

Reproductive Competition and Its Impact on the Evolution and Ecology of Dung Beetles

Leigh W. Simmons^{1,2} and T. James Ridsdill-Smith²

¹*Centre for Evolutionary Biology, The University of Western Australia, Crawley, Western Australia*

²*School of Animal Biology, The University of Western Australia, Crawley, Western Australia*

1.1 Introduction

Beetles make up one quarter of all described animal species, with over 300,000 named species of Coleoptera, making them the most speciose taxon on planet earth (Hunt *et al.*, 2007). One of the larger groups is the Scarabaeoidea, with approximately 35,000 known species including the stag beetles, the scarabs and the dung beetles (Scarabaeinae) (Hunt *et al.*, 2007). Currently there are 6,000 known species and 257+ genera of dung beetles distributed across every continent on earth with the sole exception of Antarctica (Chapter 2). What better taxon could there be for the study of biodiversity, and the evolutionary and ecological processes that generate that biodiversity? Given their abundance and species richness, it is little wonder that dung beetles have attracted significant attention both from early naturalists and contemporary scientists. As we shall see throughout this volume, the unique biology of dung beetles makes them outstanding empirical models with which to explore general concepts in ecology and evolution.

The extreme diversity of beetles generally appears due to the early origin, during the Jurassic period (approx. 206–144 million years ago) of numerous lineages that have survived and diversified into a wide range of niches (Hunt *et al.*, 2007). In Chapter 2 Keith Phillips reviews our current understanding of the phylogenetic history of the dung beetles, which seem to have appeared during the Mesozoic era (around 145 million years ago), in the region of Gondwana that would later become Southern Africa.

The majority of extant species of dung beetles feed predominantly on the dung of herbivorous or omnivorous mammals. There was probably a single origin of specialist dung-feeding (coprophagy) from detritus- (saprophagy) or fungus- (fungivory) feeding ancestors, and the dung beetles are likely to have then co-radiated with the diversifying mammalian fauna (Cambefort, 1991b; Davis *et al.*, 2002b). However, throughout the dung beetle phylogeny there are numerous evolutionary transitions to alternative feeding modes, ranging from fungivory to predation (see Chapter 2), reflecting the divergence into new niches that characterizes the evolutionary radiation of beetles generally (Hunt *et al.*, 2007).

In this volume, we highlight the extraordinary evolutionary lability of dung beetles, arguing that much of their radiation is driven by reproductive competition. In their work on dung beetle ecology, Hanski & Cambefort (1991) argued that competition for resources was a major driver of the population and community dynamics of dung beetles. However, they noted the paucity of empirical studies available at that time which had actually examined reproductive competition.

Much progress has since been made. The chapters in this volume examine how reproductive competition affects organism fitness at the individual, species, population and community levels, and thereby illustrates the consequences of reproductive competition for evolutionary divergence and speciation. In this first chapter, we provide an overview of the evolution and ecology of dung beetles and introduce the detailed treatments of our co-authors that constitute the majority of the volume. While the often unique behaviour and morphology of dung beetles make them interesting taxa in their own right, the chapters highlight how dung beetles have proved to be model organisms for testing general theory, and how they have, and will, continue to contribute to our general understanding of evolutionary and ecological processes.

1.2 Competition for mates and the evolution of morphological diversity

A striking morphological feature of the Scarabaeoidea is the presence in males of exaggerated secondary sexual traits. Among the 6,000 known species of dung beetles, the males of many species possess horns (Emlen *et al.*, 2007). Darwin (1871) was the first to note the extraordinary evolutionary radiation in dung beetle horns and the general patterns of sexual dimorphism. If horns are present in females at all, they are generally – though not always – rudimentary structures compared with those possessed by the males of the species (Figure 1.1). Darwin (1871) argued that contest competition between males and female choice of males bearing attractive secondary sexual traits are general mechanisms by which sexual selection drives the evolutionary divergence of male secondary sexual traits. There is now considerable theoretical and empirical evidence to support his view that sexual selection can drive rapid evolutionary divergence among populations of animals (Lande, 1981; West-Eberhard, 1983; Andersson, 1994).

Emlen *et al.*'s studies (2005a; 2005b; 2007) of the genus *Onthophagus* have taught us much about the evolutionary diversification of horns in what is one of the most species-rich genera of life on Earth (there are already more than 2,000 species

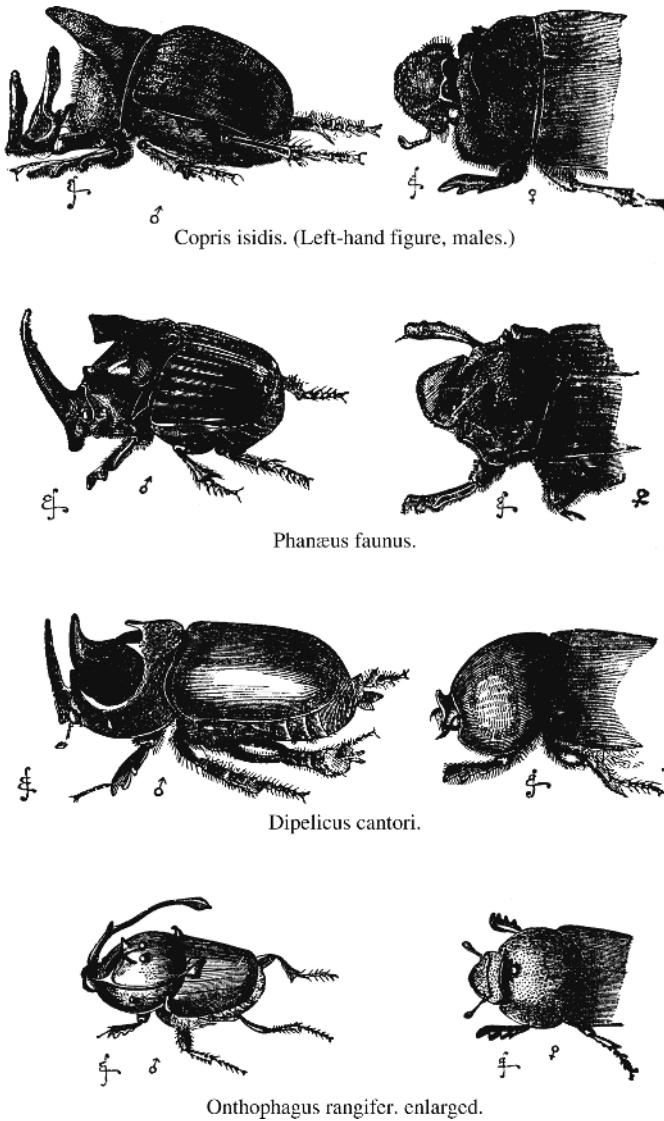


Fig. 1.1 Darwin (1871) argued that sexual selection was responsible for the evolutionary diversification of secondary sexual traits such as dung beetle horns, and he used these species of beetles to illustrate the sexual dimorphism that might be expected from selection by female choice. We now know that sexual selection via contest competition can favour the evolution of horns in males and females of tunnelling species, while female choice has not yet been shown to be important for horn evolution.

