, field
N. vespilloides	Small	May–Sept.[*]	Marsh
N. pustulatus	Large	June–Aug.	All types
N. americanus	Very large	June–July	Field

[a]Diurnal species: [*]; crepuscular species: [**]. Others are nocturnal. (Data are drawn from 1, 10, 37, 43, 47, 52, 56, 68, 74, 80, 100.)

univoltine (one generation/year) and some to be multivoltine (multiple generations/year). In each of the European and North American communities, one species, *Nicrophorus humator* and *Nicrophorus sayi*, respectively, becomes reproductively active very early in the spring. Beetles breed until early summer when other species become active. The adult young of the year cannot breed because they require a diapause for ovarian maturation (43; MP Scott, unpublished data). These populations tend not to be dense, and they are not well studied. In late spring (April in Germany and early June in northern United States), dense populations of burying beetles emerge to dominate the communities until late summer. These species, *Nicrophorus vespilloides* in Germany and *Nicrophorus orbicollis* and *Nicrophorus defodiens* in the United States, are multivoltine. *Nicrophorus vespillo* is also an early summer breeder, is active at the same time as *N. vespilloides*, is univoltine, and is now less common than once observed (47, 52). In both communities, a species, *Nicrophorus investigator* and *Nicrophorus tomentosus*, is reproductively active from late summer well into the fall. They are able to breed with approaching cold weather because, unlike the other species, which overwinter as adults, young of the fall species overwinter as prepupae and complete development in the late spring (52, 100).

Comparisons of the same species in Germany and Finland indicate that reproductive seasons are restricted farther north by colder temperatures. The Finnish populations start breeding one month later and stop a month earlier (47). Similarly, North American burying beetles are active earlier and longer in North Carolina than in New Hampshire. However, in the southern location, the late summer species, *N. tomentosus*, begins to breed not earlier but about two months later (80), thus avoiding substantial overlap with the summer breeders.

In spite of the longer seasons in southern locales, burying beetle communities are less rich in southern than northern habitats. Neither *N. sayi* nor *N. defodiens* is found in the Piedmont of North Carolina (80). These two species also seem to be absent in southern Michigan, though they are present in the northern part of the state (100). Wilson et al (100) proposed that *N. defodiens'* geographical range is probably determined by competition with *N. orbicollis*. *N. orbicollis* is larger and can displace *N. defodiens* on a carcass. Competition between the two species appears to be temperature dependent; *N. orbicollis* finds the highest proportion of experimental carcasses on relatively warm nights, but *N. defodiens* can find and bury carcasses at lower temperatures (100). Thus, cool nights are thought to serve as a temporal refuge for coexistence with *N. orbicollis*. Further south, without these cool nights, *N. defodiens* cannot compete.

The species within a community also exhibit different patterns of daily activity, with main peaks in the afternoon, at sunset, or at night. Usually, those that are active at the same time of year hardly overlap in their flight periods

(43, 100). However, this may be a less important mechanism for resource partitioning than it seems. Carcasses that become available at one time are not necessarily found and removed immediately so that they are unavailable when another species begins searching (100). Complete concealment may take from 2 to 24 h (61, 63, 97), during which time the carcass could be discovered and appropriated by a competitor.

HABITAT PREFERENCES   Most burying beetle communities are characterized by broad overlap in habitat use (1, 10, 47, 52, 68, 100). Though most species are adapted to cool, shady conditions, those that are active at the same time of season have a tendency to differ in habitat preferences. In early summer in northern Michigan, *N. orbicollis* is the dominant species in moderately wet hardwood forests and dry meadows, whereas *N. defodiens* is more often found in wet hardwood or coniferous forests (100).

Perhaps the most important habitat characteristic is the soil composition and texture (52). Smaller species find it easier to dig in damp soil that is rich in organic material and typical of coniferous forests, whereas larger species can manage in the dry, somewhat sandy soil of the hardwoods. Two species, *Nicrophorus marginatus* in Canada (1) and *N. vespillo* in Germany (47, 52), which are both fairly large, are habitat specific and are found only in fields and meadows where they have to contend with relatively hard, dry soil and a thick mat of grass roots. The two very large species, *N. germanicus* and *N. americanus*, are also field specialists (37, 52). *N. vespilloides*, which has a Palearctic distribution (3), reproduces in forests in Europe (43, 47, 52) but exclusively in bogs in southern Canada (1, 3, 10). Presumably this habitat shift allows *N. vespilloides* to coexist with *N. defodiens*, its sister species (1), with whom it is broadly sympatric in North America.

As a consequence of seasonal occurrence, habitat preferences, and local abundance, the probability of encountering a conspecific versus a congeneric varies by species, time, and habitat. Thus, the major burying beetle competitor that an individual faces may always be a conspecific, may shift seasonally, or, for uncommon species, may usually be a congeneric. For example, in Finland, *N. vespilloides* is the most common species, and in the deciduous or spruce forest that is its common habitat, most encounters during the summer are likely to be with conspecifics (47). Also in Germany, *N. vespilloides* buries over 85% of the available carcasses (16, 33), even though two species of larger, competitively superior beetles are reproductively active at the same time. In New Hampshire, *N. defodiens* has a somewhat higher probability of encountering a conspecific than a *N. orbicollis* during the first part of the summer, but by August encounters are more likely to be with *N. tomentosus* (68; MP Scott, unpublished data).

