

CHAPTER 5

Patterns of parental care in invertebrates

Stephen T. Trumbo

5.1 Introduction

The tremendous diversity of social behaviour among the invertebrates is an asset and a challenge. There is richness in both the number of phylogenetic lineages that have evolved extended parental care and the forms of care provided by parents. Fifty families of insects in more than a dozen orders have evolved parental care (Costa 2006), and sixteen separate lineages of arthropods exhibit paternal care (Tallamy 2001; Nazareth and Machado 2009). There are three principal avenues for progress in evolutionary biology: new theory to test, new technology for measurement, and new subject matter. This last avenue is still wide open for students of parental care in invertebrates. Among birds and mammals, extended parental care is universal (Chapter 4) and most forms of care have been well studied. On the other hand, new species and new forms of care in the invertebrates are being discovered yearly, permitting a creative interplay between inductive and deductive approaches. The non-eusocial invertebrates are where we will find the subject matter for understanding the origins of parental care, transitions between types of care, and manipulable systems for testing theories. Broad phylogenetic comparisons will permit testing of the ecological factors that favour different social solutions, and also whether convergent parental behaviour is built upon convergent physiological mechanisms. More narrow comparisons will reveal how closely related species can take widely divergent social paths. For studies of single species, invertebrates offer many pragmatic advantages over vertebrates. First, most

invertebrates live in a very different sensory world than humans. While this imposes barriers to our understanding, it also allows manipulations, such as observation under red light, that have minimal effect on experimental subjects. Second, the smaller size and shorter lives of many invertebrates make it practical to follow large numbers of subjects over their lifetime, often in the laboratory. Third, many invertebrates are also suitable subjects for selection experiments and genetic analysis, which will eventually allow an understanding of how interactions between genes and developmental environments produce the tremendous variation in parental care and social behaviour.

According to broad definitions of parental care, care includes all parental traits that enhance offspring fitness (Chapter 1). For the purpose of discussing the origins and transitions of extended care in the present chapter, consideration is confined primarily to post-fertilization traits that increase offspring fitness, beyond the temporary housing and passage of the fertilized egg within the female. Viviparity and ovoviviparity will therefore be discussed, but the amount of yolk in an egg and selection of an oviposition site will not. After an overview of the forms of parental care, the origins, transitions, and loss of parental care will be discussed, including male versus female care. Lastly, the microbiology of care is salient for appreciating the complexity of social invertebrates and needs to be integrated into our understanding of parental care. The physiology of care is not treated here because this topic was covered in a prior review (Trumbo 2002).

5.2 Forms of care

The evolution of parental care in many independent lineages of invertebrates has resulted in diverse forms of care (Chapter 1). An exhaustive review of all forms of care in invertebrates is not feasible. Although this chapter uses a slightly different scheme to characterize the diversity of forms of care, the categories used here can easily be fitted into the more general scheme used in Chapter 1. I start with two basic forms of parental care, the use of trophic eggs and sedentary protection of eggs. I then discuss more complex forms, many of which were built upon the initial parent–egg association.

5.2.1 Trophic eggs

Trophic eggs are food provisions that do not require direct maternal–offspring contact, and either may be the sole form of care or part of a diverse suite of parental behaviours. Reduction of sibling cannibalism may have been an important ecological need at the origin of trophic egg production. In some species, juveniles cannibalize viable eggs or opportunistically consume inviable eggs before leaving the oviposition site. In such species, the origin of trophic eggs may be preceded by kin selection on cannibalistic young to discriminate between viable and inviable eggs. To assist young in making the correct choice of which eggs to consume, maternally derived cues could be incorporated into trophic eggs that initially mimicked the kin-selected discrimination cues employed by juveniles. Production of trophic eggs might reduce cannibalism, thereby enhancing direct fitness of parents and indirect fitness of offspring (Perry and Roitberg 2006). Because accurate discrimination between eggs may not increase the direct fitness of young, the use of trophic eggs may not necessarily have originated as a form of parental care.

Although there is debate in particular species about whether a consumed egg was indeed ‘trophic’, there are also clear cases of use of trophic eggs. True trophic eggs should be easy to distinguish from non-trophic eggs, should be available at the appropriate time for developing young, and should provide a nutritional benefit not easily supplied by the mother (West and Alexander 1963).

In the wood-feeding passalid beetle *Cylindrocaulus patalis*, trophic eggs are paler, softer, and with a less complex chorion compared to viable eggs. If third instar larvae stridulate, they are fed a trophic egg by the mother (Ento et al. 2008). In the burrower bug *Canthophorus niveimarginatus*, females produce some trophic eggs at the same time as they produce viable eggs, but they also lay additional trophic eggs after the nymphs hatch (Filippi et al. 2009). In burrower bugs, trophic eggs can provide food for nymphs while the mother forages for seeds away from the nest (Hironaka et al. 2005). In each of these systems, production of trophic eggs is part of a suite of parental behaviours. Investigation of systems with only trophic egg provisioning will provide insight into its origin and allow tests of the reduction of cannibalism hypothesis.

5.2.2 Attending eggs and offspring

After a female oviposits in a selected location, a tendency to linger near the clutch might offer modest protection from predators or parasitoids. Protection requires clumping of eggs (as opposed to scattering in the environment), a behaviour that may have preceded extended care due to the enhancement of an aposematic effect, facilitation of feeding among siblings, or oviposition near a patchy food source. Subsequent to the evolution of post-ovipositional care, young may be under selection to aggregate to facilitate care. At its origin, protection of young may evolve without specialized parental behaviour. Tallamy and Schaefer (1997) have pointed out that maternal defensive behaviours in the lace bug *Gargaphia solani* are similar to those used in conspecific interactions, and were likely to have been co-opted from the former without a long period of evolutionary modification. Over time, defensive behaviour can become increasingly complex. In the treehopper *Umbonia crassicornus*, mothers tilt their elongated pronotum, and fan and buzz potential threats, protecting their young until adulthood. In the presence of a predator, offspring produce synchronous vibrations that inform the mother on which side of the aggregation the threat is more imminent (Ramaswamy and Coccoft 2009). Not all predators, however, can be deterred by active defense. Female spider mites (*Stigmaeopsis*) employ a form of

misdirection where they produce numerous ‘void’ nests in addition to the true nest that contains an egg mass. Void nests appear to reduce predator search efficiency, and ultimately reduce predator motivation (Saito et al. 2008).

