

Chapter 12

Recognition and Family Life: Recognition Mechanisms in the Biparental Burying Beetle

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Abstract Burying beetles (genus *Nicrophorus*) are one of the few insect taxa that provide elaborate prehatching and posthatching biparental care. They reproduce on dead vertebrates and both parents are known to feed and defend their young. In this chapter, I will show that both of their key characteristics, their extended biparental care as well as their reproduction on a valuable and sought-after resource gave rise to the evolution of sophisticated recognition mechanisms. They are able to recognize the sex of a conspecific, their previous mating partner, their breeding partner including its reproductive state and—using temporal cues—their offspring. I will provide an overview of the recent advances in elucidating the recognition processes of burying beetles and will demonstrate that most of the recognition mechanisms are mediated by chemical cues and signals.

Keywords Burying beetle · *Nicrophorus* · Biparental care · Chemical signals · Parent-offspring interactions

Introduction

The larva is begging for food by raising its head while waving its legs and touching the mother's mouthpart. Its mother is responding by regurgitating predigested carrion food, while the father is just chasing off an intruder intending to kill the brood. This description reflects a typical family life in burying beetles (Coleoptera: Silphidae: *Nicrophorus*) and illustrates the importance of recognition processes in insect species exhibiting extended parental care.

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Family life is crucially dependent on recognition mechanisms as parents have to recognize their offspring, offspring their parents and in the case of biparental care, the breeding partners each other. Certainly, the recognition mechanisms involved might not necessarily be very sophisticated in many species: offspring, for example, can be indirectly recognized by correctly identifying the nest or burrow. The degree of complexity of the recognition system also strongly depends on the encounter rate with undesirable senders, i.e. brood parasites or rivals that try to steal or take-over important resources necessary to raise the brood. If there is a very low risk of encountering them, the recognition system might be not very fine tuned. However, in systems in which parents defend or provide a valuable resource (i.e. provide parental care), cheats, who attempt to acquire the resource, are selected for and brood parasites are usually found to be common (see e.g. Kilner and Langmore 2011). This in turn selects for recognition processes in parents to identify and reject the parasites. A co-evolutionary arms race between host and parasite eventually leads to very fine tuned and complex recognitions system. Consequently, in species with parental care, we would expect more elaborate forms of recognition processes than in species not engaging in any kind of social behavior. For that reason, it is not surprising that burying beetles, which are well-known for their extended biparental care of young, have evolved a rather complex recognition system.

Nicrophorus is a northern hemisphere genus comprising about 72 species (Sikes and Venables 2013; Peck and Kaulbars 1987). Their peculiar habit to bury small vertebrate carcasses, mice or birds, as food for their larvae has fascinated scientists for centuries (e.g. Pukowski 1933; Scott 1998; Eggert and Müller 1997; Royle et al. 2013; Walling et al. 2008; Trumbo and Robinson 2004; Cotter et al. 2010; Steiger 2013; Suzuki and Nagano 2009; Fabre 1899). Usually it is a pair of beetle, a male and a female, which bury a corpse, thereby rolling it up into a ball, removing fur or feathers (Pukowski 1933) and treating it with antimicrobial oral and anal secretion to defend the carcass against competing microorganisms (e.g. Arce et al. 2012; Cotter and Kilner 2009; Suzuki 2001; Hall et al. 2011; Steiger et al. 2011a). The female lays her eggs singly in the surrounding soil and after the larvae have hatched they crawl to the carcass (Pukowski 1933). The parents prepare the carrion ball by opening a small feeding depression at the top, where the larvae usually aggregate. At this time the feeding of the larvae with predigested carrion food begins. The larvae show a specialized begging behavior in which they rear up and wave their legs to obtain food from their parents (Rauter and Moore 1999; Smiseth et al. 2003). Both parents engage in feeding, however, females spend more time nourishing, whereas males are more involved in defending the carcass from competitors (Fetherston et al. 1990; Trumbo 2006). Larvae are also able to self-feed directly from the carcass and the older they grow, the less time they spent begging and the more time feeding on their own. The female stays on the carcass until larval development is complete, the male usually leaves a few days earlier than the female (Trumbo 1991; Bartlett 1988; Scott and Traniello 1990). The larvae crawl into the surrounding soil for pupation and a few weeks after, adult emergence takes place (Pukowski 1933). However, in some species,

larvae stay in the soil as prepupae, and adults do not emerge until the following summer (Eggert and Müller 1997).