CARCASS SIZE   Burying beetles will bury any type of small vertebrate carcass (23, 73) and show no preference when given a choice of bird or mammal (37). Except for very small or very large carcasses, different species use completely overlapping ranges of carcass sizes. Although *N. orbicollis* is about four times heavier than *N. defodiens*, the former will bury and can rear a brood on carcasses as small as 7 g, whereas the latter will bury and rear a brood on 4-g carcasses (79, 86). In northern Michigan, over 90% of very small carcasses (4–6 g) are buried by *N. defodiens*, even though *N. orbicollis* is abundant (79). Intermediate size carcasses (21–90 g) are often buried by *N. defodiens* but later discovered and usurped by *N. orbicollis* (84, 100). Very large carcasses (120–210 g) are difficult for *N. defodiens* to bury, and virtually all are lost in competition with *N. orbicollis* before larvae are mature (84).

Although burying beetles have a suite of behavioral, physiological, and morphological characters that allow them to effectively use small carcasses, there are anecdotal reports that *Nicrophorus* spp. can rear broods on a large carcass, such as a rabbit, without burying it (49). *Nicrophorus pustulatus*, a species that is widespread in eastern North America but uncommon everywhere (3), has been proposed to regularly use large carcasses. It has never been found to have buried any of the 1000 or more carcasses put out by investigators (68, 80, 84, 100). Although, in the laboratory, *N. pustulatus* rears a brood like other burying beetle species on small carcasses (56), a female can also fully utilize a very large one (220–260 g), rearing a much larger brood than a female of other species (84). Trumbo (85) made the intriguing suggestion that *N. pustulatus* is adapted as an interspecific brood parasite. Interspecific contests of size-matched individuals were observed to be severe, and when *N. pustulatus* females lost, many *N. pustulatus* young were reared (85) in the mixed-species broods. These are otherwise very rare. The large clutch produced by *N. pustulatus* can potentially swamp that produced by the successful competitor.

Competition with Other Taxa

A carcass is a valuable resource to many organisms. The importance of competitors other than beetles varies with latitude, habitat, and season. Vertebrates such as skunks and racoons in southern Michigan remove a much higher proportion of carcasses before they can be buried by beetles than they do in the northern part of the state. Thus, *N. orbicollis* is the top competitor in the northern locale but is in considerable danger of losing carcasses to vertebrates in the south (97). Similarly, in New Hampshire, competition with flies seems to increase over the summer. Both *N. orbicollis* and *N. defodiens* abandon carcasses to flies far more frequently in August than in June and July (68; MP Scott, unpublished data), whereas *N. tomentosus* competes more effectively and rarely loses carcasses to flies even in August (63).

Burying beetles combat dipteran competitors in several ways. Adults destroy both eggs and larvae directly. They also carry phoretic mites that are reputed to pierce fly eggs (75). However, studies of beetles with and without mites have shown mixed results. In the field, mites may increase the beetles' fitness, especially when carcasses are buried shallowly (75, 96). However, laboratory studies suggest that the positive effect of mites is minimal (99) or may be negative, as some species are predators on *Nicrophorus* eggs (9, 12; MP Scott, unpublished data).

Microorganisms are more serious competitors on relatively large carcasses than on smaller ones. Small carcasses can be cleaned and rolled effectively by beetles. Beetles spread secretions over the exterior and groom the surface with their mandibles. Large carcasses are difficult to prepare, and mold often makes part or all of the carcass unusable by the beetles.

Just how the competitive environment can influence the behavior of beetles is the theme of the latter part of this review. The major source of competition, whether from intraspecifics, other burying beetle species, or other taxa such as vertebrates or flies, can affect the beetles' reproductive strategy and render inter- or intrasexual cooperation in burial and brood care either more or less effective.

BIPARENTAL CARE

Perhaps the most striking aspect of the behavior of burying beetles is their parental care. Extended maternal care is unusual in insects (14, 76, 77, 101, 103), and the substantial parental investment by males is even more surprising and raises questions concerning its evolution. Because most factors that influence the potential costs and benefits of care can be manipulated and measured easily in burying beetles, researchers studying several communities have gained considerable insight into the ecological forces contributing to the evolution of biparental care.