of described onthophagines). Based on a phylogeny of just 48 species – a mere 2 per cent of this genus – Emlen *et al.* (2005b) identified over 25 evolutionary changes in the physical location of horns on adult male beetles (Figure 1.2a). Moreover, from the reconstructed ancestral head horn shape (a single triangular horn arising from

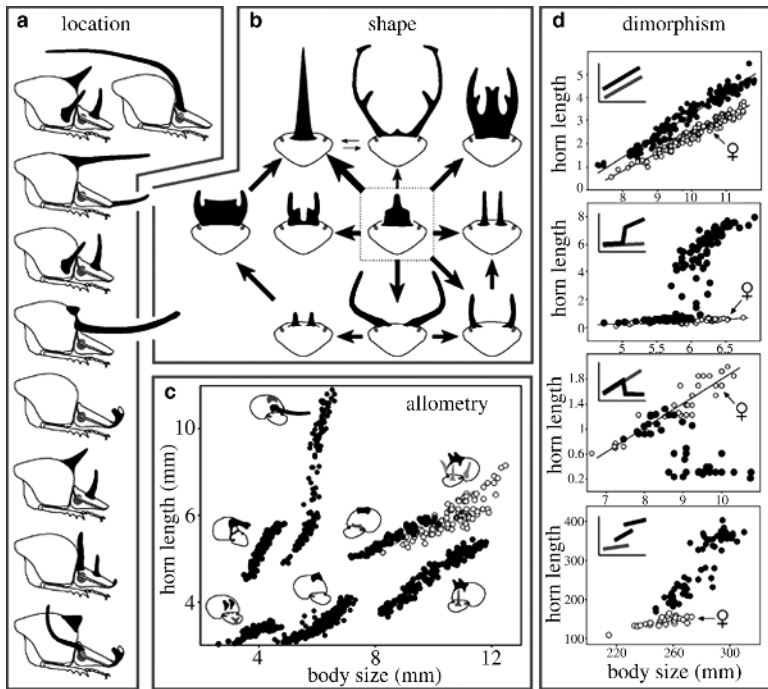


Fig. 1.2 Four trajectories of beetle horn evolution. **a:** Species differ in the location of horns; side-views of nine species of *Onthophagus* (Scarabaeinae) shown. **b:** Species differ in horn shape. Head horns shown for ten *Onthophagus* species; arrows indicate relative frequencies of changes as reconstructed from a phylogeny (from Emlen *et al.*, 2005b). **c:** Species differ in horn allometry, the slopes, intercepts, and even the shapes of the scaling relationships between horn length and body size. Data for thoracic horns of seven *Onthophagus* species shown. **d:** Species differ in the presence and nature of dimorphism in horn expression (males=closed circles; females=open circles). Top to bottom: sexual dimorphism (*O. pentacanthus*); male dimorphism and sexual dimorphism (*O. nigriventris*); reversed male & sexual dimorphism (*O. sloanei*); male dimorphism and sexual dimorphism (*Enema pan* (Dynastinae); unpublished data, JM Rowland). From Emlen *et al.* (2007); reprinted by permission of Macmillan Publishers Ltd, copyright 2007.

the centre of the vortex), there have been at least seven variant forms, several of which have themselves radiated into additional forms (Figure 1.2b).

Darwin (1871) noted that while dung beetle horns often exhibited sexual dimorphism, there was considerable within-species variation in this pattern. Indeed, in their study of 31 species of *Onthophagus*, Emlen *et al.* (2005a) identified at least 7 gains and 13 losses of sexual dimorphism. In one species, *O. sagittarius*, the horns of males are qualitatively different from the horns of females; males possess a pair of short horns at the sides of the frons and an enlarged thoracic ridge, while females possess a single long horn in the centre of the frons and a second single long horn in the centre of the thorax (Emlen *et al.*, 2005a). Thus, horn morphology in dung beetles appears to exhibit extraordinary evolutionary lability in the size, shape

and number of horns, and in the degree and nature of sexual dimorphism (see Figure 1.2 and Chapter 3, Figure 3.1).

Early researchers rejected Darwin's (1871) argument that sexual selection was responsible for the evolutionary radiation of beetle horns, and the idea of sexual selection generally, arguing that beetle horns were more likely to function as protective structures against predators (Wallace, 1891) or to arise as a correlated response to evolutionary increases in body size (Arrow, 1951). However, there is now considerable evidence that dung beetle horns *are* subject to sexual selection through their use in contest competition.

In Chapter 3, Robert Knell provides an overview of the functional significance of dung beetle horns. Among the dung beetles, there appears to be a close evolutionary association between tunnelling behaviour and the possession of horns. As we shall see, dung beetles can be broadly classified into tunnellers that nest in the soil below the dung, and rollers that construct balls of dung which they roll away from the dung pad for burial elsewhere (Section 1.3 and Chapter 2). The available phylogeny suggests that tunnelling was the ancestral behaviour pattern, and that there have been numerous evolutionary transitions to rolling behaviour (Chapter 2). Horns function primarily in blocking access to the confined spaces within tunnels, allowing males to monopolize access to breeding females (Chapter 3). In contrast, for rollers operating in an open above-ground environment, horns would be unlikely to contribute to a male's ability to monopolize access to females and/or breeding resources (Emlen & Philips, 2006).

Based on a phylogeny of 46 species from 45 genera, Emlen and Phillips (2006) showed how all of eight evolutionary origins of horns were on lineages of tunnellers, while not a single lineage of rollers included an evolutionary gain of horns (see Figure 3.4).

The monopolizability of mates and/or breeding resources is thought to be a major factor moderating the strength of sexual selection (Emlen & Oring, 1977). In Chapter 3, Knell shows how the density of breeding beetles impacts the evolution of horns even within tunnelling species. Tunnelling dung beetles that live in highly crowded environments, where their ability to control access to breeding resources is limited, are significantly less likely to have evolved horns than species from less crowded environments, where the monopolizability of mates and resources is easier (Pomfret & Knell, 2008).

