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Male Contest Competition and the Evolution of Weapons

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3.1 Introduction

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21 The spectacular horns found on many species of beetle must rate as one of the most
22 extraordinary structures found in the animal kingdom, both for their extravagance
23 and their diversity. Horned species are found in many families of the Coleoptera,
24 but the majority of them are in the Scarabaeidae, four sub-families of which have
25 significant numbers of horned species: the Dynastinae, Cetoniinae, Geotrupinae
26 and Scarabaeinae. The latter two are the dung-feeding scarabs with which we are
27 presently concerned, and in these two families there is not only a huge number of
28 horned species but also an extraordinary variety of horn morphologies. These range
29 from short single or double horns on the head (Figure 3.1C) to the extravagant
30 structures carried by species such as *Heliocopris andersoni* (Figure 3.1F) and
31 *Onthophagus sexcornutus* (Figure 3.1A), which have numbers of large, complex
32 horns arising from both the head and the pronotum. The variability in these
33 horns, even amongst closely related species, has been recognized since the mid-
34 nineteenth century, with Darwin relaying observations from Bates on the matter
35 (Darwin, 1871):

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37 ‘In the several sub-divisions of the family, the differences in structure of the horns do not
38 run parallel, as I am informed by Mr. Bates, with their more important and characteristic
39 differences; thus within the same natural section of the genus *Onthophagus*, there are
40 species which have either a single cephalic horn, or two distinct horns.’

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42 Recent phylogenetic studies have confirmed Bates’s hunch that that these horns
43 exhibit substantial evolutionary lability. Emlen *et al.* (2005b) found that within a
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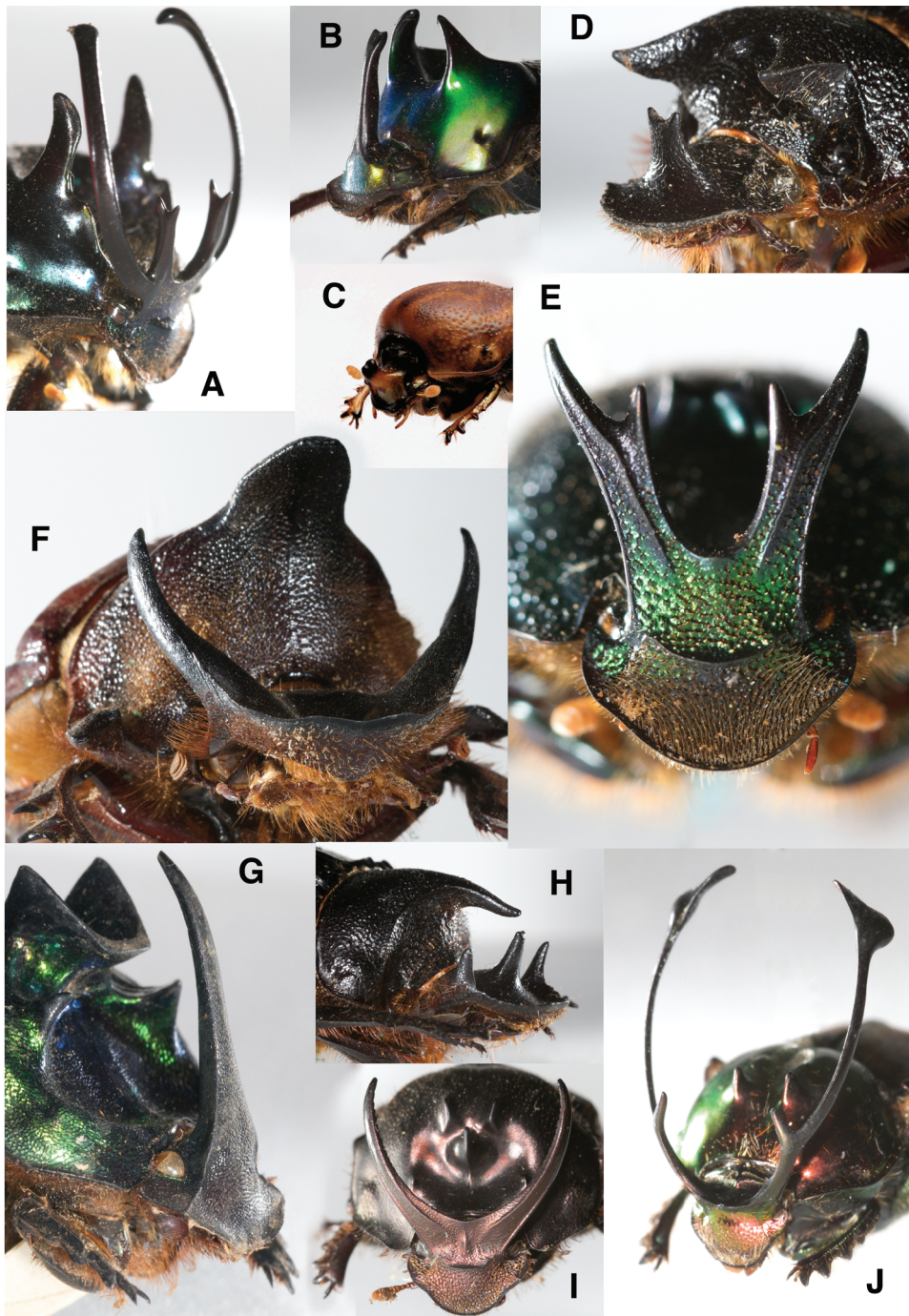


Fig. 3.1 Diversity in horn morphology in dung beetles. A: *Onthophagus sexcornutus*.
 B: *Oxysternon palaemon*. C: *Euoniticellus intermedius*. D: *Heliocoprpris hunteri*.
 E: *Onthophagus imperator*. F: *Heliocoprpris andersoni*. G: *Coprophanaeus bonariensis*.
 H: *Heliocoprpris hunteri*. I: *Onthophagus watanabei*. J: *Onthophagus rangifer*.