A "bonanza" resource such as carrion or dung selects for parental care (28, 76, 101, 102) because it is valuable and unpredictable and must be defended from a diverse group of organisms that would also exploit it (27, 31). Thus, burying beetles conceal a carcass underground and continue to guard it to prevent its use by vertebrates, other insects, and microbes. Models that treat parental care and mate desertion as an evolutionarily stable strategy (26, 39, 103) have been useful in focusing attention on the major factors promoting post-ovipositional investment. These factors include (*a*) the potential gain from each parent's ability to increase offspring survival and competitive ability and (*b*) the potential loss from reduced future fitness if additional reproductive opportunities are lost while providing care and if providing care reduces future fecundity. Usually

males of almost any species face a trade-off between increased offspring production and missed mating opportunities, whereas females suffer decreased fecundity if they provide care rather than accrue resources. However, these typical asymmetries in the costs and benefits of parental investment are mostly absent for burying beetles. Carcasses, not mates or food, limit reproductive opportunities for both males and females, and both sexes are capable of breeding again as soon as they leave a brood (7, 42, 68). Furthermore, in the laboratory, males and females are equally capable of rearing offspring as single parents (6, 25, 89). In the next sections, I examine the costs and benefits especially to males in providing extended parental investment and how they might be affected by environmental factors.

Parental Behavior and Its Effects

PARENTAL BEHAVIORS   Male and female *N. orbicollis* perform the same repertoire of parental behavior. Both spend a large proportion of their time in carrion and brood chamber maintenance, circling the brood ball, spreading preservative hindgut secretions, and removing fungi (24). Both regulate the brood size on small carcasses by committing infanticide on superfluous young (4, 57, 82, 89). Female *N. orbicollis*, however, spend significantly more time feeding larvae than do males (24), but when the female parent is removed, single males compensate for mate loss by increasing their feeding rates to match those of single females (25). The feeding frequency of paired male *N. vespilloides*, however, may not differ from that of paired females (6). In all species investigated, the survival or final weight of larvae does not differ if they are reared by single male or single female parents (6, 83; MP Scott & L Sherwood, unpublished data).

FEEDING   Just before eggs hatch and larvae reach the carcass, parents prepare the brood ball by opening a small feeding depression at the top that they treat with regurgitated oral fluids (52). Larvae beg and are fed by parents, or they can feed directly from the treated carcass. Larvae of large species, *N. orbicollis* and *N. sayi*, are extremely dependent on parental regurgitation and die before they reach second instar if they receive no parental care; larval *N. defodiens* and *N. tomentosus* can develop normally without any parental feeding (82, 84). Similarly, the two large European species, *N. investigator* and *N. humator*, also require parental feeding (BP Springett, cited in 84). *N. vespilloides* survives without parental feeding (55), and Pukowski (52) reported, probably with reference to *N. vespillo*, that these larvae also feed and develop normally in the absence of parents. Trumbo (84) pointed out that it is the larger species that require parental feeding and argued that this allows more rapid larval growth. He proposed that, because larvae of the near relative *Ptomascopus morio* do not require any parental care (48), feeding is not the primary selective force for

the evolution of parental care in *Nicrophorus*, but rather feeding is the price paid for rapid larval growth to a larger size (84). Nonetheless, even when not required or when extended beyond the period that it is required, feeding often improves larval survival and growth; longer maternal care by *N. orbicollis* does result in offspring of greater mass (68).

When considered in the absence of competition, the quantity or quality of parental care is not the principal determinant of reproductive success; the size of the carcass is. In all studies conducted either in the laboratory or in the field, the number of larvae reared and the total mass of the brood is strongly positively correlated with carcass mass and not with the number of parents present, their size, or how long they provide care (10, 37, 47, 89, and references therein). If males consume some of the resource of very small carcasses, biparental care may even reduce the number of larvae reared (60, 66, but see 83). However, competition is a very important factor in the field both before and after the carcass is buried, and it appears to be the major selection force in the evolution of biparental care in burying beetles.

DEFENSE AGAINST COMPETITORS AND PREDATORS   Male assistance in defending the brood and carcass may be important at various times. Before the carcass is buried it is vulnerable to many types of scavengers; two beetles were long assumed to be able to conceal the carcass faster than one, even though their interactions are not at all coordinated (23, 40, 52, 77). However, male assistance in burial does not account for very much of the variance in the speed with which a carcass is buried (61, 97). Microhabitat differences, such as soil texture and underground runways, and temperature are more important in determining the effectiveness and speed of burial (61).

Both before and even after burial, flies may lay their eggs on a carcass, and most beetle species abandon carcasses that are already infested with maggots (96). Adult beetles, perhaps with the aid of their phoretic mites, can often rid the carcass of fly eggs and larvae that are still on the surface. However, *N. defodiens* buries shallowly, and single females are significantly more likely to experience brood failure, mostly caused by competition with flies, than are females assisted by males (85).

Fungi, subterranean ants, and insect predators can also contribute to brood failure. Microbes and fungi can outstrip the beetles' ability to preserve the carcass. *N. defodiens*, for instance, suffers significantly more brood failure on large carcasses than on small ones, which reflects the greater difficulty in preparing and preserving a large carcass (85). Male assistance may help keep fungi in check. The effectiveness of beetles' defense against ants has not been studied. By and large, larvae can be defended from insect predators, such as staphylinids, by single female parents (4, 52, 61); females of small beetle

species, *N. vespillo* and *N. vespilloides*, lose their lives only to large staphylinid predators (52). Predation on burying beetle eggs has been suggested to be a serious threat (but has not been tested), especially for *N. vespilloides*, a species that buries shallowly and oviposits in the top layer of the soil (4, 42). Whether either or both parents are more effective in defending their eggs is not known. *N. vespilloides* readily produces replacement clutches after brood failure (42), more so than some other species (MP Scott, personal observations), which may be an adaptation to high egg predation.