Importantly, there are now several within-species studies from a number of genera which confirm that horn size is a strong predictor of the outcome of disputes between competing males (see Chapter 3). Moreover, the form of sexual selection, estimated from the slope of male reproductive success on horn length, has been shown to be directional for increasing horn length within experimental populations of *O. taurus* (Hunt & Simmons, 2001) (see Figure 6.1b). Interestingly, directional positive linear selection has also recently been documented for horn length in female *O. sagittarius*. In this species, females compete for dung with which to build brood masses, and differences in horn length predict the amount of dung females can monopolize and, therefore, the number of offspring they are able to produce (Watson & Simmons, 2010b). This study represents the first demonstration of selection acting on female secondary sexual traits for any species, and it suggests that sexual selection is likely to be



important in the many evolutionary origins of female horns in dung beetles (Emlen *et al.*, 2005a).

Darwin (1871) noted that horn morphology could be just as variable within species as it was among species. Thus, in discussing onthophagines, he noted that, 'in almost all cases, the horns are remarkable from their excessive variability; so that a graduated series can be formed, from the most highly developed males to others so degenerate that they can barely be distinguished from the females.' (Figure 1.3). This extreme morphological variability is now known to be associated with alternative mate-securing tactics, in which minor males remain hornless and sneak matings with females guarded by horned males. The tactic adopted depends critically on the amount of dung provided by a male's parents when they provisioned his brood mass. Thus, brood size influences adult body size, and males exceeding a threshold body size develop horns and adopt the fighting and mate-guarding tactic (see Figs. 1.2d and 7.3).

In Chapter 6, Joseph Tomkins and Wade Hazel provide an overview of the general theoretical issues surrounding the evolution of such phenotypic plasticity and show how dung beetles have contributed significantly to our understanding of this area of developmental biology. They demonstrate how an interaction between environmental cues and genetic variation can influence the expression of alternative male phenotypes in onthophagine dung beetles, and specifically the position of the body size threshold at which males switch between alternative phenotypes, thereby generating variation within and among populations in the proportion of males that adopt the horned fighting tactic.

In Chapter 7, Armin Moczek penetrates this subject to the genetic level, using the latest genomic techniques to identify the genes responsible for horn development and to reveal the signalling pathways responsible for switching the developmental trajectories that lead to the horned and hornless phenotypes. These studies of *Onthophagus* are providing us with detailed insights into the developmental mechanisms that underpin morphological diversity in dung beetles, while at the same time contributing to the emergence of the cross-disciplinary research fields of evolutionary developmental biology and ecological developmental biology (Chapter 7).

Moczek shows us that beneath the apparently extreme evolutionary lability in phenotypic diversity among onthophagine dung beetles lies a rather small and conserved set of regulatory pathways. These pathways can readily account for the multiple evolutionary gains and losses of horns within and between the sexes, and for the phenotypic plasticity and nutrient sensitive growth that collectively generate



Fig. 1.3 Darwin (1871) noted the extreme variability in horn development within species of dung beetles, as illustrated by these images of *Proagoderus* (*Onthophagus*) *lanistra*, which show both sexual dimorphism and male dimorphism. Females (left) do not develop horns. Large males (majors) develop exaggerated horns, while small males (minors) remain hornless, resembling females. These alternative phenotypes are associated with different mating tactics whereby major males fight for females and assist with brood production, while minor males sneak copulations when major males are collecting dung or fighting with other major males for the possession of females. From Emlen *et al.* (2007). Copyright (2007) National Academy of Sciences, USA.

the extraordinary phenotypic diversity which characterizes the genus *Onthophagus* (Figure 1.2).

The adoption of sneak mating behaviour by a subset of the male population generates a sexual selection pressure that was not appreciated by Darwin – that of sperm competition (Parker, 1970; Simmons, 2001). Whenever a female mates with two or more males, the sperm from those males will compete to fertilize the few eggs that she produces during her lifetime.

Sexual selection is predicted to favour any morphology, physiology or behaviour that enhances a male's success in competitive fertilization. In Chapter 4, Leigh Simmons reviews sperm competition theory and shows how dung beetles in the genus *Onthophagus* have been important in its empirical evaluation. Within the onthophagines, the considerable among-species variation in the proportion of males adopting the sneaking tactic generates variation in the strength of sexual selection arising from sperm competition and provides an opportunity to test the theoretical expectation that sperm competition should influence the evolution of male investment in sperm production. Thus, across a phylogeny of 18 species of *Onthophagus*, evolutionary increases in the proportion of males adopting the sneaking tactic were found to be positively associated with evolutionary increases in male investment into their testes (Chapter 4). Moreover, within species, by virtue of their mating tactic, sneaks are always subject to sperm competition and tend to invest more in testes growth than do horned fighters (Simmons *et al.*, 2007).

Interestingly, these studies have revealed important nutrient allocation trade-offs between traits involved in competition for mating opportunities (horns) and competition for fertilizations (testes). Both within and among species, males that invest more in their testes tend to invest less in horn expression (Chapter 4).

Nutrient allocation trade-offs are likely to contribute greatly to the evolutionary diversification of dung beetle horns. Morphological traits that develop in close proximity will compete for the same pool of resources, thereby constraining each other's patterns of growth (Emlen, 2001). The strength of selection acting on one trait is then expected to shape the allocation of resources to the other.

For example, thoracic horns develop in closer proximity to testes than do head horns, and Simmons & Emlen (2006) found that novel gains of thoracic horns were far less likely in lineages in which there were alternative sneak tactics (and thus intense sperm competition) than in lineages without sneak tactics. Thus, pre- and post-copulatory processes of sexual selection can interact in determining the evolutionary diversification of male morphology.

In a similar manner, during development, horns at the rear of the head compete for resources with eyes, while those at the front of the head compete for resources with antennae, and thoracic horns compete for resources with wings (Emlen, 2001). In Chapter 9, Marcus Byrne and Marie Dacke provide an extensive survey of the visual ecology of dung beetles, illustrating the considerable evolutionary diversification in dung beetle eye morphology and visual acuity. They point out how nutrient allocation trade-offs between horns and eyes may dictate the evolutionary response to sexual selection. Indeed, across a phylogeny of 48 species of *Onthophagus*, Emlen *et al.* (2005b) found losses of horns located at the rear of the head, where horn development results in reduced eye size, were concentrated on lineages

that have switched from diurnal to nocturnal flight behaviour, where greater visual acuity would be required.

As noted in Chapter 5, the detection of olfactory cues is also critical for locating ephemeral resources. Gains in horns at the front of the head tend to be associated with forest-dwelling lineages, where odour plumes from dung are perhaps more likely to persist and trade-offs with antennae are therefore less costly compared to open pastures (Emlen *et al.*, 2005b). Much more work is required in this area, but the data clearly suggest that ecology plays an important role in modulating the evolutionary responses in male weaponry to sexual selection.