1 phylogeny of 48 species of *Onthophagus* there had been more than 25 evolutionary
2 gains or losses of five types of horn. It seems that the ancestral condition in this
3 particular group of beetles was the possession of a single horn on the head, and that
4 horns have repeatedly been lost, have been gained, and have diversified from this
5 original form.

6 Not all taxa of dung beetles are horned, however, with many important genera
7 such as *Sisyphus* being entirely hornless. This tremendous morphological variability
8 is clearly in need of an explanation, as are the patterns in the presence and absence of
9 horns. In this chapter I will first focus on the function of these horns and how horn
10 morphology and size are related to the fitness of the bearer. I will then consider how
11 these patterns of diversity in horn presence and morphology might arise, with
12 particular emphasis on the roles of breeding biology, population density and sex
13 ratio.

14 15 16 **3.2 Dung beetle horns as weapons**

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18 Early workers on beetle horns were not sure of their function. Darwin (1871)
19 discusses them at length in *The Descent of Man and Selection in Relation to Sex*, and
20 concludes that there is little evidence that they are used as weaponry, and that they
21 must therefore be ornaments for attracting females. Although Beebe (1947)
22 described the use of horns in combat between males of a dynastid beetle, it was
23 only towards the end of the 20th century that empirical evidence started to appear
24 that demonstrated a similar role for the horns of dung beetles. This long delay in
25 establishing the function of these remarkable and well-described structures can be
26 attributed to the fact that horned dung beetles usually fight in tunnels (Emlen &
27 Philips, 2006), making observation difficult.

28 Palmer (1978) was the first to realize that tunnelling beetles will readily excavate
29 in soil between sheets of glass, and used this to observe contests between males of a
30 Geotrupine beetle, *Typhoeus typhoeus*, during which they used their horns as
31 weapons to push each other. The same technique has since been used for species
32 from the Scarabaeinae, and the use of horns as weapons in fights between males has
33 been observed in *Phanaeus difformis* (Rasmussen, 1994), *Onthophagus acuminatus*
34 (Emlen, 1997a), *O. taurus* (Moczek & Emlen, 2000), *Euoniticellus intermedius*
35 (Pomfret & Knell, 2006b), *O. nigriventris* (Madewell & Moczek, 2006) and
36 anecdotally in several more species. These studies, combined with observations
37 of the use of horns as weapons in a number of other beetle species (Brown &
38 Bartalon, 1986; Eberhard, 1979; Eberhard *et al.* 2000; Otte & Stayman, 1979;
39 Siva-Jothy, 1987), have led to a broad consensus among biologists that the horns of
40 beetles are used as weapons during fights, usually between males competing for
41 access to females.

42 By contrast, there is no evidence of female choice for horns in either *O. taurus*, *O.*
43 *australis* (Kotiaho, 2002), or *E. intermedius* (Pomfret, 2004). In *O. binodis* there is
44 some evidence for an association between horn length and mating success in the
45 absence of rival males, in that long-horned 'major' males experience higher mating
46 success, but this is attributed by the author to a body size effect rather than a horn
47 effect, with large beetles having higher courtship rates (Kotiaho, 2002). In general,

1 female *Onthophagus* appear to choose their mates based on courtship rate rather
2 than horn morphology (see Chapter 4 of this volume). There is therefore little
3 reason to believe that female choice has played a role in the evolution of beetle
4 horns. However, it cannot be ruled out in every case; possible signalling roles for the
5 horns of Phanaeini, and for the horns carried by some of the more extravagantly
6 ornamented *Onthophagus*, are discussed in the next section.

3.3 Functional morphology of horns

11 As we have seen, dung beetle horns are extraordinarily diverse, yet we only have
12 detailed descriptions of horn use from a few of these species. This lack of knowledge
13 means that a good understanding of the functional morphology of these structures is
14 still some way away, but a series of studies over the last twenty years have given us an
15 understanding of how the horns are used in some systems. Here I shall relate the
16 form of dung beetle horns to their function, with an emphasis on these systems, and
17 discuss the possible use of horns in some less well-known systems in the light of this
18 knowledge.

19 Probably the most common horn type is the long, gently curved cephalic horn,
20 often coupled with pronotal sculpturing, as found on most males in the Phanaeini,
21 all male *Copris*, and also on males in many other taxa (Figure 3.1G). These are
22 reminiscent of the cephalic horns carried by many Dynastinae, such as *Oryctes*
23 *rhinoceros* and *Golofa porteri*, some of which are known to fight by inserting their
24 cephalic horns underneath their opponents. Once this has been achieved and the
25 opponent's grip on the substrate is broken, the defeated opponent can either be
26 flipped onto his back or lifted and held between the cephalic horn and the pronotal
27 horns or sculpturing, allowing the victor to throw his rival to the ground or off the
28 stem where the fight is taking place (Beebe, 1947; Eberhard, 1977; 1979).

