This book describes the evolutionary and ecological consequences of reproductive competition for scarabaeine dung beetles. As well as giving us insight into the private lives of these fascinating creatures, this book shows how dung beetles can be used as model systems for improving our general understanding of broad evolutionary and ecological processes, and how they generate biological diversity. Over the last few decades we have begun to see further than ever before, with our research efforts yielding new information at all levels of analysis, from whole organism biology to genomics. This book brings together leading researchers who contribute chapters that integrate our current knowledge of phylogenetics and evolution, developmental biology, comparative morphology, physiology, behaviour, and population and community ecology. Dung beetle research is shedding light on the ultimate question of how best to document and conserve the world’s biodiversity. The book will be of interest to established researchers, university teachers, research students, conservation biologists, and those wanting to know more about the dung beetle taxon.

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Cover image: Onthophagus nigriventris dung beetle, major male. Courtesy of Alex Wild
Cover design: Nicki Averill Design
Ecology and Evolution of Dung Beetles
Ecology and Evolution of Dung Beetles

Edited by
Leigh W. Simmons & T. James Ridsdill-Smith
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Scarabaeine dung beetles feed on the dung of herbivores as adults, and bury dung masses as provisions for their offspring. The subfamily contains about 6,000 species and is found in all continents except Antarctica. Beetles of different species are attracted to the same pad of fresh dung, but they occupy many different niches, thus reducing competition. Activity of the beetles is clearly visible to the casual observer and it fascinated the early Egyptians and Greeks, who considered the rolling of dung balls as representing the sun being rolled across the sky.

In the 19th century, J.H. Fabre described cooperation between male and female beetles in the formation of brood balls, the female role in oviposition and, in some cases, brood care, while Charles Darwin used the horns of adult male beetles to illustrate his theory of sexual selection. The biology and taxonomy of many species continued to be described through the 20th century, and books have been published summarising dung beetle natural history by Halffter & Matthews (1966), reproductive biology by Halffter & Edmonds (1982), ecology by Hanski & Cambefort (1991) and, most recently, a general overview of their evolutionary biology and conservation by Scholtz, Davis & Kryger (2009).

Our thesis in this book is that the wealth of information now available on dung beetles elevates them to the status of ‘model system’. Dung beetles have proved remarkably useful for broad-scale ecological studies that address fundamental issues in community and population ecology and its extension to conservation biology. At the same time, they are providing valuable laboratory tools to explore fundamental questions in evolutionary biology; Darwin’s theories of sexual selection have been validated through work on dung beetles and they are contributing to our understanding of the evolution of parental care. Moreover, their utility for studies of phenotypic plasticity is contributing to emerging research fields of evolutionary developmental biology (‘evo-devo’) and ecological developmental biology (‘eco-devo’).
The development of genomic tools for dung beetles will no doubt invigorate future research on this important taxon. Thus, our aim with this book is to provide detailed and focused reviews of the important contributions dung beetles continue to provide in evolutionary and ecological research.

Leigh W. Simmons and T. James Ridsdill-Smith
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Reproductive Competition and Its Impact on the Evolution and Ecology of Dung Beetles

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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
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
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* (Scarabaeinae) shown. 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

**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.
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) lanistria, 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*, *Gymnopleurus*, *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 Halfifer and his colleagues (Halfifer & Mathews, 1966; Halfifer & 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 (Halfifer & 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 (Halfifer 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