Ironically, in the absence of firm evidence for competition among males, Darwin (1871) thought that sexual selection through female choice was likely to be the more powerful selective force in the evolution of beetle horns. It is becoming clear, however, that while female dung beetles do exercise mate choice, they do not appear to use male horns as cues to mate quality. Thus, studies of several species of *Onthophagus* suggest that females choose among males based on their overall genetic and phenotypic condition, not on the length of their horns (Kotiaho *et al.*, 2001; Kotiaho, 2002; Watson & Simmons, 2010a; Simmons & Kotiaho, 2007a). As Simmons shows in Chapter 4, females rely on pre-copulatory (courtship) and post-copulatory (sperm competitiveness) performance as predictors of male genetic quality, and in so doing they are able to produce offspring that are more likely to reach reproductive maturity.

However, female choice in dung beetles remains poorly explored. In Chapter 5, Geoff Tribe and Ben Burger review what is available on the olfactory ecology of dung beetles, and in so doing they reveal a rich area for future research. They show how pheromone signalling is a key component of the breeding biology of ball-rolling species. While much is known of the chemical composition of the sex attraction pheromone in the genus *Kheper*, little is known of other species. We know nothing of within-species variability in pheromone composition or signalling effort.

Pheromone signalling has been shown to be subject to intense sexual selection in other insect groups (Wyatt, 2003; Johansson & Jones, 2007), so it is highly likely to be an important aspect of reproductive competition in dung beetles as well, at least among ball-rollers, where males often attract a female to a location somewhat removed from the dung source (Chapter 5). Almost nothing is known of semiochemicals in tunnelling species, but the occurrence of sexually dimorphic chemical-producing glands on the cuticle suggest that here, too, chemical signals are likely to play an important role in species mate recognition and mate choice.

1.3 Competition for resources and the evolution of breeding strategies

The breeding behaviour of dung beetles is perhaps the most conspicuous aspect of their biology. The early Egyptians observed dung beetles emerging from the soil in spring, which they believed represented reincarnation, and when beetles made and rolled perfect spheres of dung it represented to them their god Kheper, rolling the sun across the sky (Ridsdill-Smith & Simmons, 2009). They revered the beetles as

symbolizing rebirth; scarab amulets are found on paintings and in tombs to simulate reincarnation and they were used by the living to bring good luck. Also, identifiable beetles are often found preserved in tombs.

The breeding biology of several dung beetle species was described in exquisite detail in the works of the early French naturalist, J. H. Fabre. Fabre (1918) studied representatives from most of the major genera, including *Scarabaeus*, *Gymnopterus*, *Copris*, *Onthophagus*, *Oniticellus*, *Onitis*, *Geotrupes* and *Sisyphus*. Not only did he describe the major nest-building behaviours and the patterns of parental care, but he also made the first detailed observations on the developmental biology of many of the species he studied.

For example, in his studies of the ontology of *O. taurus*, Fabre discussed extensively the pupal horns and their loss prior to adulthood. He was at a loss to explain the functional significance of these structures, asking, ‘What is the meaning of those horny preparations, which are always blighted before they come to anything? With no great shame I confess that I have not the slightest idea.’ As Moczek describes in Chapter 7, we now know that pupal horns probably function in releasing the head capsule during the pupal moult; they are not always lost, being the precursors of thoracic horns in the adults of some species.

Fabre’s important observations were followed by the formal classification system of Halffter and his colleagues (Halffter & Mathews, 1966; Halffter & Edmonds, 1982). The nesting behaviour of dung beetles can be broadly classified into telecoprid (the rollers), paracoprid (the tunnellers), and endocoprid (the dwellers). These can be further classified on the complexities of brood mass and/or nest construction and the extent of parental care (Chapter 2 and Figure 1.4):

- Paracoprids dig tunnels in the soil beneath the dropping and carry fragments of dung to the blind ends of those tunnels, where they are packed into brood masses. A single egg is laid in an egg chamber and the brood mass sealed with dung (Halffter & Edmonds, 1982).
- The males of telecoprids fashion a ball of dung before emitting a pheromone signal to attract a female, either at the dropping or after rolling the ball away from the dropping and burying it in a chamber below ground (Chapter 5 and Figure 1.4). The female enters the chamber to fashion a brood ball with the supplied dung, and in some species she will remain with the brood until the adult offspring emerge (Halffter and Edmonds, 1982).
- Endocoprids fashion brood balls within the dropping (Figure 1.4).

As noted above, current evidence suggests that tunnelling is the ancestral nesting behaviour of dung beetles and that there have been several evolutionary gains of telecoprid behaviour (Chapter 2). There have also been several evolutionary gains of brood parasitism or kleptoparasitism, in which females deposit their eggs into the broods provisioned by telecoprid or paracoprid species (Hanski & Cambefort, 1991; González-Megías & Sánchez-Piñero, 2003; 2004).

Reproductive competition for dung has undoubtedly played an important role in the evolutionary diversification of breeding behaviour. Hanski and Cambefort (1991) suggested a competitive hierarchy among dung beetle species in which rollers and fast tunnellers are competitively superior to slow tunnellers, who are