5.2.3 Protection and facilitating feeding of mobile young

Mobile young feeding out in the open are vulnerable to predators and parasitoids (Tallamy and Wood 1986). In some species, the protective mother simply follows her young around. For example, in the acanthosomatid bug *Elasmucha dorsalis*, protection lasts for over two months while the nymphs feed on fruits or flowers (Kûdo et al. 1989). The presence of the mother can also facilitate cooperative behaviour among juveniles, such as in scorpions where groups of young are able to subdue much larger prey than young feeding alone (Mahsberg 2001). The benefits of mass action or byproduct mutualisms among aggregating juveniles may exceed the costs of heightened predation only in the presence of a defending parent. Mothers can also play a more direct role in facilitating feeding. Mothers of the treehopper *Umbonia crassicornus* make a series of spiral slits down the stem of the host plant where their young aggregate to feed. Parental females stand nearby, not only threatening potential predators, but stroking wandering nymphs (Wood 1976). Such ‘herding’ behaviour has evolved convergently in folivorous beetles (Windsor and Choe 1994), as well as in fungus feeding beetles of the genus *Pselaphacus* (Preston-Mafham and Preston-Mafham 1993). In this latter group, the mother shepherds her larvae from fungus to fungus, first sitting over them and then walking off, some young underneath and some straggling behind in a line, perhaps following a pheromone trail. Some mothers appear to lead larvae out to feeding sites each day and back to a hiding place each night, permitting a rapid development that may be as short as four days.

5.2.4 Brooding behaviour and viviparity

An alternative form of protection is to carry eggs or young either internally or externally. Brood

pouches are common among non-insect invertebrates. In an exceptional case, mothers of the tailless whipscorpion *Phrynus marginemaculatus* protect their young for at least 11 months. Others, such as fathers of all species of sea spiders, simply carry eggs on ovigerous legs (Barreto and Avise 2008), as does the mother in the only squid species known to have post-spawning care (Seibel et al. 2005). Viviparous scorpion mothers extend care by assisting in birth and then transferring young to her back. During transfer, young that have difficulty separating from their birth membranes are more likely to be cannibalized by the mother, salvaging nutrients from offspring unlikely to thrive (Mahsberg 2001).

Leeches provide diverse forms of care, ranging from the production of a protective cocoon for eggs, via brooding of eggs and young, to feeding of young (Kutschera and Wirtz 2001). In the hermaphroditic leech *Helobdella papillornata* the parent carries young on its venter for up to 60 days and provisions them with gastropods. Paez et al. (2004) argue that although parental care in this sit-and-wait predator is costly, it may be less so than it would be in leeches that actively hunt. Cockroaches are also known for carrying young in a variety of ways. Oviparous species carry an ootheca externally, false ovoviviparous species retract the ootheca into the abdomen, true ovoviviparous cockroaches carry eggs and then the young in a brood sac without producing an ootheca, and viviparous species nourish young internally with secretions (Nalepa and Bell 1997). In the ovoviviparous *Thorax porcellana*, care is extended when hatching nymphs ride in a specialized compartment on the dorsum (Fig. 5.1) and obtain liquid nourishment through pores of the mother by using their mandibles to pierce the mother’s cuticle (Bhoopathy 1998). These specialized mandibular ‘teeth’ are lost at a later instar when young no longer associate with the mother.

In aquatic environments, oxygen availability can be a fundamental constraint on the number of embryos that can be brooded and there can be considerable costs to making oxygen available to the centre of a large embryo mass (Fernández et al. 2000). Smith (1997) has related how the back-brooding male giant water bug must keep eggs moist to prevent desiccation, yet periodically push

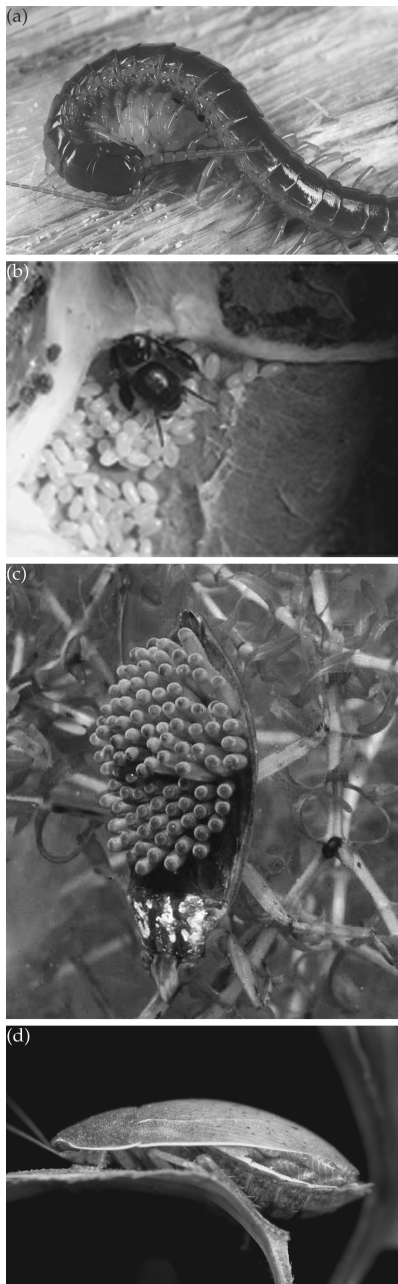


Figure 5.1 (a) Centipede (believed to be *Scolopendra subspinus*) wrapped around her eggs (Scott Camazine); (b) a webspinner (*Partenembia reclusa*) mother emerging from underneath her silk nest (Janice Edgerly-Rooks); (c) a male giant water bug (*Belostoma flumineum*) carrying eggs of two females who oviposited close in time (Scott Kight); (d) the cockroach *Thorax porcellana* carrying nymphs in a specialized compartment on her dorsum beneath the carapace (Natasha Mhatre).

the eggs above the water surface to increase oxygen availability. Where paternal care is so essential, it is predicted that male sexual advertisement might reflect his parental ability (Kelly and Alonzo 2009). The belostomatids would be an attractive model for this question because the pumping sexual display of males shares many features in common with the vigorous oxygenating behaviour during care. The ancestral pattern within Belostomatidae of ovipositing eggs on emergent vegetation adequately met the oxygen demand, but necessitated that the male imbibe and regurgitate water onto the eggs, or else stand above the egg cluster and dribble water down toward the clutch (Ichikawa 1988). These extraordinary adaptations for aerating and hydrating eggs may be necessitated by selection for large eggs that must rely on passive diffusion of oxygen (Smith 1997).

5.2.5 Nest building and burrowing

The ability to create and maintain a long-term favourable microenvironment for eggs or young (nesting) is a foundation for many of the remarkable social behaviours found in invertebrates. Web-spinners build a branched silk tunnel system that not only protects against predators, but provides a favourable physical environment by elevating humidity and reducing temperature (Edgerly 1997). Enhancing offspring fitness by environmental buffering is most evident in extreme environments such as the desert where burrow systems make the habitat tolerable (Rasa 1998). A remarkable example of transition to a niche widely divergent from the ancestral state occurs in the crab *Metopaulias depressus*, which maintains a nursery in water-holding epiphytic bromeliads. During a 9-week period the mother removes debris that reduces substrates for oxygen-consuming decomposers, and adds shells to increase the availability of calcium carbonate (Diesel and Schuh 1993).