Vertebrate carrion is a rare and ephemeral resource, but because of its high nutritive value, extraordinary valuable and sought-after. Not surprisingly, a carcass often attracts many animals, and—to be able to use it for one's own reproduction—burying beetles have to defend it against intra- and interspecific competitors as well as to find appropriate mating and breeding partners (Eggert and Müller 1997; Scott 1998). Even buried carcasses have to be protected against hetero- and conspecifics that try to kill the brood and use the resource for their own reproduction (Trumbo 1990a, 1994; Robertson 1993; Scott 1990). Moreover, intraspecific brood parasitism is known to occur: competitively inferior females do not always leave the carcass immediately, but may stay near the carcass and lay eggs of their own (Müller et al. 1990). Hence, discrimination against unrelated young should be selectively favored to avoid wasting resources on foreign offspring. It goes without saying that recognition is a necessary skill for burying beetles to either effectively defend the carcass, to mate with appropriate partners or to care for their own offspring. For the diverse task they have evolved an indirect time dependent recognition system as well as different social recognition systems, from familiar and class level recognition to nearly true individual recognition (see Gherardi et al. 2012 for definition of social recognition systems). In some cases, they appear to have innate representations of the cues of desired individuals, in other cases they learn the cues of senders and use the memory as a template afterwards in their discrimination decisions. Although burying beetles are known to produce sounds through stridulation during fights, prior to mating and during offspring feeding (Pukowski 1933; Niemitz and Krampe 1972; Huerta et al. 1992), all direct recognition mechanisms investigated to date are mediated by chemical cues and signals. Burying beetles release a vast array of chemicals: they possess a complex mixture of lipids on their cuticle (Steiger et al. 2007) and they also emit more volatile substances into the surroundings (Haberer et al. 2008, 2010).

In this chapter, I provide an overview of the recent advances in elucidating the social recognition processes of burying beetles. I start with the most fundamental type of recognition, the recognition of mating partners (i.e. recognition of species and sex), then I proceed with the more special features of burying beetles, the recognition of breeding partners and parent-offspring recognition.

Recognition Mechanisms Between the Sexes

Long-Range Mate Recognition

It has long been known that male burying beetles release a volatile sex pheromone, thereby adopting a headstand-like posture, pointing their head down and raising the abdomen (Pukowski 1933). Males engage in pheromone emission after having found a carcass suitable for reproduction as well as in the absent of

a carcass, in a daily routine towards the end of the species-typical daily activity period (Eggert and Müller 1989b; Müller and Eggert 1987; Beeler et al. 1999). Females recognize the species-specific pheromone and are attracted to it from a distance. They appear not to be able to discriminate between resource owner and non-owner: a field study has shown that males that have buried a carcass prior to pheromone emission are equally effective in attracting females as males that have not (Eggert and Müller 1989a). Even if the males are not in the possession of a carcass, females are not reluctant but will accept copulation, although they usually fly off after one mating event (Eggert and Müller 1989a). In this situation, females do not gain a resource for reproduction, but they may still benefit by gaining fresh sperm that enables them to reproduce alone in the case they find a carcass suitable for reproduction later on. Interestingly, also conspecific males respond to the sex pheromone, most likely because there might be a chance to take over a carcass from the calling male or to mate with surplus females the pheromone emitter attracts (Müller and Eggert 1987). The sex ratio of the attracted beetle is, however, usually biased towards females. The opportunity to take-over a resource might also explain the asymmetric heterospecific cross-attraction that can be observed in field studies: larger, and therefore in a fight superior *Nicrophorus* species eavesdrop on and react to the male sex pheromone of smaller species, but not vice versa (Haberer et al. 2011; Müller and Eggert 1987). The larger *Nicrophorus humator*, for example, is attracted to its own as well as to the sex pheromone of the smaller *Nicrophorus vespilloides*, whereas *N. vespilloides* does not respond to the sex pheromone of *N. humator* and is exclusively attracted by its own male pheromone (Haberer et al. 2011). Although all burying beetles studied to date are known to release a sex pheromone, only the sex attractants of *N. vespilloides* and *N. humator* have been identified yet. Both species release an ester, the first species ethyl 4-methylheptanoate (Haberer et al. 2008), the second methyl 4-methyloctanoate (Haberer et al. 2011).