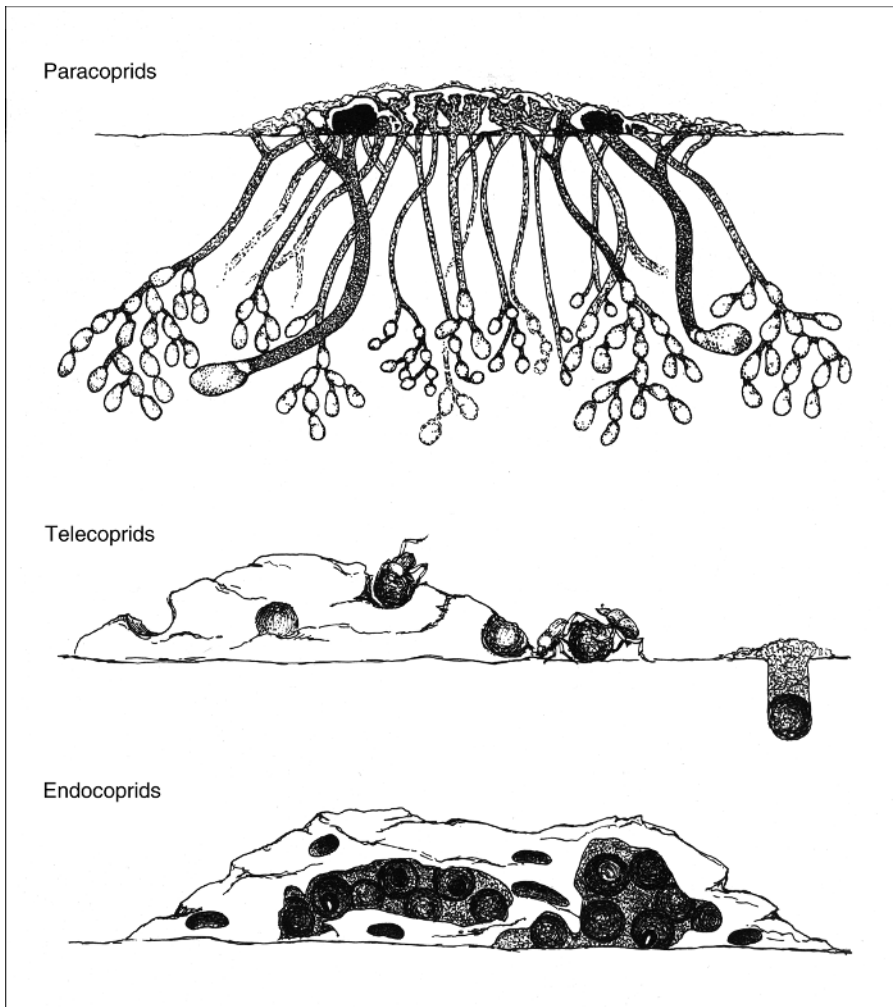


Fig. 1.4 Nesting behaviours of scarabaeine dung beetles can be broadly classified into three major types. In tunnelling or paracoprid species (a), beetles dig tunnels beneath the dung pad and pack fragments of dung that they bring from the surface into the blind ends of tunnels before laying a single egg into the brood chamber. A brood mass provides all the resources for the development to adulthood of a single offspring. In rolling or telecoprid species (b), beetles build a dung ball and roll it away from the pad before burying it in the soil. The dung ball can be used as food for the adults or fashioned into one or more brood balls. In dwelling or endocoprid species (c), beetles build broods within the dung pad itself (reproduced from Bornemissza, 1976).

competitively superior to dwellers (see Section 1.4), and it is certainly easy to imagine how telecoprid behaviour might arise in response to competition among paracoprid species that are rapidly burying dung in the soil beneath the dropping.

The African scarab *Scarabaeus catenatus* appears to adopt both tunnelling and rolling tactics (Sato, 1997; 1998b). When tunnelling, a pair of beetles will dig a nest

within 1 m of the dropping, and will move back and forth from the dropping with small fragments of dung to provision the nest. Alternatively, the male may roll a ball of dung up to 15 metres from the dropping to establish a nest, a behaviour more typical for a telecoprid.

Sato (1998b) observed that male competition was far greater for those adopting the tunnelling tactic because of interference from other tunnellers for dung and space around the dropping. Males adopting the rolling tactic did not suffer from competition but, because they did not return to the dropping, they obtained a smaller share of dung for brood production. The average reproductive success obtained from the two tactics was equal for males, but not for females, who fared better when adopting the tunnelling tactic (Sato, 1998b). Such differences in reproductive pay-offs are predicted to generate sexual conflict between males and females over which breeding tactic to adopt (Arnqvist & Rowe, 2005).

Perhaps the most interesting aspect of dung beetle breeding biology is the often extensive level of parental care that limits their lifetime fecundity to as few as three offspring in the rolling *Kheper* (Edwards, 1988), and over 100 in the tunnelling *Onthophagus* (Hunt *et al.*, 2002; Simmons & Emlen, 2008) (see Table 3.2 in Hanski & Camberfort, 1991). It is often the case that males and females cooperate in brood production. In both *Kheper* and the tunnelling *Copris*, males and females will cooperate in excavating a nest and supplying it with dung (Edwards & Aschenborn, 1988; Halffter *et al.*, 1996; Sato, 1988; 1998a; Sato & Hiramatsu, 1993). Cooperation may have arisen in response to the need to sequester dung quickly in the face of intense intraspecific and interspecific competition for the limited resource.

Paternal care appears to cease after the nest is provisioned with dung. The female will use the dung provisions to build brood masses and will remain with her broods and tend them until the adult offspring emerge. Female *Copris lunaris* keep the brood balls upright and will repair them should they break open during the development of the larvae (Klemperer, 1982).

Olfactory communication may be important in interactions between females and their developing young. For example, in *C. lunaris*, females will not right or repair broods that do not contain larvae unless dichloromethane extracts from *C. lunaris* broods have been added (Klemperer, 1982). Moreover, female *C. diversus* have been shown to reallocate dung from broods within which an offspring has died to viable broods, so that the size of surviving adult offspring is increased (Tyndale-Biscoe, 1984).

Numerous experimental removal studies have shown that brood survival is dependent on maternal care. Thus, in *K. nigroaeneus*, maternal care increases egg-to-larva survival by 20 per cent, larva-to-pupa survival by 39 per cent and post-feeding survival by 20 per cent (Edwards and Aschenborn, 1989). Likewise, egg-to-adult survival is increased by maternal care in several species of *Copris* (Klemperer, 1982; Tyndale-Biscoe, 1984; Halffter *et al.*, 1996). Female *Copris* spend a considerable proportion of their time tending to brood balls, compacting and smoothing their surfaces (Halffter *et al.*, 1996). Broods that do not receive maternal care appear vulnerable to invasion by fungi *Metarrhizium anisoplae* and *Cephalosporium* sp. (Halffter *et al.*, 1996) and also to predation by other soil invertebrates (Sato, 1997).

Maternal care is also likely to be an important guard against reproductive competition from brood parasites. Thus, the brood parasite *Aphodius* reduces host brood survival by as much as 68 per cent, with 12 per cent of *S. puncticollis* nests being parasitized (González-Megías & Sánchez-Piñero, 2003). Klemperer (1982) observed that female *C. lunaris* would attack and kill *Aphodius* larvae when they were encountered in the nest.

Dung beetles have proved to be ideal model organisms with which to test empirically the extensive theoretical models that have been developed around the evolution of parental care. In Chapter 8, John Hunt and Clarissa House review the extensive and detailed work on biparental care in *Onthophagus* and show how the study of this genus has contributed to our general understanding of parental care. Biparental care is common in this genus, where horned males assist females by delivering fragments of dung to the brood chamber where the female constructs the brood mass. Although females can construct broods alone, male assistance increases the number and weight of broods produced, thereby improving female and offspring reproductive fitness (Palestrini & Rolando, 2001; Hunt & Simmons, 2000; Sowig, 1996a; Lee & Peng, 1981).

Unlike *Kheper* and *Copris*, neither sex of *Onthophagus* provide care after oviposition is completed. Nonetheless, biparental provisioning of the brood mass has dramatic effects on offspring fitness. In Chapter 8, Hunt and House show how parental provisioning is optimized, depending on the costs and benefits of provisions to offspring and parental fitness. Behavioural interactions between male and female *O. taurus* during provisioning influences the relative amounts of dung that each parent provides, as well as how males adjust their investment facultatively to the risk of sperm competition from sneak males, and thus their confidence in paternity of offspring they help to provision.