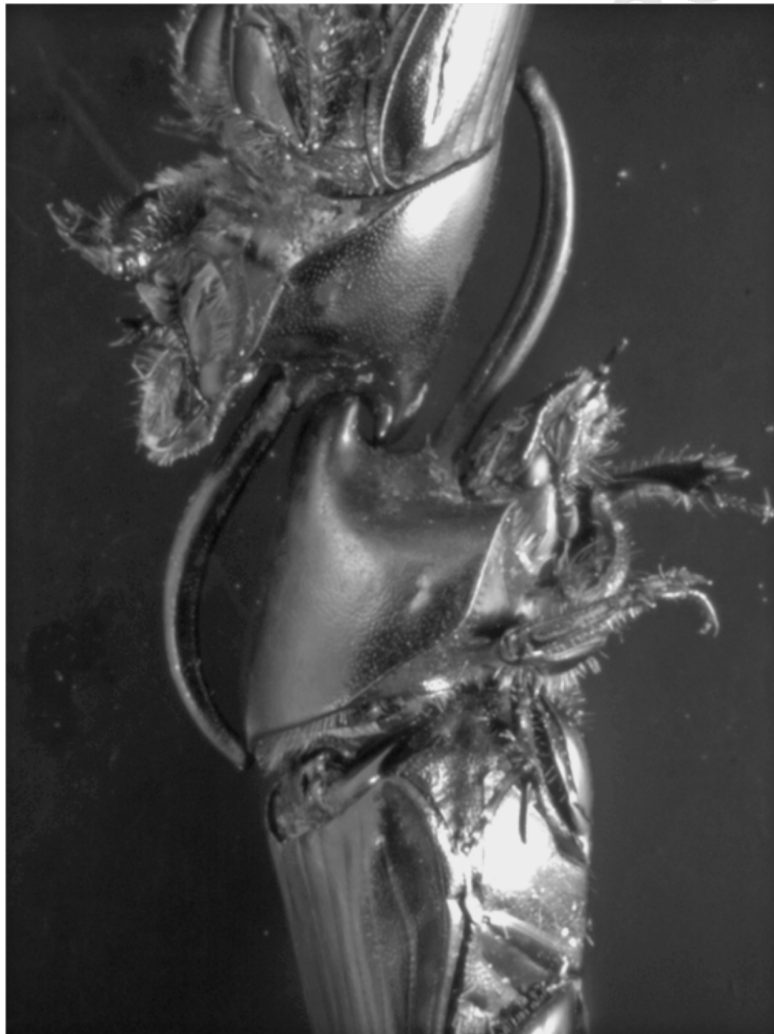
29 Rasmussen (1994) describes similar contests between male *Phanaeus difformis*,
30 with males inserting their cephalic horns beneath opponents and turning them over,
31 and notes that in one case a large male lifted a rival and pinched him against his
32 pronotum using his horn. Rasmussen also reports that *P. difformis* males only fight
33 in this way on the ground at burrow entrances; when males encounter each other in
34 tunnels, the contests are restricted to pushing contests, presumably because the
35 confined space in the tunnels does not allow rivals to be turned over.

36 Many species of *Phanaeus* will facultatively roll dung some distance prior to
37 burying it, and fights have been reported between males attempting to accompany
38 females rolling dung across the ground (Price & May, 2009). It is tempting to
39 suggest that the ubiquity of long, curved cephalic horns in this genus is a conse-
40 quence of this habit of fighting on the ground surface, which allows males to lift and
41 flip their opponents. Otronen (1988), however, describes male *Coprophanaeus*
42 *ensifer*, which also carry long curved horns, as inserting their horns underneath each
43 other in tunnels to allow them to lift and push their opponents, indicating that the
44 use of these horns can vary between taxa.

45 Many species of dung beetle carry horns that seem to be adapted for pushing,
46 rather than lifting, opponents. Males of the Minotaur beetle, *Typhaeus typhoeus*
47 (Geotrupinae) carry three forward-facing pronotal horns, and Palmer (1978)

1 described their use in detail. Unescalated fights are simple head-on horn-to-horn
2 pushes but, if neither opponent backs down, then one beetle will invert himself in
3 the tunnel so that the two large outer horns engage on the rival's pronotum. The
4 beetles will then engage in a contest of strength that can last up to 75 minutes. A
5 third tactic was described by Palmer as a 'defensive block', whereby a defending
6 beetle edges himself in a tunnel side-on with his back to the aggressor. In these cases,
7 the aggressor uses his horns to lever the defender via the lower edges of the elytra.

8 Major males of *O. nigriventris* also fight with one male inverted in relation to the
9 other (Figure 3.2), which allows the small posterior horns to engage with the hollow
10 in the cuticle between the anterior and posterior horns, while the longer anterior



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46 **Fig. 3.2** The typical fighting position for *Onthophagus nigriventris*, illustrated using dead
47 specimens (originally published in Madewell & Moczek, 2006).

1 horn is placed along the curved top of the opponent's pronotum and, in some cases,
2 engages with the gap in the exoskeleton between the pronotum and the elytra
3 (Madewell & Moczek, 2006). While locked together in this position, the beetles
4 will push each other in contests lasting roughly nine minutes, until one is expelled
5 from the tunnel.

6 Many other beetles have similar horn morphologies, with one or more horns
7 projecting forwards that will engage with an opponent's head or pronotum, and it
8 seems reasonable to suggest that they are likely to be used in a similar way. As an
9 example, consider the three *Heliocopris* species shown in Figures 3.1D, F and H.
10 While the morphologies of these beetles' horns are all different, the overall effect is
11 similar in each species, with a forward-pointing pronotal horn or horns combined
12 with one, two or three upward-pointing cephalic horns. With the head lowered and
13 the cephalic horns ~~are~~ pointing forwards, the beetle will present a thicket of pointed
14 weaponry to its opponents. Smaller opponents with less well-developed horns will
15 find their rival's horns fully engaged against their pronotum and head, while they
16 struggle to gain purchase because their own shorter horns are unable to engage their
17 rivals to the same extent.

18 Rather than the multiple horns found in beetles like these *Heliocopris* spp., many
19 beetles carry more modest armament that is also used for pushing, rather than lifting,
20 opponents. As described above, the two curved horns of major *O. taurus* males
21 engage with the rival's pronotum during contests (Moczek & Emlen, 2000) and the
22 short single horn of *E. intermedius* (Figure 3.1C) is used to pry and push at an
23 opponent's head (Pomfret & Knell, 2006b). It is likely that many of the short, straight
24 or slightly bent cephalic horns carried by other beetles are used in the same way.