Whether females extract more information from the male sex pheromone, beyond species and sex, is not very well investigated. There is only one study that had looked into this topic: Beeler et al. (2002) has shown that female *Nicrophorus orbicollis* discriminate males of different body sizes from a distance preferring males of larger size. However, as the pheromone of *N. orbicollis* has not identified yet, it is not clear, whether this preference is based on quantitative or qualitative differences in the sex attractant.

Short-Range Mate Recognition

A vertebrate carcass as well as a burying beetle's sex pheromone often attracts several beetles of both sexes (Eggert and Müller 1989b; Müller and Eggert 1987). Hence, the long range sex pheromone is not enough to guarantee an appropriate mating partner, but the sex of an encountered conspecific has to be recognized at

a short range as well. Both males and females are able to discriminate between the sexes upon contacting them with their antennae: attracted to a carcass suitable for reproduction, males will fight with males, but tolerate females and vice versa (Pukowski 1933). Moreover, although same sex sexual behavior occasionally occurs (Engel et al. 2015), males usually discriminate between the sexes and copulate with females only. This class level recognition is mediated by contact pheromones on the cuticle: males covered with female cuticular lipids are perceived as females and females covered with male cuticular lipids as males (Steiger et al. 2009). However, although it is known that the composition of the cuticular pattern is sexually dimorphic (*N. vespilloides*: Steiger et al. 2007; *N. orbicollis*: Scott et al. 2008), the substances responsible for mate discrimination have not been identified yet. As in many invertebrate systems, the mate recognition process is innate, i.e. the beetles have not to learn the cues of a conspecific male or female to be able to discriminate. *N. vespilloides* beetles that had never contact to an adult male or female throughout their life, because they were raised in the absence of parents and afterwards kept in isolation, have still the ability to recognize an appropriate mating partner (personal observations).

The Coolidge Effect

If mating entails costs and there is little benefit to re-mating with the same female, selection should favour the evolution of mechanisms that allow males to preferentially mate with novel females (Adler 1978). The Coolidge effect, defined as a decline in the propensity of a male to copulate repeatedly with the same female combined with a heightened sexual interest in novel females (Wilson et al. 1963; Dewsbury 1981), is expected to be a widespread phenomenon among animals. Although the Coolidge effect has been documented in several vertebrates (mammals: e.g. Rodriguez-Manzo 1999; birds: e.g. Pizzari et al. 2003; reptiles: e.g. Tokarz 1992; amphibians: Donovan and Verrell 1991; e.g. fishes: e.g. Kelley et al. 1999), surprisingly few cases are known in invertebrates (e.g. in the red flour beetle *Tribolium castaneum*: Arnaud and Haubruge 1999; in the pond snail *Lymnaea stagnalis*: Koene and Ter Maat 2007; but not e.g. in the decorated cricket *Gryllodes sigillatus*: Gershman and Sakaluk 2009; or the freshwater snail *Biomphalaria glabrata*: Häderer et al. 2009). One possible explanation for its rareness in invertebrates might be that the Coolidge effect requires an individual's ability to distinguish between its previous partner and a novel mate. However, a study of Steiger et al. (2008a) has demonstrated that burying beetles have this ability and males show greater sexual interest for novel females, irrespective whether these females are virgin or had already mated with other males. There are at least three good reasons, why male burying beetles have evolved the ability to discriminate against a previous mate. First, there is evidence that the supply of sperm in males is not limitless and that frequent mating can leave males sperm-depleted (Eggert 1990). Hence, males should invest

their sperm strategically (Wedell et al. 2002). Second, the carcass as valuable resource for feeding and reproduction promotes a temporal clumping of beetles and therefore, there is a risk of remating the same female. Third, there are situations in which copulation with a particular female involves costs in terms of lost opportunities to copulate with other females. Frequently, several females are attracted to a carcass, but most of these potential mates are available for a limited time only, as same sex individuals usually engage in violent fights until only one of them remains in a central position of the carcass (Pukowski 1933; Müller et al. 1990; Eggert and Müller 1997; Scott 1998). Defeated females either leave the carcass immediately for the search of a new one, or stay near the carcass and may succeed in producing some offspring as intraspecific brood parasites (Müller et al. 1990, 2007; Scott and Williams 1993). Therefore, a male investing time by copulating repeatedly with the same female will miss the opportunity to sire some additional offspring with subordinate females that are ultimately expelled from the carcass.