Hunt and House also show how brood provisioning, rather than egg production, represents the major cost of reproduction for *Onthophagus*, and how male assistance can ameliorate the female's costs of reproduction. This finding is consistent with the fact that ovariole development is inhibited, and the terminal oocyte resorbed, during the period when females are provisioning and caring for their offspring (Klemperer, 1983; Sato & Imamori, 1987, Anduaga *et al.*, 1987). In other words, females spend much more of their resources on caring for young than they do in manufacturing eggs.

The amount of maternal and paternal provisions are an important source of environmental effects that contribute to offspring fitness. Where provisioning has an underlying genetic basis, these parental effects can generate evolutionary responses to selection in traits that they affect, such as offspring body size, even when there is little or no additive genetic variance for those traits (Wolf *et al.*, 1998). As Hunt and House point out, parental care can thereby have important, yet unappreciated, implications for the evolutionary diversification of dung beetles.

The very different environments in which dung beetles must operate will also generate different selection pressures on their morphology. Rollers are often characterized by adaptations to the hind tibia for ball construction and rolling (seen in its extreme in the hind legs of *Neosisyphus*), while the tunnellers have relatively short robust forelegs and specialized structures on the head for moving soil (see Figure 17.2 in Hanski & Cambefort, 1991). Moreover, as we have

discussed above, both sexes of tunnellers can have horns with which to defend their tunnels, an adaptation that comes at a cost to visual acuity.

In Chapter 9, Marcus Byrne and Marie Dacke show us how the morphology of the eyes vary between tunnellers and rollers, and between diurnal and nocturnal species. Indeed, they show us how well the eyes of rollers are adapted to the need to roll balls of dung away from the source of resource competition. The dorsal rim of the eye is adapted to function as a polarizing compass that allows the beetles to follow an accurate bearing when rolling a ball away from the dropping – and, more importantly perhaps, for those flightless species, to return to their nests by the quickest straight-line path once they have secured additional pieces of dung (Chapter 9).

1.4 Ecological consequences of intraspecific and interspecific competition

Intraspecific interference competition is common in the scarabaeine dung beetles (Hanski & Cambefort, 1991). The annual peak adult activity of scarabaeine dung beetles tends to occur for short periods. For species active in summer, these periods follow rainfall events in months when temperatures are highest. As a result, large numbers of dung beetles of many species can arrive at the same fresh dung pads (Figure 1.5). Over 1,000 beetles can be caught in one dung-baited trap over 24 hours (Hanski & Cambefort, 1991; and see Tables 12.1 and 12.2 in this volume). There is not sufficient dung for all females in the pad to breed, and oviposition is affected by competition.

However, intraspecific interference competition between beetles can occur in pads long before any shortage of dung generates exploitation competition (Ridsdill-Smith, 1991). For example, a negative exponential curve described the fall in number of eggs per female per week with increasing beetle density from 2 to 100 *Onthophagus binodis* on one litre of cattle dung (Ridsdill-Smith *et al.*, 1982). Dung burial, calculated from the volume of each brood mass, reached a maximum of



Photo P. Edwards

Fig. 1.5 Dung beetles competing for dung in Mkuzi Park in Southern Africa. Main beetles are *Pachylomera femoralis* (large) and *Allogymnopleurus thalassinus* (smaller).

45 per cent with 20–30 beetles. Egg production of both *Onthophagus ferox* and *O. binodis* was greatly reduced by intraspecific competition (71 per cent and 85 per cent reduction respectively, between low and high density populations) (Ridsdill-Smith, 1993b).

In Chapter 12, James Ridsdill-Smith and Penny Edwards describe the serial introduction of exotic dung beetle species to pasture sites where there was a surplus of cattle dung. They show how in single-species populations, the large native species, *O. ferox*, was unable to increase its population size to utilize more than 30 per cent of the available dung, while the smaller exotic species, *O. binodis*, used only 50 per cent of the available dung. Over 14 years, the total number of beetles trapped increased with the number of exotic species present (Figure 12.6), and they presumably used more of the available dung. Intraspecific competition thus appears to be a more important factor limiting the growth of dung beetle populations than the supply of fresh dung.

Most of the examples of interspecific interference competition given by Hanski & Cambefort (1991) are for rollers, where it is relatively easy to observe contests over dung balls. In general, larger species capture dung balls from small species (Hanski & Cambefort, 1991). In laboratory studies, large tunnelling species bury more dung and show asymmetric competition with smaller species (see Chapters 12 and 13). Egg production of the large tunnelling species, *Copris elphenor* and *Catharsius tricornutus* were not affected by the smaller species *Onitis alexis*, but egg production of *O. alexis* was reduced in the presence of the larger beetles (Giller & Doube, 1989). Similarly, at high beetle densities, egg production of the larger species *O. ferox* was unaffected by the smaller species *O. binodis*, but egg production of *O. binodis* was reduced in the presence of the larger *O. ferox* (Ridsdill-Smith, 1993b).

In both of these studies, the larger species showed pre-emptive dung burial behaviour, burying relatively more dung on the first day, which was then used to produce brood masses on subsequent days. In contrast, the smaller species buried only enough dung for one brood mass on the first day, and then again on subsequent days. In the field, the pad can be disturbed very quickly when beetles are very abundant, resulting in interspecific as well as intraspecific exploitation competition, so that any beetles returning to the pad from their tunnel in the soil after a day or two are unable to obtain dung to produce any further brood masses (Ridsdill-Smith, 1991).

1.4.1 Niche expansion

Competition for resources will reduce individual fitness and generate selection on traits that reduce the intensity of competition. For example, when two species exploit the same resource, those individuals within each species that compete least with members of the other species are expected to have a higher fitness, generating disruptive selection that can drive niche divergence (Slatkin, 1980; Day & Young, 2004; Rundle & Nosil, 2005; Abrams *et al.*, 2008). Likewise, when individuals within a species compete for resources, divergent selection is expected to favour individuals that compete least, i.e. individuals who differ from the average competitor phenotype. Thus, both interspecific and intraspecific competition can drive

phenotypic divergence and promote niche expansion and subsequent speciation (Schluter, 1994; Pfennig *et al.*, 2007; Agashe & Bolnick, 2010).

A very striking feature of the scarabaeine dung beetles is the niche separation of co-existing species (Chapter 2). Different species have evolved to fill the same niches in different geographical regions, and different species within the same regions have evolved differences in diet, nesting behaviour, thermal tolerances or visual acuities to fill different niches.