25 The horns of other beetles are likely to be used to engage rival's horns directly
26 rather than the pronotum or head. Consider the horns of *O. imperator*
27 (Figure 3.1E); these animals might lower their heads and engage opponents with
28 the points of the horns, but the shape and location of the horns, coupled with the
29 head extending downwards and parallel to the plane of the horns, suggests the
30 possibility that they are held vertically to block tunnels. Alternatively, the forked
31 ends of the horns would engage with the small pronotal horns, were the beetles to
32 fight with one inverted in relation to the other.

33 The function of some of the more elaborate horns is harder to understand and has
34 been little studied. In some cases at least, the morphology of the horns might reflect
35 specific details of the beetles' mating systems or the nature of the contests. This is
36 known to be the case in bovids and cervids, where both the overall size and the
37 morphology of the horns or antlers is correlated with factors such as group size,
38 territoriality (Brø-Jørgensen, 2007) and the way that the animals use their weapons
39 in contests (Caro *et al.*, 2003). In the absence of detailed studies of the mating
40 systems of large numbers of dung beetle species, it is difficult to carry out similar
41 studies at present, but this is certainly an area of research that is likely to be fruitful as
42 our knowledge of these animals improves.

43 Looking at specific details of some of these species with very exaggerated horns,
44 it is possible that the long, curved outer horns carried by species such as
45 *O. sexcornutus* (Figure 3.1A), *O. elgoni* and *O. panoply* function in a similar
46 manner to those of *O. taurus*. However, their great length begs the question of how
47 the bearer manages to bring them forwards in the confined space of a tunnel. Some

1 of these animals carry horns extending upwards from the pronotum, and these
2 might be important during fighting if the males brace themselves within tunnels by
3 pushing up with their legs and pressing the pronotum against the top of the tunnel,
4 as is known to happen in *O. taurus* (Moczek & Emlen, 2000) and *E. intermedius*
5 (Knell, *personal observations*).

6 The question of how the horns are used is even more acute in the case of
7 *O. rangifer*, which carries horns that are almost the same length as its body
8 (Figure 3.1J), and which are normally carried folded back along the animal's
9 back. Lowering the head raises the horns to the upright position seen in
10 Figure 3.1J, something that would be impossible in most beetle tunnels, which
11 are only a little larger in diameter than the excavator. The horns must therefore
12 either be used in wider tunnels, in the open, or remain parallel to the animal's
13 body when used.

14 Finally, the females of some dung beetle species carry horns. These are either
15 reduced versions of the male horn (e.g. *Phanaeus difformis* (Rasmussen, 1994)) or
16 different structures that appear to have independent evolutionary origins from male
17 horns (e.g. *Onthophagus sagittarius* (Simmons & Emlen, 2008)). In the case of *P.*
18 *difformis*, females are reported to fight with other females that attempt to steal dung
19 or take over burrows, but whether the horns are important in these contests is not
20 clear (Rasmussen, 1994).

21 On the other hand, female *O. sagittarius* use their horns in fights with other
22 females in contests over limited supplies of dung (Simmons & Emlen, 2008; Watson
23 & Simmons, 2010b). Like the males of *O. nigriventris*, the horned females of *O.*
24 *sagittarius* fight with one individual inverted in relation to the other, such that the
25 cephalic horn engages in the area between the pronotal horn and cephalic horn of
26 the opponent (Watson & Simmons, 2010b).

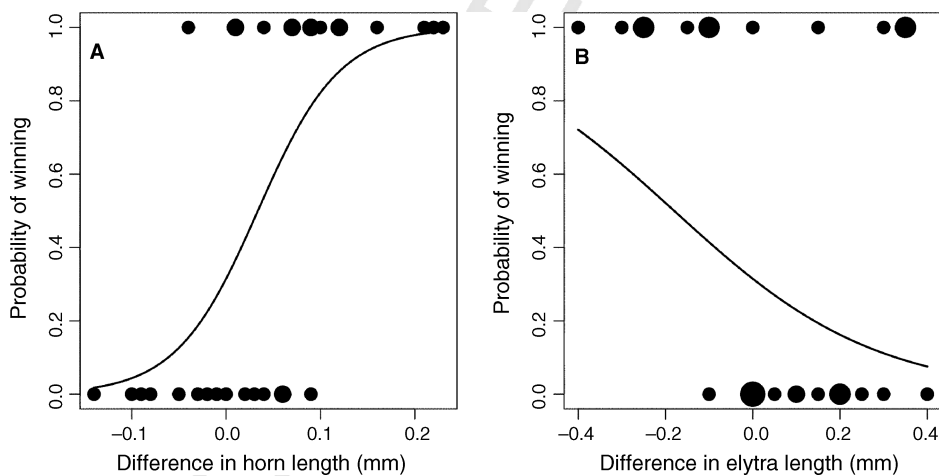
27 28 29 **3.4 Horns as predictors of victory**

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31 It is now clear that not only are horns used in fights between (usually) male beetles,
32 but that horn length is an important predictor of victory in these fights. Horn length
33 co-varies with body size, which could be an important predictor of fighting ability,
34 so experimenters have controlled for body size by staging contests between pairs of
35 males matched for size but not for horn length. This technique has demonstrated
36 that males with longer horns are much more likely to win fights in *P. difformis*,
37 (17 out of 20 contests won by the male with the longer horn (Rasmussen, 1994)),
38 *O. acuminatus* (14 out of 16 contests won by the longer horned male when the
39 difference in horn length was ≥ 0.2 mm (Emlen, 1997a)) and *O. taurus* (22 out of
40 27 contests won by the longer horned male (Moczek & Emlen, 2000)).

41 Both Emlen (1997a) and Moczek & Emlen (2000) also demonstrated that the
42 probability of winning was related to the magnitude of the difference in horn length.
43 In the case of *O. taurus* (Moczek & Emlen, 2000), 15 out of 15 fights were won by
44 the male with the longer horns when the difference in length was greater than 1 mm,
45 whereas 4 out of 12 fights between beetles with horns that differed by less than
46 1 mm were won by the animals with the shorter horns (in this species, horns grow up
47 to around 4.5 mm long).