The most important competitors for the carcass both before and after it is buried are other burying beetles. Both sexes face strong intrasexual competition when more than one male or female discovers a carcass. The winner is almost always the largest (7, 46, 47, 52, 85, 97) of each sex. Losers do not always depart but often may remain nearby for 24 h or more and attempt to lay eggs or sneak copulations (6, 46, 58, 85, 97). Even after the carcass is buried, it can be discovered and usurped by other beetles (6, 52, 57, 61, 62, 79, 81, 83, 100). Because body size determines the outcome, members of a larger species can usurp the carcass from small species; for example, *N. orbicollis* often replaces *N. defodiens* (62, 79, 100). Larger conspecifics can also replace same-sex residents on a carcass; when they do so, they kill the residents' young and either reinseminate the resident female or oviposit so as to rear their own young (61, 81). However, male assistance greatly reduces the probability of an intraspecific takeover (57, 61, 79, 83). Although there is no evidence of any intersexual cooperation in the initial intrasexual competition before the carcass is buried (52), after it is buried and eggs have been oviposited, both males and females appear to assist their mates; even intruders larger than the same-sex resident are seldom successful (61, 79). Males and females benefit by assisting their mates to avoid eviction. Although a remaining original resident can produce a replacement clutch with a successful intruder, it is smaller than the original clutch (42, 57, 81) and continues to be vulnerable to competitors.

In addition to the benefit of male assistance in defense, male assistance in burial and preparation may make the carcass less vulnerable to detection in the first place. *N. defodiens*, a small species, makes only shallow burial chambers, and chemical cues from the carcass may escape. However, carcasses buried by a pair attract fewer free-flying congeners than those buried and prepared by single females (85).

Duration of Paternal Care

Because of the variety of competitors faced by burying beetles, the major benefit of biparental protection varies (see Figure 1). The effectiveness of this protection also varies with the type of competitor, and, as we might expect, this is reflected in the duration of parental care. In most species, but not all, females
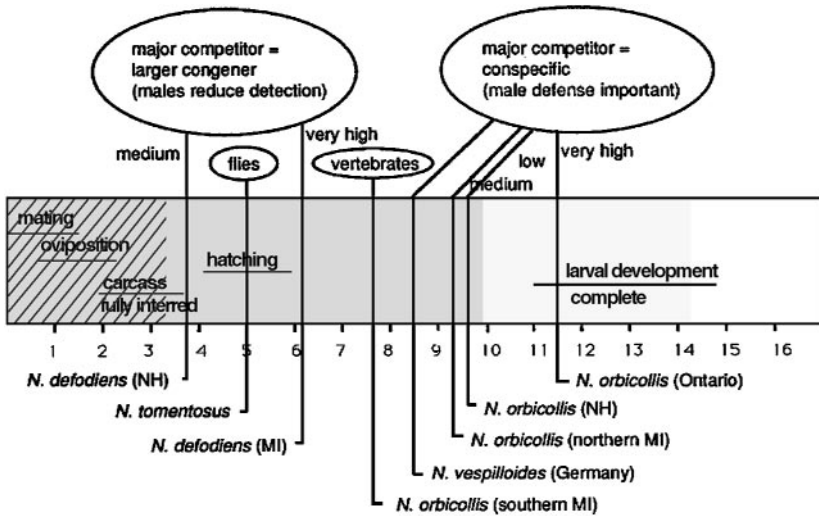
Figure 1 Duration of paternal care plotted along a generalized time line (1–16 days) of carcass preparation and larval development. *Shading* corresponds to the depletion of the carcass and the reduction of its value to vertebrates and other burying beetles. *Hatched lines* correspond to the period when beetles must prepare the carcass to reduce the probability of its detection and to rid it of flies. *Ovals* denote the major source of competition experienced by each population and thus the primary benefit of paternal care. The intensity of a given threat is indicated as low, medium, or very high. (Data are drawn from 6, 13, 57, 62, 68, 79, 83.)

on average remain until larval development is complete or nearly so. The duration of male care is quite variable both among species and among populations (57, 68, 83), and it is related to the vulnerability of the brood and dependent on the stage of larval development and carcass depletion (83).

TIMETABLE OF LARVAL DEVELOPMENT AND PARENTAL CARE   Females begin to oviposit as soon as 12 h after the carcass is discovered (*N. tomentosus*; 65) and usually within 48 h. At 20°C, eggs hatch on average 56 h later (*N. vespilloides*; 45). Larvae of large species (e.g. *N. orbicollis*) complete development and disperse to pupate in the soil in 6–8 days (68), and those of smaller species require about a day less (MP Scott, unpublished data). The time from burial to larval dispersal is less on small carcasses than on larger ones because the former require less time to prepare (83). Therefore, depending on the temperature, size of carcass, and species of beetle, the potential duration of parental involvement with larvae could range from 9 or 10 days to 15 or 16 days.