Most scarabaeine beetles fly upwind to locate fresh dung pads, attracted by the volatile odours given off by the dung, in particular, 2-butanone (Chapter 5). Beetles can also distinguish between dung from different mammals and, although they do not specialize on any one dung type, they can show clear preferences when presented with alternatives (Chapter 5; Dormont *et al.*, 2007).

Other species feed on alternative food resources such as carrion, fungi, millipedes or fruit, and they use different volatile cues to find each resource. Seeds of plants may be present in dung, and dung beetles can also be attracted to volatiles from the seeds. For example, *Pachylomera femoralis* is attracted to seeds of spineless monkey orange trees, and Tribe and Burger have identified volatiles from the seeds that will attract the beetles (Chapter 5). In the European flightless species *Thorectes lusitanicus* (Geotrupidae), adult beetles are attracted by oak acorns, and feeding on acorns can increase female fitness through enhanced ovarian development (Verdú *et al.*, 2010). Thus, dung beetles can exhibit considerable variation in the types of resources they exploit, both within and among species.

We saw in Section 1.3 that dung beetles have evolved three major patterns of nesting behaviour: tunnelling, rolling and dwelling (Figure 1.4). Within these groups there is much variation, based on how deep the brood masses are placed in the soil under the pad, the speed with which the dung is buried and the amount buried (Doube, 1990). Some species bury all the dung in the first two days, in preemptive dung burial, while other species bury dung over longer periods (Doube *et al.*, 1988a; Ridsdill-Smith, 1993b). In *S. catenatus*, beetles can adopt either the rolling or tunnelling nesting tactic (Sato, 1997) and the amount of brood provisions per offspring can vary, depending on the type of dung exploited or whether males cooperate in brood provisioning (Hunt & Simmons, 2004; see Chapter 8).

It is reasonable to expect that dietary preferences and/or nesting behaviours harbour underlying genetic variation which would, when coupled with intraspecific or interspecific competition, facilitate niche evolution (Agashe & Bolnick, 2010). Indeed, brood provisioning has a genetic basis in *O. taurus*, and Hunt and House propose that plasticity in brood provisioning, particularly in response to environmental factors such as soil moisture, has the potential to play an important role in promoting niche expansion in onthophagines (Chapter 8).

Another striking feature of the scarabaeine dung beetles is the intensity of sexual selection, a form of intraspecific competition that favours traits, such as increased body size and condition, that contribute to success in reproductive competition (Chapters 3 and 4). Theory suggests that sexual selection can play an important role in niche expansion. Under good gene models of sexual selection, traits that females find attractive in males, or which give males a competitive advantage over other males, are reflective of the underlying genetic quality or condition of an individual, so that these individuals also have higher non-sexual fitness (Chapter 4). As such,

sexual selection can accelerate the fixation of advantageous alleles (Proulx, 1999; 2002) and the purging of disadvantageous alleles (Whitlock & Agrawal, 2009), processes that can, in theory, accelerate the rate of adaptation to new niches (Lorch *et al.*, 2003).

Empirical tests of this idea are few, and the evidence for a role of sexual selection in promoting adaptation to new niches is contradictory (Candolin & Heuschele, 2008). Studies of *Drosophila* suggest that sexual selection may not influence adaptation to new thermal or resource environments (Holland, 2002; Rundle *et al.*, 2006), but studies of bruchid beetles, *Callosobruchus maculatus*, demonstrate clearly that adaptation to a novel resource is accelerated by sexual selection (Fricke & Arnqvist, 2007). The later study is informative because the authors found evidence that the costs of sexual selection, bought about by sexual conflict, may depress population fitness once a species has adapted to its new niche.

An important fitness trait in the context of sexual selection is adult body size (Chapters 3, 4, 6 and 8). In Chapter 10, Steven Chown and Jaco Klok explore the importance of body size from an ecophysiological perspective. They demonstrate a significant physiological advantage to beetle size that has important ramifications for species richness and the structuring of beetle communities. For example, they describe the ability of species over 2 g in weight to be endothermic regulators in flight, while species below this mass have thoracic temperatures similar to ambient. Elevated body temperatures will give the larger beetles considerable advantage in exploiting a range of foraging options that might otherwise not be open to them, and in making and rolling balls of dung faster than species at ambient temperature (Heinrich & Bartholomew, 1979). Ball-rolling species occupying similar trophic habits showed very different thermal niches (Verdú *et al.*, 2007a).

Chown and Klok also point out how thermal tolerance influences the range of new habitats that species are able to exploit, and how thermal tolerance can account for the altitudinal and latitudinal gradients of species richness and abundance, thus playing a role in niche separation and the reduction of interspecific competition. Climatic and abiotic factors influence the structure of local communities at a regional scale (Hanski & Cambefort, 1991). Species richness of dung beetles tends to be greater near the equator and to decrease with latitude (Fig 11.2 in Chapter 11), as predicted from their ecophysiology (Chapter 10).

1.4.2 Regional distribution and seasonal activity

In Chapter 11, Tomas Roslin and Heidi Viljanen provide a broad overview of the factors thought to underlie the distribution and abundances of dung beetle species, contrasting the dung beetle fauna of Finland and Madagascar to illustrate broad geographical patterns. Like Chown and Klok, they identify an important role of body size associated with the regional distribution of dung beetle species. Using mark recapture data, they show how the large *Aphodius fossor* can move over a much larger spatial scale than the small *Aphodius pusillus*, illustrating how body size can influence a species ability to expand its range and, potentially, exploit new niches.

The dung beetle fauna of open and forested habitats differ markedly. The low species richness of scarabaeine dung beetles in pastures, compared with the high species richness in forests, is particularly evident in warmer regions nearer the

equator. Examples of this are given in this volume from Madagascar (Chapter 11), Australia (Chapter 12) and South America (Chapter 13). Indeed, the low species richness in pastures was the basis for the biological control programme which introduced exotic dung beetles to utilize cattle dung in Australia (Chapter 12). Pasture species can disperse rapidly (Chapter 12). Most forest species, however, remain strictly confined to the forest habitat and, as Roslin and Viljanen show, habitat discontinuities provide a strong barrier to dispersal (Chapter 11).

The dung beetle faunas of adjacent forest and savannah are completely different, but finer-scale subdivision of habitats can also influence the composition of the dung beetle community (Chapter 13). These broad-scale ecological patterns are reflected in the population genetic structuring of species. For example, the Madagascan forest dwellers have large and stable populations, with restricted gene flow, but for species in Finnish pastures there has been a recent and rapid expansion of populations, with pasture species having a larger range size and a strong ongoing gene flow (Chapter 11). These patterns suggest that the opportunities for niche expansion and speciation are far greater in forest than pasture habitats.