1 The technique of staging contests between pairs of beetles that are matched for
 2 size is useful, but it does not tell us about the relative importance of body size and
 3 horn length in determining the outcome of fights. This can be investigated by
 4 staging fights between beetles varying in size and horn length and by designating one
 5 beetle in each pair as the ‘focal male’. The outcome of the fight is then coded as 1 or
 6 0 for a win or loss by the focal male, and a generalized linear model is fitted to the
 7 data, with the differences in horn size and body size between the focal male
 8 and his rival as predictor variables (Hardy & Field, 1998; Pomfret & Knell,
 9 2006b). To date, this approach has only been used with one species of dung beetle
 10 – *E. intermedius*. In this species, both body size and horn size differences were
 11 significant predictors of victory when small beetles fought each other but, when
 12 fights occurred between large beetles, only horn size predicted victory (Figure 3.3).

13 Looking beyond the dung-feeding Scarabaeidae, a similar analysis of fights
 14 between males of the dynastine beetle *Trypoxylus (Allomyrina) dichotoma* also
 15 found that horn length, but not body size, predicted victory. In this case, the authors
 16 confirmed this result by staging contests between animals matched for horn length
 17 but not for body size (Karino *et al.*, 2005). These results contradict the conventional
 18 wisdom that size is the most important factor in contests between animals; future
 19 work on the use of horns in contests should clarify whether this is a general pattern.
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 38 **Fig. 3.3** Horn length predicts victory in contests between large males of *Euoniticellus*
 39 *intermedius*. **A:** The x-axis gives the difference in horn length between two male beetles and
 40 the y-axis shows the fitted probability of victory from a generalized linear model. The data
 41 points show the outcomes of experimental contests, with a zero indicating a loss for the focal
 42 male and a one indicating a victory. **B:** The relationship between the difference in elytra size
 43 for the same set of experimental contests and the probability of victory. The x-axis gives the
 44 difference in elytra length and the y-axis shows the fitted probability of victory. Note that the
 45 slope of the line in A is highly statistically significant ($p < 0.0002$), but that in B is not. The size
 46 of data points indicates the number of contests corresponding to each point, with the
 47 largest representing four contests and the smallest representing one. Figure redrawn using
 data originally published in Pomfret & Knell, 2006b.

3.5 Are beetle horns simply tools?

Beetle horns are used as weapons in contests, usually between males. There is strong evidence that animals with larger horns tend to win contests and, in some species at least, horn size is more important than body size in determining the outcome of fights. These facts lead us to ask whether beetles with longer horns win their fights because their larger horns are tools that in some way enable them to do so, or whether they win because of some other aspect of their biology that the horns are correlated with. In the latter case, the horns might be functioning to transmit information about the bearer's fighting ability to opponents rather than enabling the bearer to beat an opponent by mechanical means.

I would suggest that beetle horns carry out both functions. Observations of fights between horned beetles, and a consideration of the functional morphology of beetle horns, can lead to little doubt that the horns of many of these animals are used actively in contests to push, pry and lift opponents. In the case of beetles such as *P. difformis*, which uses its cephalic horn to lift opponents (Rasmussen, 1994), a longer horn will enable a male to get his horn into position beneath the body of an opponent, while the shorter-horned opponent is unable to do so, and this may also allow greater leverage to be applied while the opponent is lifted. When considering beetles with multiple horns that fight in tunnels, long pronotal horns can hold a less well-endowed opponent at a distance and allow a cephalic horn to be used against an opponent which is unable to retaliate.

Many dung beetle horns clearly function as tools, therefore, but it is questionable whether all of them do. The horns carried by major males of *O. taurus*, for example, are used in combat and engage with the opponent's pronotum, but whether a longer set of horns provides much mechanical advantage to the carrier is questionable. The males are in contact not only through the horns but also through the head, and it is likely that this is where the majority of the force used to push the opponent is transmitted, rather than through the slender and somewhat flexible horns. Similar questions can be raised about the horns of many other beetles, an obvious example being *O. rangifer* (Fig 3.1J). It is hard to imagine how such long and delicate structures would make effective weapons. In this case, at least, the use of the horns more as signalling structures than weapons has to be considered a possibility.

Evidence is starting to accumulate that horn length is correlated with other traits that will influence fighting ability. In *E. intermedius*, horn length is a better predictor of maximal strength and endurance than body size – both traits that have an obvious connection to fighting ability (Lailvaux *et al.*, 2005). In *O. taurus*, maximal strength is also correlated with horn length once body size has been controlled for, although this relationship is dependent on the animal's condition, with males in poor condition having low strength no matter what their horn length (Knell & Simmons, 2010).

Furthermore, horn length in *E. intermedius* is also correlated, independent of body size, with immunity (Pomfret & Knell, 2006a – see also Cotter *et al.*, 2007, for a study of immunity and morph in *O. taurus*) and, interestingly, with weight gain following eclosion (M. Head & R. Knell, in prep.). The weight gain result is particularly interesting because horn length is determined during metamorphosis, before the maturation feeding period. A possible explanation of these data is that

1 ~~these~~ beetles differ physiologically in their ability to assimilate food both as larvae
2 and adults. Horn length is influenced by larval feeding or digestive efficiency, which
3 co-varies with adult assimilation efficiency, so horn length co-varies with the
4 animal's weight gain during maturation.

5 Finally, it has been suggested that in one case at least, horns might act as visual
6 signals. Most horned dung beetles interact in dark tunnels, so their horns are
7 unlikely to act as visual signals, but, as we have seen, beetles from the Phanaeini
8 frequently interact above the ground and are diurnal (Price & May, 2009). These
9 animals are often brightly coloured and iridescent, and the horn is often a darker
10 colour than the bright pronotum behind it.