5.2.6 Food provisioning

More complex parent–offspring interactions can develop subsequent to the evolution of nesting. In addition to trophic eggs (see Section 5.2.1), there are four basic types of food provisioning based

on a nest: 1) mass provisioning for each offspring, 2) mass provisioning with a large resource (e.g. carrion) for multiple offspring, 3) nesting within the food source that is modified to serve as shelter by the parent (e.g. a log or tree), and 4) progressive provisioning of young. In a classic work, Evans (1958) outlined a series of increasingly more complex nesting behaviours among wasps, from mass provisioning of a single food item for each larva, to progressive provisioning of smaller items. Diversity of forms of provisioning behaviour is also seen in spiders. The simplest form, and perhaps the origin of provisioning in spiders, might have occurred when a mother tolerates young for an extended period near a site where she stores food (Buskirk 1981). Progressive provisioning occurs in many social spiders in which parents and sometimes juveniles cooperate to capture numerous prey, and in some cases (e.g. *Anelosimus studiosus*) the young stay until maturity (Jones and Parker 2002). The spider *Stegodyphus lineatus* regurgitates repeatedly to young and then makes the ultimate sacrifice, allowing the young to feed upon her body (Salomon et al. 2011).

Some dung- and carrion-feeders are mass provisioners of a sort. The nutrient-rich resource typically requires ongoing maintenance to control microbial competitors and ward off potential usurpers (Hanski and Cambeport 1991). Dung feeders match the available food resource to brood number by partitioning the resource for each larva, while burying beetles adjust the total number of young to match the size of the indivisible carrion resource (Wilson and Fudge 1984). Wood feeders typically live inside their food resource, which also provides shelter. After egg-laying, parents can progressively extend tunnel systems to meet the demands of growing young who feed off wood, fecal material, or fungi that use wood as a substrate (Kirkendall et al. 1997; Schuster and Schuster 1997).

For many types of food provisioning, there is the potential for feedback from young to alter subsequent parental care. Mass provisioners such as burying beetles and dung beetles, and progressive provisioners such as burrower bugs and earwigs, adjust their parental behaviour to cues from offspring. Overlap of parents and offspring and parent-offspring communication can be co-opted

for the elaboration of more complex social behavior. For example, permanent-social behaviour is seen in progressively provisioning spiders (Avilés 1997), eusociality evolved from progressive provisioning Hymenoptera, and eusociality from wood-feeding in bark beetles (Kent and Simpson 1992).

The most intimate parent-offspring interactions are observed when parents feed young by regurgitation (stomodaeal trophallaxis). Regurgitation allows parents to soften food, add digestive enzymes, and transfer symbionts. Parents may respond to cues from offspring as in the earwig *Forficula auricularia*, which increases provisioning to high quality offspring (Mas et al. 2009). Regurgitation behaviour may be especially critical for altricial young with poorly developed sensory abilities and unsclerotized mouthparts, as found in the woodroach *Salganea* (Nalepa et al. 2008). In the burying beetle *Nicrophorus vespilloides*, parents respond to the hunger level of offspring, while offspring increase begging in response to a chemical cue from the parent (Smiseth et al. 2010). Mutual adjustment of provisioning and begging behavior by parent and offspring suggests a complex co-evolution in which conflicts over the amount of care are resolved.

5.3 Origins and transitions of parental care

5.3.1 Factors promoting care

Students of evolutionary biology are taught very early that an understanding of the maintenance of an adaptation does not explain its origin. The origin of parental care has not attracted as much attention as other issues (Clutton-Brock 1991), such as which sex provides care, transitions between types of care, or the origin of eusociality from 'presocial' behavior. The universality of extended care among birds and mammals, and their origins in a distant reptilian past, explains some of the neglect. Biologists studying ectotherms, in which different forms of care have evolved many times independently, have shown more interest in this issue, stimulated by the opportunity for comparative work (Reynolds et al. 2002). Using dung beetles, Halfpenny and Edmonds (1982) outlined an increasing complexity of parental

provisioning across extant species that is suggestive of a past progressive evolutionary sequence. The diversity of parental care within some groups (e.g. no care, maternal care, paternal care, amphisexual care in harvestmen) show promise of uncovering the ecological tipping points that nudge different species toward one evolutionary pathway or the other (Machado and Macías-Ordóñez 2007). Theory and broad phylogenetic analyses, long employed for topics such as which sex provides care, have been a relatively recent approach for understanding the origins of care.

The first modern attempts to explain the origin of parental care among invertebrates emphasized ecological pressures. The prime movers of care were proposed to be stable and structured environments (K selection for parental investment), harsh environments (care as a buffer allowing expansion of the realized niche), use of rich, ephemeral resources (enhanced competition often leading to biparental cooperation), and intense predation pressure on eggs (Wilson 1975). There are two practical problems with using this framework. Most care-giving species, such as the bromeliad crab described earlier, exhibit multiple forms of care, making it difficult to determine which adaptation and which prime mover was important at the origin of care. Secondly, while most insects face at least one of these ecological challenges, extended parental care is rare (about 1% of insect species, Costa 2006). Among other groups of invertebrates, however, parental care is quite common.

Barriers to care among insects are thought to exist both because of a lack of clear benefits of care and the substantial hurdle of evolving necessary innovations. The insect ovipositor allows eggs to be dispersed in the smallest hiding places, and the remarkable ability of the insect egg to allow gas exchange while retaining even smaller molecules of water, greatly reduces the benefits of care for many species (Zeh et al. 1989). Even if the potential benefits of parental care were substantial, small-bodied, short-lived insects with limited means to modify the environment or deter predators might have difficulty evolving effective care-giving (Zeh and Smith 1985; Tallamy and Wood 1986). Only an innovation such as the modification of an ovipositor into a sting or the evolution of burrowing legs or

silk production might provide a pathway through the adaptive landscape to reach parental care.

A second ecological approach to the origin of parental care emphasizes food resources, particularly their persistence, dispersion, and nutritional value (Tallamy and Wood 1986). Folivores, which often feed out in the open, tend to provide care in the form of protection against parasitoids and small predators. Detritivores, which typically feed on dispersed sources, either must forego feeding during care (e.g. earwigs) or carry their young with them (e.g. cockroaches). The use of protein-rich resources such as carrion and dung, or the use of sheltering wood may select for biparental guarding of the resource, which in turn may set the stage for protection of young (carrion and dung) or nutritional assistance (wood). Insect predators feed on unpredictable resources and sacrifice foraging opportunities to provide care. Tallamy (2001) noted that six of the seven insect lineages that have evolved male-only care have a predatory lifestyle, suggesting that maternal care would entail high fecundity costs. The association between a predatory habit and the absence of maternal care, however, does not hold as well for non-insects. The possession of effective defence mechanisms such as venoms has perhaps promoted extended maternal care among predatory centipedes (Fig. 5.1), spiders, and scorpions (Costa 2006).