But how do burying beetle males discriminate between their previous mating partner and a novel one? The possibly simplest mechanism that does not require any cognitive abilities, would be to chemically mark the mate during copulation and utilize chemosensory self-referencing to recognize recent mates. There would be no need for learning, rather they could directly compare their own scent with that of the individual with whom they interact (on-line processing sensu Hauber and Sherman 2001). Indeed, this mechanism has been shown in the cricket *G. sigillatus*. In this species, it is the female that discriminates against a previous mate (Ivy et al. 2005). Weddle et al. (2013) has shown that females imbue males with their own unique cuticular hydrocarbon signatures during mating and identify their previous mate based on these cues. However, burying beetles do not appear to transfer any cuticular lipids during mating to mark females. Instead, experiments have shown that they learn their mates' individual specific cuticular pattern during mating: when a male encounters a novel female that is experimentally treated with the same cuticular substances as his previous mate, he mistakes the novel female to be a familiar mate (Steiger et al. 2008a). Although this mechanism is no true individual recognition sensu Gherardi et al. (2012) but an example for familiar recognition, it is still quite sophisticated. First, the chemical cues of females have to be more or less individual-specific, otherwise a male would not be able to discriminate between two random females out of a population, but would make many mistakes. Second, a male must be capable to perceive and learn these individual specific chemical patterns. The composition of the burying beetle's cuticle is highly complex comprising about 100 substances and shows considerable inter-individual variation in their relative proportion (Steiger et al. 2007, 2008a; Engel et al. 2015). The variation of female patterns is even higher than that of males (Steiger et al. 2008a). However, it is currently unknown which of the substances a male can perceive and how many substances he is learning. It would be interesting to see how accurate this recognition system is and how often novel females are confused with previous ones within a population.

Recognition Mechanisms Between Breeding Partners

Even buried carcasses have to be defended by the adult beetles as the corpses can still be discovered by competitors. Successful intruders kill and eat the residents' brood and use the resource for their own reproduction (Robertson 1993; Trumbo 1990c; Trumbo and Valletta 2007; Scott 1990). Infanticide can occur with both, hetero- or conspecifics, and by both, male and female intruders (Scott 1994; Koulianos and Schwarz 2000; Trumbo 1994). When resident beetles encounter intruders, violent fights ensue and males and females assist their mate to drive off intruders of either sex (Scott 1990; Trumbo and Wilson 1993; Trumbo 1991). Hence, individuals rearing a brood on a buried carcass are able to discriminate between their breeding partner and intruding conspecifics (Trumbo and Wilson 1993). However, the beetles do not recognize their individual partners, but their breeding status, i.e. the fact that they have been on a carcass caring for larvae: familiar and unfamiliar brood caring individuals of the opposite sex are generally accepted as nest-mates, whereas non-breeding beetles are attacked (Müller et al. 2003; Fig. 12.1a). Individual recognition is not necessary to defend the offspring, as beetles that are caring for young do not kill larvae of other conspecifics (Müller and Eggert 1990) and are therefore no threat to the brood. Moreover, on larger vertebrate carcasses joint breeding of several males and/or females can be observed (Müller et al. 2007; Scott et al. 2007; Eggert and Müller 1992; Trumbo 1992). Therefore, class-level recognition might be favoured, as learning the individual signature of more than one breeding partner is likely to be a more complicated mechanism than simply to recognize the breeding status of a encountered beetle. Behavioural assays in *N. orbicollis* and *N. vespilloides* have shown that the beetles use chemical recognition cues to discriminate between breeding and non-breeding beetles (Scott et al. 2008; Steiger et al. 2007, 2009). They accept dead breeding beetles and non-breeding beetles that are covered with the chemical cues, i.e. the whole body extract, of breeding beetles. Previous experiments could already exclude the possibility that the cues are merely acquired through contact with or ingestion of carrion (Müller et al. 2003). Chemical analysis via gas chromatography coupled with mass spectrometry revealed that the composition of the cuticular pattern changes within a breeding cycle (Scott et al. 2008; Steiger et al. 2007), and breeding *N. vespilloides* males and females are characterized by a higher proportion of polyunsaturated hydrocarbons, i.e. hydrocarbons with several double bonds, than non-breeding beetles (Steiger et al. 2007, 2008b). In addition, headspace analyses (a technique to elucidate the odour compounds present in the air surrounding an object) brought to light that at least breeding females emit high amount of (*E*)-methyl geranate, a terpenoid, that cannot be detected in females not caring for larvae (Haberer et al. 2010). Behavioural experiments strongly suggest that males rely on both, (*E*)-methyl geranate and cuticular lipids to identify a female's breeding state (Haberer et al. 2010; Steiger et al. 2011b). Interestingly, (*E*)-methyl geranate is structural quite similar to juvenile hormone III (JH III), it only lacks the epoxidised isoprenoid group of JH III. Both molecules most