EFFECTIVENESS OF MALE DEFENSE   For some species, the major threat to successful breeding is the discovery and usurpation by conspecifics. Two parents are much better than one in preventing this. Males of these species remain in the brood chamber for a relatively long time. In northern Michigan and in New Hampshire, *N. orbicollis* is the top competitor, and therefore the major threats are from conspecifics. Similarly, in northern Europe, *N. vespilloides* is much more likely to meet a conspecific than a member of another species in competition over a carcass. Thus, although *N. vespilloides* is not the largest species, its major competitors are also conspecifics because of its abundance. Males of both of these species exhibit relatively long paternal care (Figure 1). In southern Michigan, the threat of a vertebrate scavenger is much greater than it is in northern Michigan (97). Presumably there is little either a male or female can do if the brood chamber is discovered by a vertebrate. Male *N. orbicollis* in the southern population provide significantly shorter care. Only 13% of the males remained in the burial chamber on the tenth day in the south, whereas 40% were still present at the northern site (P = 0.001; analyzed from 97). Similarly, in southern Ontario, the threat of discovery and usurpation is greater than it is in northern Michigan. Pairs lost 37% of medium-size carcasses to conspecifics in Ontario and 19% in Michigan (P = 0.07), whereas single females lost 83% and 40% at each site respectively (P = 0.005; analyzed from comparison of 57 and 83). In Ontario, male *N. orbicollis* can effectively prevent takeovers, and they do provide longer care (11–12 days versus 9 days for *N. orbicollis* in northern Michigan).

The risk of takeover changes over time as the larvae grow and consume the carcass. When pairs or single female *N. orbicollis* of the New Hampshire population were systematically challenged by introducing a potential intruder near the brood chamber on different days, the risk on carcasses guarded by single females remained high until after the eighth day (66). On average, males of this population remain 9.5 days. A dynamic optimization model developed by Scott & Gladstein (66) to examine the effect of the risk of takeover on the duration of male care predicted that males would optimize their reproductive success, which balanced the gain from their present brood with the probability of breeding again, if they remained 10 days on large carcasses and 9 days on small ones (66). Only when the probability of breeding again became very high (4–6%/day) were males predicted to cease parental care altogether. Thus, the duration of male care seems to reflect the potential benefit of male assistance in defense of the brood and carcass.

N. tomentosus is also the top burying beetle competitor in Michigan and New Hampshire by the time it breeds in August and September. However, males provide relatively short care (Figure 1). In addition to conspecifics, flies are important competitors (68). Males assist in cleaning and preparing the carcass,

but after the initial fly eggs and maggots are removed, competition from flies ceases to be important. The benefit of continued paternal care is reduced.

N. defodiens faces intense competition from the larger *N. orbicollis*. Males of *N. defodiens* provide very short care. Studies examining the benefits of male assistance in interspecific competition have had conflicting results. Whereas one study demonstrated that females aided by males were more likely than single females to avoid takeovers by *N. orbicollis* (79), another suggested that one or two beetles were equally ineffective (62). The former study was unmanipulated and compared the natural occurrence of takeovers of carcasses guarded by pairs or single females, whereas the latter study examined the outcome of competition with an introduced competitor. A comparison of these methods suggests that male assistance might reduce the probability of discovery if not the effectiveness of defense; the presence of a male significantly reduced the number of competitors that discovered the carcass (85) perhaps because the carcass was more completely buried by pairs or because treatment of hindgut secretions from two beetles reduced odors. In either case, the benefit of continued male care is somewhat less after the carcass is fully buried. Males of this species depart sooner than do males of species whose primary benefit is through better defense against conspecifics.

FACULTATIVE ADJUSTMENTS OF DURATION OF PATERNAL CARE   Males seem to use the developmental stage of the larvae, not just the length of time with the carcass, as a cue to depart (83). As the larvae develop, the carcass is depleted and its value to competitors reduced. The question arises whether males will adjust the duration of their care to broods when circumstances change the costs or benefits of that care. If the female parent dies, deserts, or is removed experimentally, the benefit of male care is increased. Males that are single parents remain with the brood significantly longer—as long as the average duration of maternal care (83). The risk of usurpation is generally less on relatively small carcasses (61, 66, 83), thus the benefit of male presence is reduced on small carcasses. *N. orbicollis* males provide significantly shorter care on small carcasses than on larger ones. This effect is statistically independent from the effect of the shorter development time of larvae on smaller carcasses (83, 84).

A dynamic optimization model of the duration of paternal care (66) predicts that the duration of care should not be very sensitive to either the probability of finding another carcass or the intensity of competition. Several studies have attempted to manipulate the male's perception of the availability of carcasses or the level of competition (beetle population density) to observe the effect on the duration of his care. They have had mixed results. Male *N. orbicollis* do not significantly reduce the duration of their care with their second carcass (83; MP Scott, unpublished data). Similarly, males do not increase the duration of their

care when the density of intruders is experimentally increased (57). However, males reared and maintained in the laboratory with four to five others provided significantly longer care than those reared in complete isolation (14.5 $\pm$ 4.9 days vs 9.1 $\pm$ 3.1 days, respectively; P < 0.001; MP Scott, unpublished data).