A third ecological approach proposes that a primary barrier to the evolution of parental care is the cost of future reproduction (Trivers 1972; Tallamy and Schaefer 1997). Parental care is not only an adaptation that can solve an ecological problem, but may incur substantial fitness costs to parents. Among species with indeterminate growth such as fish and many marine invertebrates, parental care will subtract resources that otherwise could be allocated toward adult growth. Because fecundity is often related to body size by positive allometry, care will have high costs in species with the potential for large body size. This may explain the association of parental care and small body size in many ectotherms with indeterminate growth (Strathmann and Strathmann 1982).

Consideration of life-history trade-offs, feeding ecology, and Wilson's prime movers provides a plausible explanation of why some insects exhibit

parental care. Left unanswered are the questions why other insects exploiting the same resources in the same habitats do not provide care, and why some invertebrate groups (spiders, scorpions, pseudoscorpions, centipedes, octopuses) are primarily parental (Costa 2006)? There are thousands of species of invertebrates that use small vertebrate carrion as a resource, some facultatively, some obligatory. Only the burying beetles (65 species) and some of the tropical scarabs have evolved parental defence of the carcass from competitors, and provisioning of food to larvae. Other carrion specialists have taken diverse parental and non-parental evolutionary routes. The sarcophagid flies employ an alternative form of parental care, bypassing an external egg stage and depositing larvae directly on the resource. Many other dipterans simply maximize speed, locating and ovipositing on a carcass within minutes of availability, while other non-parental invertebrates are latecomers and consume the leftovers. One predisposition for subsocial behavior occurs when organisms have been selected to modify their microenvironment, a process that increases the variance in environmental quality. Creating highly favourable environmental space selects for adults to remain in such spaces, and also provides an advantageous place for eggs and young to develop (Nowak et al. 2010). Such different approaches to the same resource, leading to alternative forms of parental care or to the absence of extended care, are only to be understood by overlaying life-history and ecological approaches on a phylogenetic framework.

Phylogeny will also be necessary to understand why parental care is present or absent in non-insect invertebrates. While most insects use an ovipositor to selectively locate and protect their eggs without extended care, many groups employ viviparity (scorpions), brood pouches (pseudoscorpions, tailless whipscorpions, amphipods, isopods), or egg cases (spiders) to protect young. Viviparity has also evolved numerous times among diverse marine invertebrates and in selected groups of insects such as dipterans (Reynolds et al. 2002). To understand why flies should evolve viviparity, but rarely other forms of extended parental care, will require a thorough understanding of the physiology of female reproductive systems and embryo development.

Difficult, but rewarding work in evo-devo may be the only path to understand phylogenetic biases in the intensity and forms of parental care.

Gillespie and McClintock (2007) and Poulin et al. (2002) argue that historical biogeography is also needed to understand patterns of parental care. Among echinoderms, more species exhibit brooding behaviour in the Antarctica than near the Equator. While the difficult environment has been proposed to be a prime mover for care, in this case an evolutionary as well as an ecological time scale must be considered. Poulin et al. (2002) suggest that the extinction of phytoplankton during periodic shifts to colder climates may have eliminated the food source for planktotrophic echinoderms, favouring non-broadcasting species that brood their young. Brooding species are thought to have greater opportunity to buffer environmental conditions for young, allowing young to subsist (indirectly) on the food sources of their mothers.

As opposed to the extrinsic hypotheses for the origin of parental care, an intrinsic factor, haplodiploidy, is thought to predispose some groups toward care, specifically maternal care, especially when inbreeding is prevalent (Linksvayer and Wade 2005). Although haplodiploidy is well known to be associated with eusociality, it appears to be more strongly linked to subsociality (Alexander et al. 1991). Subsocial behaviour in mites and ticks is found only among haplodiploids (Saito 1997), and also in haplodiploid bark beetles (Kirkendall et al. 1997), thrips (Crespi and Mound 1997), and of course, Hymenoptera. Reeve (1993) proposed the protected invasion hypothesis to explain why the loss of dominant alleles for care and allocare to genetic drift is rarer in females of haplodiploid species. Analysis of this hypothesis has focused almost exclusively on the evolution of eusociality and awaits testing by students of subsocial behaviour.

5.3.2 Male versus female care

From the earliest days of the field, sociobiology has provided novel insights into conflicts among individuals, including conflict between males and females over mating and parenting (Trivers 1972). In this section, invertebrate models that appear

particularly favourable for addressing the questions of which sex provides care, why exclusive male care has evolved, and how transitions between the various parenting systems might occur, are highlighted. In the next section, cooperation and conflicts between males and females in biparental systems are discussed.

Attractive systems for understanding the origin of male versus female care are those, like the *Rhinocoris* assassin bugs or the harvestmen, that exhibit a diversity of parental behaviour despite living in similar habitat, having a similar feeding ecology, and having the same mode of fertilization. Using a model that does not restrict parents to caring for one brood at a time, Manica and Johnstone (2004) demonstrate that female care can be favoured when the time to produce a second batch of eggs (processing time) is long and population density is low as in *Rhinocoris carmelita*, and paternal care is favoured when processing time is short and population density is high, as in *R. tristis*. Encounter rates with available females is a critical factor in allowing males to care for multiple broods, and in the evolution of exclusive male care (Gilbert et al. 2010). As a caveat, we cannot know whether the life-history and ecological conditions required by the model were present at the origin of care. Even greater diversity of care-giving (no care, maternal care, paternal care, amphisexual care) is found among harvestmen (Buzatto and Machado 2009; Nazareth and Machado 2010). Paternal care in the harvestman *Pseudopucroliia* seems to be best explained by sexual selection, as guarding males are more attractive to mates than non-guarders, so much so that males will initially guard unrelated eggs.

Exclusive male care has evolved in at least 16 independent lineages among the arthropods. As with *Rhinocoris* and harvestmen, most cases are explained by territoriality that initially allowed males to provide a benefit to young (protection) at low cost, while still attracting additional mates. This pathway to polygyny (Paternal Care Polygyny) is distinct from other forms of polygyny (Resource Defence, Female Defence, Lek) in that females are attracted to males that have initiated care-giving for another brood. Even with exclusive male care, there can be sharp conflicts between the interests of

males and females. In *R. tristis*, eggs are better protected under leaves, but many males care out in the open on stems where they are more likely to attract other females. Presumably this divergent caring behaviour is maintained by the trade-off for males between less effective care for more eggs and more effective care for fewer eggs, and by the high costs for females of searching for caring males under leaves (Gilbert and Manica 2009). In other cases, exclusive male care may be a solution enhancing the reproductive potential of both sexes. In the polychaete worm *Neanthes arenaceodentata* the transfer of parental costs from the female to the male may directly benefit the male by allowing the female to put all of her resources into eggs. The female produces extremely large eggs for polychaetes, and dies soon after mating, after which she is often eaten by the male who obtains more energy for brooding (Schroeder and Hermans 1975).