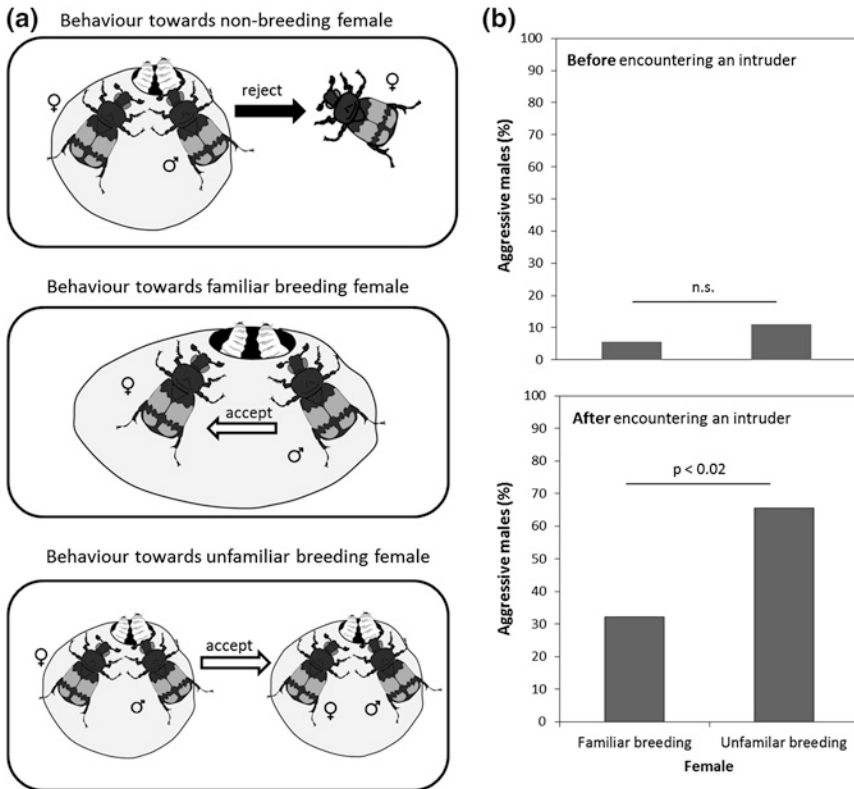


Fig. 12.1 Breeding partner recognition system of the burying beetle *N. vespilloides*. **a** Simplified scheme of the partner recognition system. Breeding males (1) behave aggressively towards non-breeding intruding females, (2) tolerantly towards their own breeding partner, and (3) tolerantly towards unfamiliar breeding females. *Note* it also works for females as receiver and males as sender of the recognition cues. **b** Shift in acceptance threshold. (1) Before encountering an intruding female, breeding males accept both, a familiar and an unfamiliar breeding female and do not discriminate between them. (2) After encountering a female intruder, breeding males become more aggressive towards an unfamiliar than towards a familiar breeding female (Fisher’s exact test). *Note* the original experiment was performed with elytra of females, instead of entire females. n.s. = not significant. Modified after Steiger and Müller 2010

likely share the same biosynthetic pathway, the mevalonate pathway (Bellés et al. 2005). In the course of a breeding attempt, females undergo major physiological changes which include an increase in JHIII (Scott et al. 2001; Trumbo et al. 1995; Trumbo 1997; Scott and Panaitof 2004). Therefore, caring females are characterized by very high hormone titres in contrast to non-caring females and they might signal their hormone titre by emitting (*E*)-methyl geranate to make them distinguishable from non-breeding, intruding females (Haberer et al. 2010). Indeed, an additional study revealed that (*E*)-methyl geranate is a signal that has been selected by the effect it has on the receiver and is not simply an unintentional

metabolic by-product of JH synthesis (Steiger et al. 2011b; see also Steiger et al. 2011c for definitions of chemical cues and signals). Female burying beetles can reproduce alone successfully, they do not necessarily need a male partner to bury a carcass and raise their young (Müller et al. 1998; Scott 1989). Uniparental care occurs regularly in the field (Müller et al. 2007). However, as there is no male partner (i.e. a receiver) in such uniparental situations, there is no need to signal the breeding state to make oneself distinguishable from intruders. In fact, single breeding females have been shown to produce only trace amounts of (*E*)-methyl geranate, 200 times less than paired females (Steiger et al. 2011b).