CONFLICT OF INTERESTS BETWEEN MALES AND FEMALES   In species with high parental investment by both males and females, there is usually much less conflict in their interests than in species with high female-only investment (78). For the most part, the interests of male and female burying beetles coincide, so much so that we might not expect male burying beetles to be either more or less inclined to provide care than females (78). However, males and females are not equally likely to be the first to desert. Females of all species provide longer care, and several hypotheses have been suggested for why this might be so. The cost of deserting may be less for a male, even if a male intruder replaces him, than it may be for a female if she is replaced. Sperm displacement is not complete (44, 70, 81, 90); a male might still be the father of some of the replacement clutch, whereas the female would be the mother of none (68). Furthermore, males, but not females, have the opportunity to increase their fitness when they mate away from a carcass (16, 58), either when they meet females feeding on a large carcass or when they emit a "calling" pheromone to attract females (see next section). Also, males may have a greater expected benefit in early desertion because a female's, but not a male's, potential reproductive success may decline with successive breeding attempts (68, 82, 83, but see 90).

Although we might reasonably assume that it is in the female's best interests to retain the male's assistance as long as possible, this does not always seem to be the case. Some evidence indicates that males may be forcibly evicted, especially from very small carcasses. Pukowski (52) reported that she observed female *N. vespillo* forcing males to leave soon after burial. When breeding on very small carcasses (5 g) in the laboratory, males may even be killed by females, presumably while being driven off (6; MP Scott, personal observations). To the female, the potential benefit from male assistance in defending a small, less attractive carcass is outweighed by the cost inflicted if the male depletes the resource by feeding from it (66). However, from the male's perspective, feeding from the carcass may still offer a net gain. Alternatively, parental care is likely to be hormonally mediated (87), and males cannot leave directly after burial while the cues are present to maintain parental behavior. Thus, continued care on very small carcasses may be the unselected consequence of strong selection for paternal care on carcasses of the sizes generally used (35).

Alternative Male Mate-Finding Tactics

If a male locates a suitable carcass and no female is present, he eventually assumes a distinctive posture and releases a pheromone to attract a female

(5, 41, 52). Males of some species, e.g. *N. vespilloides*, *N. humator*, and *N. defodiens*, take the posture and release pheromone even when they do not have a carcass (16, 18, 43). Male *N. vespilloides* may spend several hours a night advertising, whereas males of other species (e.g. *N. orbicollis*) rarely emit pheromone without a carcass (MP Scott, personal observation). Females are attracted to these pheromone-emitting males and readily mate with them (17, 18). Although these females mate with additional males, a non–carcass-holding male can expect 5–10% paternity of the female's next brood if she buries the carcass without a mate (16). As long as the frequency of uniparental care is fairly high (16, 64, 68, 97), this alternative tactic of advertising may be nearly as profitable as searching for a carcass. Thus, *N. vespilloides*, which uses this tactic, has a high rate of broods reared by single females (39%; 16), whereas *N. orbicollis*, which does not advertise without a carcass, has a lower rate [11% in Michigan (97) and 22% in New Hampshire (68)].

COMMUNAL BREEDING

Recently we have discovered that burying beetles, which have long been appreciated for their extensive biparental care, have social behavior that extends beyond such cooperation. Both males and females of some, perhaps most, species often bury a carcass and rear a single brood with others of their sex. These groups can be quite variable in composition; groups of *N. tomentosus* consist of 0–6 males and 1–7 females (64). Some adults may leave soon after burial; others remain long into the period of larval care (19, 63, 70, 92).

In an effort to understand the evolution of social behavior, the three major characteristics of sociality—cooperative brood care, reproductive castes, and overlap of generations—have been used to categorize species (38, 95, 101). Thus, the quasisocial behavior of communal brood care is thought to be more organized or complex than the subsocial behavior of biparental care. Recently, a more quantitative approach has been used to understand the range of social behavior throughout the animal world (21, 22, 36, 54, 72, 93, 94). These models focus attention on how reproduction is shared among group members and on the factors thought to be important in the evolution of cooperation. Burying beetles face limited opportunities to breed and strong competition for a valuable resource, both of which are important selection forces for cooperation.

Frequency of Communal Breeding

The frequency of communal breeding varies considerably by species. Multiple male or female *N. orbicollis* are seldom present together at any stage of carcass preparation or brood care except on very large carcasses (68, 84, 97). However, members of the smaller species, *N. defodiens*, *N. tomentosus*, and *N. vespilloides*, are all often found in cooperative associations. There is a trend for

females to enter into communal breeding more readily than males (i.e. they are more likely to be present 24 h after carcass burial) and for these associations to last longer (16, 46, 64, 97 but see 84). The longer association of females may be partially a function of their longer duration of care when acting as a member of a male/female pair, but other reasons for sex differences in intrasexual cooperation become apparent when we examine the factors that promote it.