The paternal care polygyny hypothesis for uniparental male care does not explain why females would oviposit where another female has placed a clutch. Two ideas for the origin of this behaviour have been proposed. Tallamy (related in Costa 2006, p. 35) suggests that multiple females might initially oviposit in the same location for reasons unrelated to care such as to facilitate feeding of her offspring, to enhance an aposematic display, or to dilute predation pressure. If so, males might be selected to intercept females directly before oviposition by defending the site against rival males. Trumbo (1996) offered an alternative possibility that females previously selected for dumping eggs in the clutch of another female could transfer that behaviour instead toward a territorial male. A male with a clutch might be more attractive to a female looking to dump eggs. This has the result of females copying the mate choice of prior females, establishing the potential for polygyny right at the origin of paternal care (Ridley 1978).

A second type of exclusive male care, found in sea spiders (Barreto and Avise 2008) and giant water bugs (Smith 1997), occurs when the male carries eggs. In these circumstances care is likely to be more costly and it is less clear whether the potential for polygyny is important. The lack of suitable oviposition sites and high fecundity costs of maternal care may have been the driving forces

for male care (Tallamy 2001). Although there may be some potential for polygyny in the giant water bugs, it does not appear to be great. The number of eggs a male can carry is limited by his backspace and it may be inefficient for males to carry eggs oviposited at widely different times. When a male is carrying a partial brood, for a short time he may accept a partial brood of a second female (see Fig. 5.1). Males, however, may remove a partial brood from a first mate to make room for a full complement from a second female, suggesting that simply adding eggs from multiple females is not always a good option (Kruse 1990; Kight et al. 2000). The back-brooding belostomatids are thought to have evolved from territorial males that protected and hydrated eggs that females oviposited on emergent vegetation, as occurs in extant *Lethocerus* in which the potential for polygyny may have been greater (Ichikawa 1988). An exemplary comparative study integrating the ecology, phylogeny and physiology, of care in these groups can be found in Smith (1997).

The evolutionary pathways leading to exclusive male care or exclusive maternal care are not well understood. Models of biparental care suggest that biparental care can be unstable when either parent can desert, forcing the other parent into a 'cruel bind' where it either must provide care or experience no reproductive success (Trivers 1972). Investigators of invertebrate parental care, however, have not proposed such a pathway for exclusive male care, exclusive female care, or asymmetric biparental care. In three insect systems with biparental or amphisexual care, we know the response when one parent deserts or is experimentally removed. The responses indicate that one parent could easily manipulate the other into providing more parental care, but this seems to be rarely done. In the reduviid, *Rhinocoris tristis*, males typically provide all parental care. It was noticed, however, that if the male were removed, the female parent would return and provide care until young hatch, acting just as aggressively as a male parent. Beal and Tallamy (2006) argue that female care is rare in nature, however, because the male rarely deserts and males will guard unrelated eggs if given the opportunity. Male care is likely maintained by the ability to attract mates, rather than by female parenting decisions.

In the harvestmen *Serracutisoma proximum*, which shows female uniparental care, females guard eggs within a male's superterritory. If one of a male's females is temporarily removed, the male will guard the clutch for 2–9 days (Buzatto and Machado 2009). Although males will not guard for the entire period of egg development (37 days), the male's response suggests that females could take considerable advantage of the male's willingness to care for moderate intervals. Females will occasionally do so for several hours during cold periods, but could be expected to exploit the male's response for longer periods of foraging during warmer periods. Females, however, seem to fail to do so.

In burying beetles (*Nicrophorus* spp.) with biparental care, the female typically provides care until the larvae disperse from the carcass (10–15 days), while the male leaves several days earlier. If the female dies or is removed, the male compensates by providing more care and staying until larvae disperse, achieving the same degree of reproductive success as the female (Trumbo 1991; Fetherston et al. 1994). Females, however, are almost never known to exploit this paternal response by leaving early. Female behaviour may be constrained because she has to completely abandon her brood to induce the male to provide more care. If she simply reduces her level of care while remaining in the nest, the male does not compensate (Suzuki and Nagano 2009). Paternal care can lessen the lifetime costs of care for the female (Jenkins et al. 2000), but there is no invertebrate system in which this has been hypothesized to be the route to the complete abandonment of care by the female, as proposed for birds (Emlen and Oring 1977). In each of these three systems (*Rhinocoris*, *Serracutisoma*, *Nicrophorus*), the parent that normally provides more care seems to do so primarily because of its own costs and benefits.

5.3.3 Biparental care

While competition for a resource or the necessity of two parents to construct a nest may explain the origin of biparental care, it does not explain how extended cooperative biparental associations can be stable through evolutionary time. The sources of

conflict that might destabilize biparental care are now well modelled (Chapters 6 and 9). Both parents profit from high productivity of the parental pair, but each parent does better by having its partner bear the costs of care, allowing resources to be saved for future reproduction (Trivers 1972). An understanding of conflict and cooperation at multiple levels in primitively eusocial insects might provide a framework for also understanding biparental care. Groups with more cooperative members can achieve higher group output (number of reproductively capable offspring) than competing groups with less cooperative members. Within the group, however, conflicts exist because individuals can attempt to shift costs to group members. An additional source of conflict occurs over genetic representation in offspring produced. In species with biparental care, intraspecific brood parasitism by females that mate with the paired male, and sperm storage by the paired female, place the male and female in direct conflict. Despite these sources of conflict, both primitively eusocial and biparental groups persist. Stabilizing features of social units include an alignment of genetic interests, mass action by a larger group, policing, insurance against death of a group member, division of labour with or without task specialization, and a lack of future reproductive opportunities (Oster and Wilson 1987; Keller and Reeve 1999). Among invertebrates, biparental care is usually associated with a nest (Eickwort 1981), a structured environment that can facilitate selection for division of labour, and a valuable resource that must be protected.

There are some tasks that a single parent cannot finish within the requisite time for successful brood production (necessity of mass action). Time constraints appear to be important for many invertebrates that take advantage of transient reproductive opportunities in severe habitats. In the desert isopod *Hemilepistus reamuri*, both parents fashion a burrow system to moderate temperature and increase microhabitat humidity (Linsenmair 1987). Similar constraints occur for the tenebrionid beetle *Parastizopus armaticeps* in which the male takes over burrow building from the female while the female begins foraging. When food is made available experimentally, the female has more time to assist

in working on the burrow, a critical feature of reproductive success in the desert (Rasa 1998; Rasa 1999).