The chemical composition of the cuticular profile of both, males and females, changes with breeding status, and both, breeding males and females are discriminated from intruders by their partners. The question remains, however, why only breeding females, but not males emit (*E*)-methyl geranate. A proximate reason might be that males have a much lower JH titre (Panaitof et al. 2004) and are therefore not able to produce high amounts of (*E*)-methyl geranate. On an ultimate level, there are at least two non-exclusive explanations. Firstly, the chemical signal has an additional, but hitherto unknown function. Secondly, the task specialization of the sexes is responsible for the differences in chemical signaling. Male burying beetles have a greater tendency and greater ability to guard the brood against conspecific intruders, whereas females spend more time feeding the young (Trumbo 2006). This may lead to a slightly biased signaling system, where females have to be better recognizable and transmit more information than males.

Plasticity of the Partner Recognition System

In nature the cues of desirable and undesirable individuals often overlap. Depending where a receiver individual sets its acceptance threshold, it either runs the risk to make an acceptance or a rejection error. Theoretical models have shown that the optimal acceptance threshold depends on the relative benefits of accepting and rejecting desirable and undesirable senders, the costs of making acceptance and rejection errors and the frequency or future predictability of desirable or undesirable senders (Liebert and Starks 2004; Sherman et al. 1997; Reeve 1989; Davies et al. 1996). An acceptance threshold can be fixed within an individual, however, in more elaborate recognition systems, it may be flexibly adjusted to the current situation (e.g. Hauber et al. 2006). In fact, in *N. vespilloides* it has been shown that the acceptance threshold of the breeding partner recognition system changes with the risk of losing the brood due to an infanticidal intruder (Steiger and Müller 2010). As outlined above, the beetles typically discriminate between their breeding partners and conspecific intruders based on a class-specific discrimination rule and do not discriminate between their own and unfamiliar breeding individuals, but are only aggressive towards non-breeding beetles (Fig. 12.1b). After they have encountered an intruder, however, rejection rate increases, which is manifested as a shift from class-specific to a more or less individual-specific discrimination: beetles

suddenly begin discriminating between their own breeding partner and an unfamiliar breeding individual, and are more aggressive towards the latter (Steiger and Müller 2010; Fig. 12.1b). The experiments highly suggest that breeding beetles learn the individual specific chemical cues of their own breeding partners and use it as a template, but set their acceptance threshold depending on the risk of encountering an intruder. When the risk is low, the acceptance threshold is more permissive and they also accept conspecifics with cues that are less similar to their template (i.e. unfamiliar breeding beetles). When the risk is high, the acceptance threshold is more restrictive and they only accept conspecifics with cues that are identical or almost identical to their template (i.e. own partner) (Steiger and Müller 2010).

Recognition of the Breeding Partner's Fertility

Although burying beetle males prefer to mate with novel females, they nevertheless mate repeatedly with their breeding partner. In fact, video observations revealed that they mate on average 170 times during a breeding attempt, which lasts about 10 days in *N. vespilloides* (Engel et al. 2014). However mating rate is not constant; it is high in the beginning, but it drops at the time the larvae arrive at the carcass and no mating occurs, when young larvae are present. The copulation pattern corresponds to the oviposition pattern of the females. They lay their eggs in the beginning of the reproductive event over a period of about two days, but during the time of larval feeding, they do not engage in egg laying (Müller 1987). Only if the brood is lost to predators or competitors, females will resume egg-laying (Müller 1987). If females are manipulated experimentally into producing such replacement clutches, males do not cease to mate, but continue to engage in frequent copulations (Engel et al. 2014). Further experiments brought to light, that males do not use the presence or absence of larvae as a cue to adjust copulation rate, but instead use female-produced cues/signals and are able to recognize a female's period of fertility or temporarily infertility (Engel et al. 2014). During parental care, females might either reduce the emission of a substance that otherwise triggers male mating behavior (sex pheromone/aphrodisiac), or they might increase production of a new substance that repels males (antiaphrodisiac). Further experiments are necessary to unravel the exact mechanisms of this recognition process.