CARCASS SIZE   The size of the carcass greatly affects the frequency of communal breeding for all species and populations. Multiple males and/or females of both *N. orbicollis* and *N. defodiens* are twice as commonly found on 50- to 90-g carcasses as on 20- to 30-g ones (84). Similarly, 50% of 40- to 45-g carcasses but 75% of 55- to 60-g carcasses were buried and prepared by more than one male and/or female *N. tomentosus* (64). The same pattern is apparent in laboratory studies; females form cooperative associations and exclude one another less frequently when breeding on a relatively large carcass (19, 63, 64, 84, 92). Multiple females may remain long enough to be observed feeding larvae side by side (19, 84, 92).

Communal breeding is more common on relatively large carcasses for several reasons. Although the size of the carcass is the principal determinant of reproductive success, there is an upper limit to the number of eggs that a female can lay that will hatch more or less synchronously. Thus, a smaller carcass can be fully utilized by a single female, whereas a larger one cannot. Two females can rear more larvae than one on relatively large carcasses but not on smaller ones (63, 92). Thus, a dominant female may lose less by allowing a subordinate female to join her on a large carcass than on a small one. Larger carcasses are also more difficult to exploit than smaller ones: They take longer to fully conceal and prepare; they are less likely to be well prepared and preserved; and they are more likely to be found by competitors (63, 84). Although there is no evidence that a greater benefit comes from tolerating consexuals on larger carcasses (i.e. that intrasexual cooperation improves concealment, preparation, and defense), there may be a greater cost in preventing it on larger carcasses. More consexuals are attracted to larger carcasses (91), and it may be harder to defend from consexuals either because the greater surface area reduces the encounter rate (19) during burial and preparation or because of the greater motivation to contest a larger, more valuable resource.

RELATIVE BEETLE SIZES   Consexuals have been suggested to be more likely to coexist on a carcass when they are close to the same size and competitively equal. However, neither communally breeding males or females are closer in size than random individuals in the field, nor are females of similar size more likely to form associations in the laboratory (92, 97). Size differences between

females do not predict the length of their associations either. Nonetheless, some evidence shows that conflict is more intense between individuals of similar size; the first female to leave the brood chamber, the subordinate, is more likely to suffer an injury when she is similar in size to the dominant female (92).

Outcome of Communal Breeding

Although the relative sizes of communally breeding females does not predict the likelihood that an association will form, it is an important determinant of the dominance relationship. The largest female is almost always the one to provide the longest care (19, 46, 63, 70, 92), just as the largest male provides longer care than smaller males (63). Relative duration of care is positively correlated with relative reproductive success within each association, and duration of care by subordinate males or females correlates with the proportion of the brood parented by them; subordinates with few young leave sooner than those with more (70).

Several methods have been used to determine the division of reproduction in communally breeding associations: polymorphic laboratory strains (19, 46, 92), molecular markers (11, 70, 71), and dyed eggs (65). Relative size and, even more strongly, relative duration of care are strongly positively correlated with relative reproductive success. On large carcasses, reproduction is divided between two females equitably, or at least randomly, most of the time. On small carcasses, reproduction is usually significantly skewed in favor of the larger female (19, 46, 65).

Individual females of *N. tomentosus*, and perhaps of other species as well, use several methods to achieve a bias in reproduction in their favor. First, females increase the proportion of their young in the brood through differential destruction of their competitors' eggs. Eggs are laid along a tunnel by females of some species (52, 53), but females of species that readily breed communally (e.g. *N. vespilloides* and *N. tomentosus*) lay eggs randomly in the soil (46, 65), which may make them more difficult to locate and destroy. Second, females have resting-stage ovaries and low titers of juvenile hormone as they search for a carcass. Hormone levels rapidly increase (87) and ovaries undergo vitellogenesis (67, 98) in response to the discovery and assessment of the carcass. Burying and preparing a carcass communally stimulates the ovarian development of the dominant female and slows it for the subordinate (65), which allows the dominant to oviposit sooner and possibly more than the subordinate. Third, larger females of species that often breed communally (especially *N. tomentosus*) are both more likely to be dominant and more fecund. Female fecundity is correlated not with carcass mass but with female size, which is the common pattern for insects. However, this pattern is reversed in species (e.g. *N. orbicollis*)

that do not readily cooperate; fecundity is correlated with carcass size and not female size (65).

Polyandry and Polygyny: The Male Perspective

Relatively little attention has been paid to the male's perspective in communal breeding. It is theoretically more perplexing that males should tolerate other males on a carcass (8, 77, 78). Polyandry should be rare because males are expected to maximize the number of mates and a single male could inseminate all females burying a carcass. However, on medium-size carcasses, the frequency of male *N. tomentosus* associations is as high as that of females but, unlike that of females, does not increase on larger carcasses (64). The costs of communal breeding to males remain the same on medium and large carcasses because, unlike females, a single male can fully utilize a large carcass (88). Like females, the largest male usually provides longer care and is the father of the largest share of young in the brood (*N. tomentosus*; 63–65, 70). Presumably, dominant males bias reproductive success in their favor through more frequent copulations, as males achieve greater paternity assurance with multiple copulations (44).