Biparental care occurs in log-inhabiting cockroaches in which slow-growing young are dependent on parents for an extended period (Nalepa et al. 2008). Reproductive attempts may be abandoned if one parent dies early in the nesting cycle, suggesting the combined effort from two parents is necessary to prepare the nest. Abandonment of reproduction with the death or desertion of a partner suggests the potential for a form of policing in which continued cooperation depends on a minimal level of partner presence and effort. Female *Trypoxylon* wasps will not forage for the brood unless a male is present to guard the nest. Such female decision rules would select for the male to make his presence known. Communication might promote stability of biparental care by coordinating and monitoring activity. Acoustic and chemical communication between partners is varied and complex in the passalid beetle *Odontotaenius disjunctus* (Schuster and Schuster 1997) and in the burying beetle *Nicrophorus vespilloides* (Steiger et al. 2009). Disruption of acoustic communication in *N. mexicanus* prevents coordination between partners (Huerta and Halffter 1992). Repeated interaction of just two individuals in a confined area such as a nest provides an available mechanism for both monitoring partner effort and to increase confidence of parentage.

Parents are expected to be more likely to provide care to related than unrelated young. House et al. (2008) explored the genetics of repeated mating in burying beetles and its effect on paternity. They found that males are under strong selective pressure to mate repeatedly to increase paternity while females are not under strong selection to refuse copulations because the costs are small. The sexual dynamic results in numerous, brief copulations in the first 24 h on a carcass before oviposition begins, with males siring > 90% of the brood (Müller and Eggert 1989). Although species with male care are generally expected to have high paternity, the effect of variation in the confidence of parentage on parental behaviour (Chapter 11) has received little attention in invertebrates. The burying beetles provide an attractive system for manipulating expectation of parentage because of frequent visits to the nests by intruders of either sex.

If young need at least one parent to survive until independence, then the presence of a second parent can act as insurance should one parent disappear or die. If insurance is important for biparental care, then analysis might reveal that one parent performs most parental tasks, and the second parent only becomes active if the first parent is gone (or the second parent switches to tasks normally performed by the first parent). Removal of one parent has demonstrated this effect in several insects with biparental care, demonstrating the compensating plasticity of parental behaviour, and perhaps also giving the false impression that specialization is limited. In the composting beetle *Cephalodesmius armiger*, the female will take over the male's tasks if he is removed (Dalglish and Elgar 2005). In burying beetles paired males will do less feeding of young or nest maintenance than the female but will almost completely compensate if the mate is removed (Rauter and Moore 2004; Smiseth and Moore 2004).

Division of labour is a key component of cooperation in social insects. Division of labour can occur without task specialization, where individuals take turns performing a task or when two non-specialists work at different locations. Benefits are realized by reducing inter-task travel time, by performing two tasks simultaneously, and by coordinating activity. In burrow builders, it is common for one parent to work (or guard) outside the burrow or near the entrance while the second parent works underground (Monteith and Storey 1981; Linsenmair 1987; Hunt and Simmons 2002). The presence of biparental care despite the ability of a single parent to complete all tasks suggests that some benefit is achieved even without specialization.

Detailed behavioural analyses of biparental invertebrates have uncovered sex-role specialization of parental tasks. In the dung beetle, *Canthon cyanellus*, the male pushes and the female pulls the first dung ball toward the burrow. The male then excavates under the dung ball that the female covers with soil. The female shapes the dung ball into a pear shape while the male gathers additional dung balls. The female is also specialized to produce antifungal secretions from sternal glands (Favila and Díaz 1996). In the bark beetles, a male makes a nuptial chamber, guards the entrance, and

removes frass and debris while the female constructs egg galleries (Kirkendall et al. 1997). A similar degree of specialization is found in diverse dung beetle species (Monteith and Storey 1981), ambrosia beetles (Kirkendall et al. 1997), and burying beetles (Walling et al. 2008; Cotter and Kilner 2010).

To maximize efficiencies from specialization, an individual with a tendency to perform a task more frequently should also be superior in performing that task. A correlation between superior performance and biased behavioural tendency has been demonstrated most convincingly in the burying beetles where males have both a greater tendency to guard and are superior defenders (reviewed in Trumbo 2006). Biparental care may be unstable if both parents can perform all tasks equally and either one will fully compensate for a reduction in the amount of care provided by its partner (Houston et al. 2005). Incomplete compensation, on the other hand, is thought to promote extended biparental care. Many models of biparental conflict assume that each parent is a phenocopy of the other in regards to care-giving, rather than viewing the biparental association as a potential synergism (Motro 1994). With specialization, incomplete compensation is inherent because the non-specialist cannot perform the neglected tasks equivalently (Trumbo 2006).

An interesting class of specialization occurs when a conspecific threatens a nest. Paradoxically, sexual conflict over protection of the nest and offspring can promote extended biparental associations. A conspecific may attempt to expel the same-sex rival and pair with the partner, committing infanticide as part of the takeover (Trumbo 2006; King and Fashing 2007). The costs of a takeover are much greater for the same-sex resident. In both the burying beetle, *Nicrophorus orbicollis* and the passalid beetle *Odontotaenius disjunctus* adults with young are more aggressive toward the same-sex intruder (Valenzuela-González 1986), suggesting that each parent must stay to protect its reproductive interests, promoting an extended association (Trumbo 2006). The potential for competitive takeovers may be the primary reason that high value resources are thought to be a driver of biparental care (Wilson 1975).

Specialization of parental tasks may evolve without a long history of selection for specialization (Lessells 1999). Key aspects of specialization may be present from the origin, beginning with differences in behavioural tendencies of the two sexes, as hypothesized for female co-foundresses in social insects (Fewell and Page 1999). In many biparental lineages, male care has been hypothesized to have evolved from guarding of the female or a critical resource (Alcock 1975). Defensive behaviour is reported as a male-biased behaviour in many biparental species (Kirkendall et al. 1997; Rasa 1999). After plasticity of parental behaviour has evolved, specialization can be maintained by differences in response thresholds for stimuli eliciting parental behaviour (see a similar rationale for specialization among social insect workers, Robinson and Page 1989). Small differences in thresholds of response can result in exaggerated differences in behavioural repertoires as the more sensitive individual reduces the task-inducing stimuli that would eventually trigger a response in the less sensitive individual. Considerable task specialization is facilitated while allowing rapid plasticity of behaviour when, for example, one parent is absent and task-related stimuli abruptly change. Flexibility of behaviour, even among task specialists, can be important to resolve conflict in species with costly parental care (Royle et al. 2010).