Recognition Mechanisms Between Parent and Offspring

The Parents' Viewpoint

When two females compete for a small carcass the defeated females usually do not leave immediately, but lay eggs close to the carcass. This situation has been described as intraspecific brood parasitism, because (1) subordinate females

typically abandon the carcass prior to the appearance of larvae and do not provide parental care and (2) the reproduction of subordinate females reduces the dominant's reproductive success (Müller et al. 1990). Subordinate females frequently have some surviving offspring, the composition of the brood, however, is severely skewed in favor of the dominant female. Lab as well as field studies have shown that the brood contains on average 6 % parasite offspring, often not more than one to two young (Müller et al. 1990, 2007). Although the reproductive skew can partly be explained by the loser's inability to produce as many eggs as the winner because of limited access to the carcass and therefore nutrition (Eggert et al. 2008), two different mechanisms of parent-offspring recognition has been found to contribute to the lower reproductive success of the subordinate female. In *N. tomentosus* (Scott 1997), but not in *N. vespilloides* (Eggert et al. 2008), there is some evidence that females increase the proportion of own offspring in a brood by selective ovicide. Although it is not known how they are able to discriminate between their own eggs and the foreign ones, it is possible that individual specific cuticular lipids or other chemicals left behind on the egg surface serve as recognition cues (see e.g. Endler et al. 2004). In *N. orbicollis*, intruders into the brood chambers are also known to destroy eggs of the resident pair before starting their own reproductive attempt (Robertson 1993). However, this is a different situation, as they have not to distinguish their own eggs from the residents' one. Nevertheless, it illustrates that the beetles are able to recognize conspecific eggs and are selected to exhibit oophagy.

The second known mechanism of parent-offspring recognition in burying beetle is a time-dependent recognition mechanism. In general, parental beetles are unable to directly distinguish their own larvae from unrelated conspecific larvae. Dominant females, however, are known to kill all larvae they encounter prior to hatching of their own larvae (Müller and Eggert 1990; Eggert and Müller 2011). Females switch from infanticidal to parental behaviour at about the time their own larvae hatch, and subsequently, they accept newly hatched *Nicrophorus* larvae indiscriminately (Müller and Eggert 1990; Trumbo 1994; Oldekop et al. 2007). Once females have begun to care for larvae, they remain 'parental' until the larvae have completed development on the carcass (Müller and Eggert 1990). That individuals rely on temporal cues as indirect indicators of relatedness to distinguish between their own and unrelated young is not *Nicrophorus*-specific, but is also known from a range of other organisms (Elwood 1994). In burying beetle, such time-dependent recognition mechanism is quite effective in destroying brood-parasitic young: dominant females have been shown to kill over half of the subordinate's larvae by using temporal cues (Eggert and Müller 2011). Certainly, the prerequisite of this mechanism is that some of the subordinate's larvae hatch earlier than that of the dominant one. But exactly this is the case in *N. vespilloides*. Subordinate females have shown to start oviposition nearly one day earlier than dominant ones (Eggert and Müller 2011). The reason for this oviposition pattern is unknown. Both, dominant and subordinate would benefit from late oviposition, as the dominant would improve discrimination between own and foreign young and the subordinate would save its young. However, it is possible that subordinates

are constrained to oviposit earlier because of nutritional limitations or injury risk (Eggert and Müller 2011). Interestingly, the temporal recognition mechanism is plastic, too, and the dominant's acceptance threshold depends on the presence or absence of a subordinate. Females breeding with a parasite remain infanticidal until 4 h after their own larvae begin to hatch, whereas singly breeding females begin accepting larvae already 8 h before their own offspring hatch (Eggert and Müller 2011). Though dominant females risk destroying some of their own young by shifting the switch from infanticidal to parental care to a later time, they may be able to kill a greater proportion of the unrelated larvae. Killing own larvae may be less costly than accepting subordinate ones, as female are anyway known to produce surplus hatchlings on small carcasses (Bartlett 1987; Trumbo 1990b).