Seasonal activity of dung beetles is influenced by interactions between seasonal rainfall and temperature. Most adult dung beetles are active in summer and, while immatures can spend dry seasons in the soil, they do not survive in cold, wet seasons. For species in winter rainfall areas, the winter is spent in the adult stage.

Beetles breed in spring or after the commencement of rain, when dung quality is high. Seasonal changes in dung quality as a result of changing patterns of plant growth can have a substantial impact on the rate of egg production of many dung beetle species (Chapter 12). It is possible for winter active and summer active beetle species to co-exist at the same sites (Chapter 12), but this does not always occur, and the mechanisms involving interspecific competition that allow coexistence between these species are not well understood.

1.4.3 Community dynamics

Despite competition, it is possible for many species to coexist in a dung beetle community and, as we have seen, in any one community, the different species occupy many different niches. In addition, dung beetle distribution between pads tends to be aggregated (Hanski & Cambefort, 1991; Lobo & Montes de Oca, 1997; Slade *et al.*, 2007), so that high numbers of beetles of different species may not occur in the same pads. Small species tend to be more aggregated than large species, possibly as a result of having smaller niche differences.

The high species richness of many tropical communities makes an analysis of the factors influencing community structure hard to assess. At a broad level, Hanski & Cambefort (1991) note that large rollers and fast-burying tunnellers are usually the top competitors, while dwellers are the weakest competitors.

The dung beetle community in pastures grazed by cattle supports fewer species and is dominated by small species (Chapter 13). In Australian pastures, even though both large and small exotic species have become established, the dominant species are *Euoniticellus intermedius*, *Digitonthophagus gazella* and *O. taurus*, all considered small species (Chapter 12). Indeed, these species are far more abundant in Australian pastures than they are in their country of origin. However, large species

have established and, as noted, they remove more dung proportionally than do small species. If their abundance could be enhanced, they would increase an ecosystem function by burying more dung, with pasture productivity and fly control benefits. While this could occur naturally over a much longer time period, it has been proposed that there is a need to manage the structure of the pasture dung beetle community, perhaps by increasing the habitat complexity of vegetation (Chapter 12).

1.5 Conservation

Given their extraordinary evolutionary radiation, the dung beetles offer a good model taxon with which to address the many problems associated with the conservation of global biodiversity. This is a difficult area of research, because it involves considerable elements of human judgement, so conservation efforts need to be compatible with other aspects of human use of the environment. For example, in Spain it has been noted that the abundance of the 11 species of rollers (mostly larger dung beetles, including *Scarabaeus sacer*) collected in the Iberian peninsula has decreased from 24 per cent to 6 per cent during the 20th century, particularly as a result of the loss of coastal sandy country to urban development (Lobo, 2001). An example of the use of biodiversity to measure conservation need comes from data on temperate and tropical systems, which indicates that a regional scale decline and loss of medium to large mammals has severely disrupted the diversity and abundance of dung beetle communities (Nichols *et al.*, 2009; see also Figure 13.6).

The conservation of insects has two important components. One is the conservation of key species which are a focus for particular concern, and the second is the use of insect biodiversity to indicate the general health of an environment. In Chapter 13, Elizabeth Nichols and Toby Gardner describe the use of scarabaeine dung beetles as an ecological indicator taxon for the conservation of biodiversity.

The characteristics needed of a group to be an ecological disturbance indicator are that they must have viability, reliability and interpretability (Chapter 13). A taxonomic database is available for the scarabaeine beetles, managed by members of The Scarabaeine Research Network (www.scarabnet.org). Sampling methods using dung-baited pitfall traps have been widely tested and represent a cost-effective way to detect the effects of management on dung beetles (Figures 13.4 and 13.5). Also, dung beetles have proved very responsive to habitat disturbance of tropical forests (Figures 13.2 and 13.3, and Chapter 11).

Nichols and Gardner separate species traits into response traits, which relate resource or environment needs to species performance, and effect-based traits which, as the name suggests, are those affecting the impact of the species on the environment. The effect-based traits are listed as hard traits against the more easily measured soft traits which are commonly used (Table 13.1). Distinguishing how soft and hard traits interact with human activities is one of the cutting-edge issues in understanding the meaning of biodiversity (Chapter 13).

A key soft trait is beetle body size (a key factor in inter- and intraspecific competition), which has a disproportionate effect on the amount of dung buried. However, large beetles also have the greatest risk of local extinction, so consider-

ation should be given as to how to conserve them. In their meta-analysis, Nichols and Gardner show the importance of structurally complex habitats in maintaining dung beetle biodiversity (Chapter 13). They suggest that increasing habitat complexity in pastures could assist building communities with more large beetles and give a list of examples where dung beetles are being used as indicators of ecological disturbance, helping to develop a better understanding of the key factors.

Individual Coleoptera are underrepresented on the IUCN red list, but they are included in the Sampled Red List Index Program thanks to the Scarabaeine Research Network, who estimate that over 12 per cent of all dung beetles are threatened with extinction, with a further 9 per cent vulnerable to extinction. Dung beetle survival requires both the maintenance of intact mammal communities and tight habitat control. The reality of the threat of extinction is illustrated strikingly in Chapter 11, where the loss of 90 per cent of habitat in both Madagascar and in Finland has resulted in about 40 per cent of species disappearing in each case (Chapter 11, Fig 11.5). The dung beetles are thus proving an excellent taxon with which to investigate conservation needs of the world's tropical forests.

1.6 Concluding remarks

This volume summarizes a rich history of research on scarabaeine dung beetles. Mostly, researchers choose their subjects because of a passion or admiration for the animals in their own right, but they are also driven by research agendas, using their chosen taxon to test or advance some general scientific theory. With the accumulation of knowledge, some taxa become recognized as 'model systems' (Dugatkin, 2001). The humble fruit fly *Drosophila melanogaster* is perhaps one of the best known model systems, and much of our knowledge of genetics, developmental and cell biology, life history and evolution comes from research on this one species – research that has been invigorated by the publication of the full genome in 2000 (Powell, 1997; Markow & O'Grady, 2006).

The cumulative research available on scarabaeine dung beetles now covers a broad array of disciplines. It has given us insights into the private lives of these fascinating and endearing creatures. More importantly, it has been instrumental in developing our understanding of broad ecological processes and how they shape the evolution of biological diversity. We are seeing further than ever before, with our research efforts yielding new information at all levels of analysis from functional genomics to developmental biology; comparative morphology; physiology; behaviour; and population and community ecology.

Research on dung beetles is shedding light on the ultimate goal of how best to document and conserve the world's biodiversity. With this volume, dung beetles emerge as a model system that will continue to deliver important progress in evolutionary and ecological research. To quote Fabre (1918): 'Notwithstanding their filthy trade, the dung-beetles occupy a very respectable rank.'