11 Vulinec (1997) demonstrated strong ultraviolet (UV) reflectance from the
12 pronotum in frequencies visible to insects, and suggested that the bright pronotum
13 silhouettes the dark horn, creating a powerful visual signal that could potentially
14 be important in both intrasexual contests and in mate choice. As we will see in
15 Chapter 9 of this volume, dung beetles have acute visual sensitivity and there is
16 little reason to reject outright the idea that this sensitivity might not be brought to
17 bear of on the problem of mate and/or competitor assessment. Neither of the
18 detailed descriptions of intra- and intersexual interactions between such beetles
19 includes any behaviour that could be a visual display (Otronen, 1988; Rasmussen,
20 1994) but, in both cases, the majority of observations were made of animals
21 interacting in tunnels.

22 23 24 **3.6 The evolution of horns: rollers vs. tunnellers**

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26 Some taxa of dung beetles, such as the Sysiphinae, carry no horns. In some taxa, such
27 as the genus *Phanaeus*, all of the males are horned, while in other taxa, such as the
28 genus *Onthophagus*, there is variation between species, with males of some species
29 being horned, other closely related species having hornless males, and still other
30 species having dimorphic males, some having horns and others not (see Chapters 4,
31 6 and 7 of this volume).

32 This variation does not simply reflect variation in male behaviour. Males of
33 many hornless species frequently fight with each other. For example, male
34 *Kheper nigroaeneus* make very large, smooth brood balls that are likely to play
35 a role in attracting females, and they frequently fight with other males
36 for possession of these brood balls (Ybarrondo & Heinrich, 1996); male *K.*
37 *platynotus* fight to defend females while mate guarding (Sato & Hiramatsu,
38 1993). So why have these beetles not evolved horns? To answer this question, we
39 have to consider the evolutionary costs and benefits that these structures bring;
40 horns should only evolve when the fitness gains from their possession are greater
41 than the costs.

42 Growing horns is known to impose a cost on the bearer because resources that
43 could be used in the growth of other body parts are required to build the horn
44 (Emlen, 2001; Moczek & Nijhout, 2004; Simmons & Emlen, 2006). Emlen (2001)
45 compared three species of *Onthophagus* with horns arising from different locations
46 and showed that large horns were associated with reduced sizes of organs close to
47 the horns. Thus, in *O. sharpi*, which has a horn located on the front of the clypeus,

1 males with large horns have relatively small antennae, and in an unidentified species
2 of *Onthophagus* from Ecuador that has horns at the rear of the head, males with
3 large horns have relatively small eyes.

4 More recent experimental work has shown that these trade-offs are not restricted
5 to organs close to the horns. *O. taurus* males which had the precursor cells that
6 would grow into genitalia ablated while they were still larvae were found to grow
7 larger horns (Moczek & Nijhout, 2004), while *O. nigriventris* males which were
8 similarly prevented from developing horns grew to a larger size and developed
9 larger testes (Simmons & Emlen, 2006) Chapters 4 and 7 of this volume provide
10 detailed discussions of such resource allocation trade-offs.

11 The possession of horns can also reduce the speed or manoeuvrability of the
12 owner in tunnels (Madewell & Moczek, 2006; Moczek & Emlen, 2000), although
13 not in every case (Pomfret & Knell, 2006b). It is likely that large horns have adverse
14 effects on other aspects of the bearer's biology, such as flight ability.

15 These costs will be similar across all species, but the benefits arising from the
16 possession of horns will vary between species, depending on the details of each
17 species's breeding and feeding biology. One of the most important variables
18 determining the benefits of horns appears to be whether the contests between
19 males occur in tunnels or in the open.

20 Most modern dung beetles use either a 'rolling' or a 'tunnelling' strategy to
21 reduce the intense competition for resources that occurs in dung (Hanski and
22 Cambefort, 1991; see Chapters 1 and 2 of this volume). The tunnellers excavate
23 burrows directly beneath the dung and then drag dung down, whereas rollers
24 carve pieces from dung pats, shape them more or less into balls and roll them
25 away. Early workers thought that these two strategies had only evolved once, and
26 that the dichotomy between rollers and tunnellers was a fundamental division
27 within the phylogeny of the Scarabaeinae. However, recent phylogenetic work
28 indicates that tunnelling was the ancestral behaviour in these animals and that ball-
29 rolling behaviour has evolved independently several times (see Chapter 2 of this
30 volume).

31 Emlen & Philips (2006) mapped the presence or absence of horns onto the
32 phylogeny used for this work and tested for correlated evolution of horns and the
33 behaviour used to sequester dung (tunnelling or rolling). The analysis indicated that
34 horns have evolved eight times within this phylogeny of 46 species from 45 genera,
35 and each gain of horns occurred within a tunnelling, rather than a ball-rolling,
36 lineage (Figure 3.4). This indicates that the method used by beetles to sequester
37 dung for food and breeding has an important influence on the evolution of horns,
38 with horns apparently evolving only in tunnelling beetles.

39 The reason why this should be is probably that the tunnelling habit has the effect
40 of making resources more defensible (Emlen & Philips, 2006). Male beetles
41 defending tunnels will encounter opponents one at a time and will be able to
42 completely exclude weaker beetles. This will bring greater fitness benefits to
43 beetles carrying horns than would be the case for male beetles such as *Kheper*,
44 which guard resources such as brood balls above ground for a period before
45 burying them (see Chapter 5 of this volume). These will find it much harder to
46 exclude rivals and they will also be open to challenges from more than one
47 challenger at a time.