Sexual conflict can occur between male and female if the presence of a second female on a large carcass increases the reproductive success of a male but decreases it for the first female. The large carcass would be more fully utilized and more young would be raised, but the second female could become reproductively dominant to the first. After mating with the first female, *N. defodiens* males advertise with pheromone release for additional females on large carcasses, but not small ones, and do not do so when experimentally paired with several females; females, on the other hand, physically interfere with signaling males and knock them off of their calling perches (20, 88).

Ecological Factors for the Evolution of Communal Breeding

Several hypotheses for the occurrence of communal breeding in burying beetles have been proposed. Because carcasses are rare and the probability of independent breeding is low, subordinate individuals always benefit from joining others of the same sex as long they are able to produce some young. Therefore, it is the benefits of cooperation to the dominant individual that must be examined. When competitors are excluded in laboratory experiments, the per capita reproductive success of cooperating females decreases, which imposes costs on females that allow others to join (19, 63, 84, 91, 92). Eggert & Müller (19) suggested that cooperation by *N. vespilloides* females is just the result of the constraint of the greater difficulty of excluding consexuals on a large carcass. However, in the absence of manipulative field studies to evaluate the effects of competition, it is difficult to evaluate whether there truly is no benefit to cooperation in this species.

Field studies of *N. tomentosus* suggest that communal breeding may have some significant advantages (63). In New Hampshire, flies are an important competitor in August when *N. tomentosus* breeds (68, 69), and pairs rear fewer young than three or four beetles do when flies have oviposited on the carcass. In fact, on both medium and large carcasses, the gain to the dominant female when she allows a subordinate to join is exactly offset by the loss of offspring produced by the subordinate (63, 70).

Flies are also an important competitor to *N. defodiens* in Michigan and can cause beetles to abandon the carcass. Communal breeding reduces the probability of nesting failure that may result from many causes, including flies (86, 92). Trumbo & Wilson (86, 92, 97) proposed that the high probability of nesting failure promotes communal breeding even in the absence of immediate reproductive gains. The low expectation of reproductive benefit from a large difficult-to-secure carcass reduces the value of the resource and thus increases tolerance. The positive correlation of the probability of nesting failure and frequency of communal breeding with *N. defodiens* and *N. orbicollis* in Michigan supports this argument. The risk of nesting failure for *N. defodiens* is higher on large carcasses than on small ones and thus tolerance is promoted more strongly on large carcasses. I would add to their argument that the high risk of nest failure will increase the share of offspring that the subordinate must produce in order for her to join (54); thus, reproduction should be shared more equitably by *N. defodiens* than it is by *N. tomentosus*. This, however, remains to be tested.

Although at first it seemed that polyandry should theoretically be less common than polygyny, all of these hypotheses suggest that males should be as willing to cooperate as females. Intrasexual competition is no more profitable for males than for females when there is a high chance of failure, and it is even less profitable on large than on small carcasses. If more adults helped to rid the carcass of fly eggs and larvae, males would benefit from consexual assistance as much as females. Only the decreased costs to females on large carcasses, which cannot be fully utilized by single females, would not have a comparable decrease of costs to males. Thus, the relative importance of this single factor, constraint on clutch size on females, should explain the variation in male-female differences in tolerance.

CONCLUSIONS AND FUTURE DIRECTIONS

We are not yet at the point where we can identify with confidence the ecological factors that are important in the evolution of communal breeding in burying beetles. The ecological costs and benefits have not yet been fully explored. Trumbo's (86) model to predict the benefit of fighting or accepting a rival

suggests that beetles should tolerate a rival when the expected costs of fighting (in terms of decreased number of young in future reproduction) are greater than the gain in additional offspring from expelling the rival. We have measured the gains but know nothing of these expected costs. Injuries are common in fights but might be of little consequence if future opportunity to breed is extremely rare. The increase in young with communal breeding when flies are competitors has clearly been identified as a selection force for cooperation in *N. tomentosus* (63). However, no similar benefits to communal breeding have been identified for any other species.

Models of reproductive skew (54, 93, 94) are helpful in addressing the evolution of cooperation because they allow us to examine the expected outcome of behavioral decisions of both the dominant and subordinate. They point to a need to better understand, first, the true degree of the ecological constraint to independent breeding and, second, the change in reproductive success resulting from communal breeding. For burying beetles, the questions that remain are as follow: How limited are reproductive opportunities? Are groups better able to defend the carcass and brood? And if so, from which competitors?

The focus on the ultimate factors important to the evolution of the social behavior of burying beetles has been fruitful. Many of the costs and benefits of biparental care and communal breeding have been uncovered. Because of the richness and complexity of their behavior, burying beetles will also make excellent models to investigate proximate mechanisms. These beetles must coordinate reproduction with the location of a necessary resource that is unpredictable in time and space, and reproduction must be coordinated with a mate. Their behavior must undergo regular changes from competitive to cooperative and parental. Hormonal mechanisms are expected to play a major role in orchestrating the interplay between behavior and the social and non-social environment. Elucidation of these mechanisms has the potential to provide important new insights for insect behavioral endocrinology.

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