Both parents are known to react towards a begging larva by providing food (Pukowski 1933). There is evidence that larval begging reflects hunger level, as larvae have been observed to increase their begging behavior following food deprivation (Smiseth and Moore 2004, 2007). Parental resource distribution, in turn, is biased towards food deprived larvae, most certainly because hungry larvae spend more time begging (Smiseth and Moore 2002, 2008). As larvae touch the parent's mouthpart, mechanical cues are likely to play a role in stimulating parental feeding behaviour. However, it cannot be excluded that chemical cues are likewise important. In the earwig *Forficula auraria* (Mas et al. 2009) and the bumblebee *Bombus terrestris* (Den Boer and Duchateau 2006), for example, chemical cues of offspring contain information about nutritional condition and influence the mother's food allocation pattern. In both cases, cuticular lipids appear to be involved. In burying beetles it has never been investigated, whether chemical cues mediate parents' resource distribution within a brood, but there is evidence that chemical cues must be important for offspring recognition. Although, burying beetles are not known to reject heterospecific larvae of the same genus or the sister genus *Ptomascopus* (Trumbo 1994; Trumbo et al. 2001), there at least able to discriminate between burying beetles larvae and *Tenebrio* larvae or dipteran larvae, even there are deposited into the cavity of the carcass together with their own offspring. They selectively fight (*Tenebrio* larvae) or kill and consume (dipteran larvae) them upon contacting them with their antennae (personal observation). Unfortunately, no study has looked into this topic in more detail.

The Offspring's Viewpoint

Larvae do not beg randomly, but increase begging level when a parent is around. Hence, larvae must somehow be able to perceive the presence of a parent or at least a beetle. Although the stridulatory sound parents produce may help to orientate towards a parent (Huerta et al. 1992), it has been shown that acoustic and also behavioral cues are not necessary for triggering begging behavior, as larvae also beg towards a dead beetle (Smiseth and Parker 2008). However, if the parents' cuticular lipids are removed by washing them in pentane, begging behavior

is significantly reduced (Smiseth et al. 2010). Thus, chemical stimuli from parents play an important role in parent-offspring interactions. Parents cannot discriminate between related and unrelated offspring based on direct cues about kinship and also offspring appear to lack the ability to distinguish between related and unrelated caretakers, at least they do not show any differences in the time of begging towards their biological mother and an unrelated breeding beetle (Smiseth et al. 2010). However, whereas the parents would benefit if they could discriminate against unrelated larvae based on direct kin recognition cues, the offspring would have no obvious advantage from kin discrimination. In contrast, as a larva might originate from a brood parasite, not displaying any begging behavior towards an unrelated caretaker would reduce its growth and therefore be detrimental. Interestingly, Smiseth et al. (2010) has shown that larvae are able to discriminate between a breeding and a non-breeding and therefore infanticidal female. However, the larvae do not actively avoid non-breeding female intruder, rather they only spend less time begging in the presence of an intruder female. Therefore it is likely that this discrimination is not an adaptive mechanism for avoiding contact with infanticidal females, but is a by-product of stimulus discrimination (Smiseth et al. 2010). As already outlined above, breeding beetles have a different chemical profile than non-breeding ones and as a result chemical cues that trigger begging might be expressed differently in breeding and non-breeding beetles.

Concluding Remarks

In this chapter, I provided an overview of the sophisticated social recognition mechanisms burying beetles have evolved. They are able to recognize the sex of a conspecific, their previous mating partner, their breeding partner, the breeding female's readiness or unreadiness to lay eggs and—by using temporal cues—their offspring. Their discrimination decisions are not static, but can be flexibly adjusted to the current situation. Recognition abilities differ between the sexes. Whereas males are better in defending the brood against conspecific intruders, females are inevitably superior in recognizing offspring, as they have exclusive knowledge about the time of egg laying and therefore larval hatching. Two of the burying beetles' key characteristics, their extended biparental care and reproduction on a small carcass (a valuable and scarce resource), have profoundly influenced the evolution of their recognition system. Biparental care promotes the temporal overlap of individuals for whom mutual recognition is beneficial—breeding partners and their offspring. At the same time, the scarcity of resources essential to reproduction means that breeding beetles will often encounter competitors that are a threat to their own brood—infanticidal intruders, brood parasites and unrelated offspring; recognition of these individuals is also favored. Consequently, neither universal rejection nor universal acceptance of all encountered individuals is an optimal strategy, but discrimination was and is selectively favored in burying beetles.

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