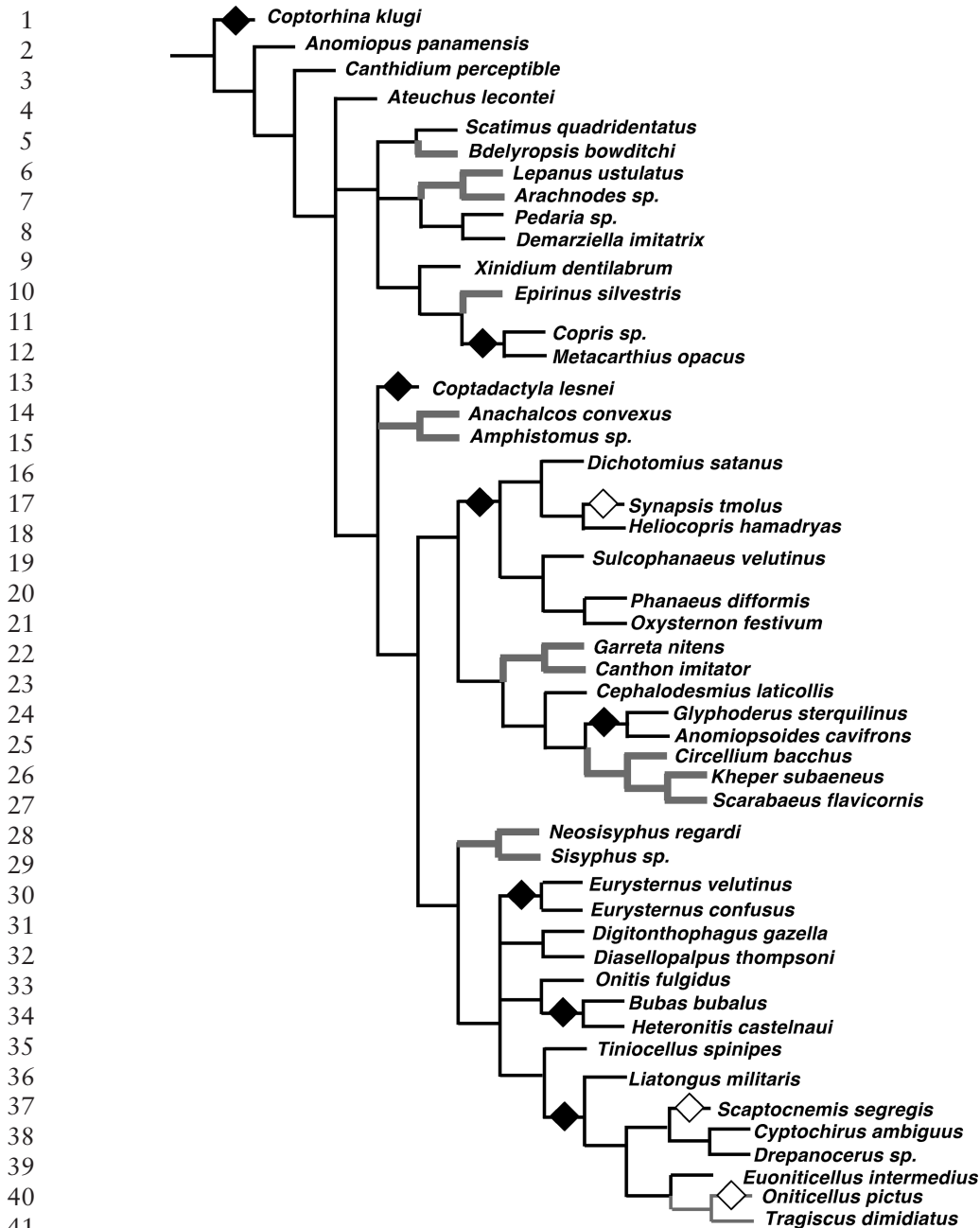


Fig. 3.4 Phylogeny of 45 species of dung beetles. Tunnelling is the ancestral behaviour, indicated by narrow branches. Non-tunnellers either breed directly within a dung pat ('dwellers'), indicated by wide grey lines, or roll balls of dung (wide grey branches). Evolutionary losses and gains of horns are indicated by open and closed diamonds respectively. All eight gains of horns occurred on 'tunnelling' branches and one of the three losses of horns occurred on a non-tunnelling branch. Redrawn from Emlen *et al.* (2006) with permission.

3.7 The evolution of horns: population density

The dichotomy between tunnellers and rollers seems to explain the larger-scale patterns in the occurrence of horns within the Scarabaeinae, but the smaller-scale patterns remain to be explained. Within some tunnelling lineages there are hornless species; five of the 48 species of *Onthophagus* considered in the phylogeny described in Emlen *et al.* (2005b) were reported as hornless, and five of the 14 species of *Onthophagini* studied by Pomfret & Knell (2008) were hornless. To explain these patterns, we must look to other ecological factors, a number of which have been put forward as potentially being important in determining the strength and nature of sexual selection (Emlen & Oring, 1977; Hamilton, 1979). These include the spatial distribution of resources; the temporal distribution of receptive females; the operational sex ratio (OSR); and population density (Emlen & Oring, 1977). Of these, population density and OSR have been studied specifically in dung beetles.

If males are competing among themselves for access to females, then, as population density increases, the strength of sexual selection should also increase. This is because contact rates between and within sexes will increase, potentially leading to increased reproductive skew within the male population as high-quality males have greater opportunities to monopolize access to females (Emlen & Oring, 1977; Knell, 2009b; Kokko & Rankin, 2006).

This might lead us to expect aggression to increase with population density, so that individuals carrying weaponry would experience increased fitness as density increases. However, empirical studies of male fitness and density have reported both increased and reduced fitness of aggressive males at high densities from different systems, indicating that the relationship between selection for aggression and density is in fact likely to be more complex than a simple increase with density (Knell, 2009 and references therein).