Two well developed biparental systems where specialization has not been reported occur in the desert isopod *Hemilepistus reaumuri* and in *Cryptocercus* woodroaches (Linsenmair 1987; Nalepa and Bell 1997). Although further study might reveal specialization, it should be noted that both of these species are semelparous. When parents have limited opportunity for re-pairing then their reproductive interests are closely aligned, reducing conflict and selecting for extended parent-offspring associations. The lack of reproductive opportunities likely contributes to the high level of care in these species, as it may also do toward the end of reproductive life in the iteroparous species discussed earlier.

5.3.4 The loss of parental care

Parental care encompasses a set of co-adapted traits integrating adult and offspring behaviour that

could be considered to be an advance in sociality (Wilson 1975). Once evolved, why would a species discard such apparent progress in social behaviour? And even if a changing environment reduced the benefits from care, correlated changes in eggs and young that occurred during the evolution of care might leave young helpless in the absence of parents. Experiments that remove parents routinely produce devastating mortality of offspring due to predators, fungal attack, or desiccation (reviewed in Tallamy and Wood 1986; Trumbo 1996). Eggs of parental species often lack antimicrobials, egg cases, toxins, and other protections commonly found in non-parental species (Zeh et al. 1989). Eberhard (1975) suggested that some care-giving species may be in a parental 'trap' that constrains the loss of care. In the pentatomid *Antiteuchus tripterus*, the guarding mother can repel generalist predators, but increases the vulnerability to a specialist parasitoid that uses her as a cue to find her clutch. While the abandonment of parental care might appear to benefit the mother, Eberhard (1975) hypothesized that clustered eggs and thin egg shells that co-evolve with parental care may now prevent the evolution of a non-parental lifestyle.

In contrast to the parental trap (Eberhard 1975) and social advancement (Wilson 1975) perspectives, which suggest that care would rarely be lost as an adaptation, Tallamy and Schaefer (1997) argue that parental care may have been common among basal groups of invertebrates but has been repeatedly lost because of the high costs of care. The primary costs of care are a reduction in lifetime fecundity and increased vulnerability to predators while giving care. Tallamy and Schaefer (1997) hypothesize that parental care is plesiomorphic within certain clades of hemipterans and that it often is ecologically less successful than a non-parental lifestyle. By example, the pentatomids are thought to be derived from a ground-nesting ancestor with an ecology similar to extant cydnid bugs (Filippi et al. 2009). Parental care was retained, or occasionally re-evolved, when host plant seasonality enforced semelparity, or when care took on additional functions such as feeding. Comparative analysis and greater knowledge of the natural history of care-givers will be necessary to evaluate these contrasting perspectives on the evolution and de-evolution

of parental care. In one such analysis of the Membracinae, Lin et al. (2004) suggest that although parental care can evolve and be lost as an adaptation, it may not be as evolutionarily labile as proposed by Tallamy and Schaefer (1997).

While there is considerable debate about the likelihood of loss of derived social traits such as parental care and eusociality, recent work suggests that male care (Reynolds et al. 2002) and complex forms of care may be more resistant to loss. A phylogenetic analysis of care in ray-finned fish suggests that viviparity has evolved numerous times, but has never been lost (Mank et al. 2005). The presence of viviparity in several diverse groups of invertebrate would make good tests for the generality of this finding. The co-evolution of provisioning behaviour and competition among offspring may also make parental care resistant to loss. Gardner and Smiseth (2011) modelled how provisioning is expected to lead to both the choice of safer nest sites by parents and to more sibling competition (provisioning being more difficult to share than guarding). Sibling competition, in turn, is expected to lead to greater provisioning and parental attendance, inhibiting the loss of care. Phylogenetic tests to examine whether guarding (such as occurs in most insect folivores) is more easily lost as an adaptation compared to more complex forms of care, remain to be done.

All investigators agree that parental care can be readily lost when care can be off-loaded onto another female or to a different species. The vulnerability of eggs and young is not an issue when there are alternative care-givers and the female achieves greater lifetime fecundity. Egg dumping into the nest of a care-giver is best documented in hemipterans (Tallamy 2005). Two females of the North American treehopper *Publilia concava* will sometimes produce a common clutch that is almost always (98%) abandoned by at least one female (Zink 2005). Non-guarding females are more likely to start a second brood (Zink 2003). The lace bug *Gargaphia solani* also dumps eggs facultatively, dumping eggs when a guarding female is available, and caring for her own eggs when this is not the case (Tallamy and Horton 1990). These condition-dependent behaviours are mediated by juvenile hormone that promotes oogenesis and abandon-

ment at the expense of guarding (Tallamy et al. 2002). Egg dumping might be beneficial for the recipient because dumpers typically lay their eggs on the periphery of the clutch where mortality is higher. Defences against egg dumping in lace bugs are therefore not well developed. Tallamy (2005) contrasts this behaviour with egg dumping in burying beetles (Müller et al. 1990) which rear young that are food-limited on small carcasses. Parasitism has clear costs for the care-giver, and potential brood parasites are vigorously attacked, occasionally fatally.

The costs of maternal care also could be transferred to others through mutualisms with other species. There are many examples of ant-treehopper and ant-lycaenid mutualisms, some involving parental and some non-parental species. The clearest case of shifting the costs of care from care-giving treehoppers to ant mutualists is *Publilia reticulata* (Bristow 1983). The presence of ants is the apparent cue for the mother to abandon her brood, her protection now superfluous.

5.4 Microbiology of care

The microbiology of care in invertebrates is a rapidly expanding subfield of microbial ecology. Close familial associations within a nest create hygienic problems for all care-giving species. Many organisms also use microbes as digestive symbionts. Some invertebrates face additional challenges, however, when species mass provision their nest with food that needs to be preserved for significant periods of time. Microbes also can be sources of nutrition because of the lesser caloric requirements of small-bodied ectotherms and the ability of dexterous mouthparts to manipulate small fungal cultures. Vertical transmission of starter fungal cultures, digestive symbionts, and microbes aiding in food preservation are facilitated by parent-offspring contact. It is rapidly becoming appreciated that an important parental task is management of the microbial community to minimize costs and maximize benefits associated with interactions with microbes.

A simple hygienic mechanism is to separate living areas from refuse areas, a behaviour that has been recorded in a burrowing cricket, bark beetles,

and even the moth ear mite that has a separate defecation chamber within a bat's ear cavity (Treat 1958; West and Alexander 1963; Kirkendall et al. 1997). When a separate refuse area is not possible, webspinners encase debris in silk to isolate it from the family (Edgerly 1997).

Grooming of eggs, typically thought to be an antimicrobial strategy, has been noted in nearly a dozen groups and may be universal among earwigs and parental centipedes (reviewed in Costa 2006). In most cases it is not clear if the defence is chemical application or mechanical removal. Some centipedes and earwigs extend grooming to young (Lamb 1976). Grooming of eggs has been speculated to be necessary in species that oviposit in organic substrates (Costa 2006). The burrower bug, *Sehirus cinctus*, is one of the few hemipterans to nest in the soil and has considerable egg grooming (Sites and McPherson 1982). Non-parental invertebrates, however, frequently oviposit in organic substrates such as rotting wood, carrion, and dung and achieve high hatching rates, so the particular selective pressures that led to egg grooming in species with parental care are not obvious. Parents can also combat microbes indirectly by eliminating substrates on which microbes grow. Male bark beetles *Ips* spp. remove frass from tunnel systems while patrolling galleries for predators or conspecific males (Robertson 1998). One of the more intricate antimicrobial strategies occurs in amphipods of the genus *Phronima* (Hirose et al. 2005). This group feeds on tunicates and uses the tunicate barrel as a nursery. *Phronima* eats the animal tissue of the tunicate, but leaves the gelatinous matrix intact. After grazing on the epidermis, tunicate cuticular layers regenerate a living layer that protects the nursery from microbes.

The coevolution of care and egg properties has taken two distinct pathways among parental insects. In some care-giving species, the ancestral egg adaptations have been retained, allowing the parent to oviposit away from the nest (e.g. burying beetles, Pukowski 1933) or away from active adult areas (e.g. bark beetles, Kirkendall et al. 1997). Displacement of eggs keeps them out of harm's way, either from normal adult activity or from ovicidal competitors (Scott 1997). Other care-giving species keep eggs close by and groom them. In

these species, experimental removal of the parent typically results in eggs succumbing to fungal attack or desiccation, indicating that adaptations typical of non-parental species have been lost. Detailed comparative study of egg anatomy of non-parental species, parental species that groom eggs, and parental species that do not groom eggs would be enlightening. One could hypothesize substantial costs of antimicrobial and antidesiccant adaptations for eggs, and that parents of some species pay a smaller cost by egg attendance.

European beewolf (*Philanthus triangulum*) moths provide antifungal protection through to the pupal stage. Females transfer an inoculum of bacteria (*Streptomyces philantii*) from glands located on the antennae to the brood cell where an egg is oviposited (Kaltenpoth et al. 2005). These bacteria produce antibiotics that protect the larvae against fungal attack. The larvae later apply the bacteria to the silk of their cocoon within which they will pupate in the soil. Wood-feeding spruce beetles *Dendroctonus rufipennis* need to maintain an entire gallery system clear of antagonistic fungi. Adults exude oral secretions that inhibit growth of invading fungi. Filtered-sterilized secretions do not inhibit fungal growth, providing evidence that bacteria within the secretions are responsible for the antifungal activity (Cardoza et al. 2011).

Mass provisioning, whether incorporating dung or carrion into a nest, or hunting for prey to stockpile for young, presents considerable microbial problems. In addition to preventing spoilage, antimicrobial application can reduce cues that might lead to detection of the nest and food by competitors. The European beewolf brings paralysed (but not dead) prey to its nest, and then licks the body surface of the prey to apply protective hydrocarbons while it makes a brood cell (Strohm and Linsenmair 2001). Both the licking behaviour and the use of paralysed prey help to prevent spoilage. The scarab beetle *Canthon cyaneellus* applies an antibiotic from its sternal glands to dung balls prepared for young (Pluot-Sigwalt 1988). Similarly, the burying beetle *Nicrophorus vespilloides* applies anal secretions by rubbing the tip of its abdomen back and forth across a prepared small vertebrate carcass (Rozen et al. 2008; Cotter and Kilner 2010). It remains to be investigated whether

these treatments should be regarded as sterilization of the resource, or the use of one type of microbe to limit growth of another, more harmful, microbe.

To exploit cellulose-rich resources such as wood or leaves, invertebrates benefit from digestive symbionts. Parental care provides a conduit for symbionts to be passed to offspring either by trophallaxis as in the woodroach *Cryptocercus* (Nalepa and Bell 1997), or by consumption of faeces as in the passalid beetle *Odontotaenius disjunctus* (Schuster and Schuster 1997). Among subsocial wood feeders, the passalid beetles have one of the shortest maturation times of young despite their soft mouthparts, benefiting from pre-digestion of wood by microbes in frass outside the body (an 'external rumen') (Halffter 1991; Schuster and Schuster 1997). Similar external digestion occurs in the composting beetle *Cephalodesmius armiger*, which macerates leaves, mixes them with faeces, and produces an artificial 'dung' ball for offspring (Monteith and Storey 1981). Another wood feeder, the stag beetle *Dorcas rectus*, consumes both wood and wood-rotting fungi, utilizing specialized abdominal pouches, mycangia, to transport fungal cultures (Tanahashi et al. 2010). Mutualist bacteria may produce chemicals that limit growth of competing, parasitic fungi. Antibiotic treatment reduced, but did not stop growth in larvae, suggesting that although bacteria may aid digestion, they are not absolutely necessary. A fascinating but little understood form of invertebrate-microbe symbiosis occurs in shield bugs of the family Plataspidae. In these species, mycetomes, specialized digestive pouches, are packed with bacteria that can be passed from mother to her eggs. In many species, mothers smear a microbial secretion over eggs, while in *Coptosoma scutellatum* the mother produces eggs that contain a packet of bacteria at the base. Remarkably, after the nymph hatches it inoculates itself, which is essential for its survival, by siphoning bacteria from the storehouse within the egg (Schneider 1940 in Costa 2006). Both nutritional and hygienic hypotheses have been generated for these taxon specific symbioses. This system seems ripe for molecular approaches that will permit a detailed exploration of the numbers and kinds of microbes involved.

Yet more complex associations with fungi are found in insects that actively manage the sub-

strate on which fungi grow. Although several additional groups, including thrips and webspinners, are known to consume fungal mycelia and/or spores, true cultivation of fungi is thought to have evolved only among Macrotermiinae termites, leaf-cutting ants, and ambrosia beetles (Mueller et al. 2005). These agriculturalists maintain the proper microenvironment to grow colonies of symbiotic fungi, alter the growth form of fungi by selective consumption, control the growth of competing fungi both by removal and the use of antibiotic-producing bacterial symbionts, and carry starter cultures to begin a new colony (De Fine Licht et al. 2005; Little et al. 2006; Scott et al. 2008). In some bark beetles, growth can be so luxurious that the crop must be harvested simply to prevent overgrowth within the tunnel system. There are a number of factors that promote mutualisms between host and symbiont (Leigh 2010). At the origin of host-symbiont associations there was presumably considerable genetic diversity among possible symbionts. Hosts that selected and vertically transmitted more cooperative strains likely would have produced more offspring than hosts working with less cooperative strains. The cultivation of fungal gardens is a rapidly growing area of research that best exemplifies the changing view of microbes as either commensals or competitors, to one where microbial interactions are actively managed by social invertebrates. For further information, readers are directed to the reviews by Currie (2001), Mueller et al. (2005), and Aanen (2006).

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