When a species occurs at low densities, males will find it difficult to locate mates and, when they do, they are unlikely to encounter rivals when they make contact. Investment into adaptations to aid in movement and the location of mates will thus bring greater fitness benefits than will investment in weaponry. As density increases, however, it will become easier to locate mates and the probability of encountering a rival male will increase, so aggressive males that invest in weaponry are expected to have increased fitness. As density increases further, however, aggressive males that guard females will be forced to spend an increasing amount of time and energy engaging in costly fights, and they will be more likely to encounter a superior competitor who will beat them and take over the resource.

A further cost to aggression will arise because the risk of sperm competition will increase with density. A given female will be more likely to have already mated before she is encountered by a particular male, and is more likely to re-mate with a rival male relatively quickly. Those resources that are invested in adaptations to increase the probability of winning fights, such as muscles and weapons, will not be available for traits that improve fitness under sperm competition, such as large testes (Knell, 2009). Studies of dung beetles have elegantly illustrated this latter point: male *O. nigriventris* that were manipulated to stop them growing horns grew relatively larger testes, indicating a trade-off between the resources available for

1 these traits (Simmons & Emlen, 2006; see Chapter 4 of this volume). Thus, the costs
2 of aggression will increase for several different reasons with density:

- 3
4 • aggressive males will pay higher costs in terms of energy, time and the risk of
5 injury because they will be fighting more often;
6 • they will lose more contests, simply because they will be engaging in more of
7 them;
8 • they will not perform well in sperm competition.
9

10 The costs of aggression, therefore, will increase as density gets higher, but the
11 benefits might not – especially in a system where males guard only one female at a
12 time, thereby limiting the degree of reproductive skew possible. At a high enough
13 density, the costs of aggression will outweigh the benefits. Hence, males that use
14 ‘scramble’ tactics, whereby they simply try to find unguarded females to mate with,
15 or that use ‘sneak’ tactics, trying to acquire matings with females who are being
16 guarded by somehow bypassing the guarding male, will have a higher fitness than
17 aggressive males that guard females (Knell, 2009).

18 This has yet to be demonstrated by direct behavioural observations in dung
19 beetles, but a study of the forked fungus beetle (*Bolitotherus cornutus*), a horned
20 tenebrionid that is found on polypore shelf fungi in the Eastern part of North
21 America (Connor, 1989), showed that longer-horned males gained a greater fitness
22 advantage in low-density populations than in high-density ones. Horn length was
23 positively correlated with the number of mating attempts per hour in the low density
24 populations only. Connor (1989) notes that in the low-density populations there is
25 usually only one male with long horns per fungus, suggesting that these males are
26 able to monopolize resource patches at low densities but not at high densities.

27 Evidence for a role of population density in the evolution of dung beetle horns
28 comes from both inter- and intraspecific studies. The latter have made use of the
29 dimorphisms that are well known in many species of *Onthophagus*, with ‘minor’
30 males that express reduced or no horns employing ‘sneak’ tactics, and horned
31 ‘major’ males aggressively guarding females (Eberhard & Gutierrez, 1991; Emlen,
32 1997a; see Chapter 6 of this volume). Within a population of males, the smaller
33 males tend to develop into minors and the larger ones into majors. These dimorph-
34 isms are believed to evolve via a process of ‘status-dependent selection’ (Tomkins &
35 Hazel, 2007), whereby small (i.e. low-status) males benefit little from competing
36 aggressively and instead pursue alternative tactics that gain them higher fitness
37 (Hunt & Simmons, 2001).

38 The proportion of the population developing into each morph is known to
39 respond to selection (Emlen, 1996), and in field populations we can draw inferences
40 about the relative fitness benefits of aggressive (majors) versus non-aggressive
41 (minors) tactics from this proportion. If the majority of the male population
42 develop into majors, for example, this implies that aggressive tactics are relatively
43 beneficial; smaller males that aggressively guard females have been selected over
44 similar-sized ones that did not. The reverse situation, with only a few males
45 developing into majors, indicates the opposite; the relative fitness benefits of
46 aggression are small, and only the largest males have historically been able to
47 acquire higher fitness by the use of these tactics.

1 One of the best studied of these dimorphic beetles is *O. taurus*. Originally found
2 in the Mediterranean region, in the 1960s and 1970s the beetle was introduced to
3 both Eastern (EA) and Western Australia (WA) and to the Eastern United States, and
4 there are now established populations in all three areas. Moczek *et al.* (2002)
5 measured the relationship between horn length and body size in beetles from the
6 latter two regions, and found that proportionally fewer male beetles from the WA
7 population develop into majors, with some intermediate-sized males that would
8 develop into majors in the Eastern US population developing instead into minors in
9 the WA population. This difference persisted even when beetles were reared in the
10 laboratory under identical conditions for several generations, suggesting that these
11 populations had diverged genetically (see Figure 7.3 in Chapter 7 of this volume).

12 A further study compared beetles from all three populations (Moczek, 2003) and
13 found that the EA population produced a proportion of major males intermediate
14 between the two other populations. Moczek discussed a variety of possible
15 explanations for the differences between these populations, including differences
16 in density of conspecifics, differences in the density of competitors from other
17 species, differences in body size and differences in sex ratio. Of these, only the
18 density of conspecifics followed the pattern that would be predicted if it were the
19 cause of the differences in the proportion of majors; the density of Eastern US
20 populations was substantially less than that of the EA populations, which were
21 themselves considerably less dense than the WA populations. This is not in itself
22 strong evidence that high population density selects against aggressive strategists,
23 and therefore against horned males. Moczek (2003) points out that these data are
24 from three populations only, and that the relationship shown is correlational, but
25 nonetheless it is certainly suggestive.

26 For further evidence for a role of population density, we must look to interspecific
27 studies. Firstly, Emlen *et al.* (2005b) scored beetle species as abundant, rare or
28 intermediate in their study of 48 species of *Onthophagus*. Abundant beetles were
29 those known to occur at high densities, that are found in most dung pats and that
30 museum collections often have many specimens of; rare species were those that are
31 only rarely encountered in the field and that are usually poorly represented in
32 museum collections. Both horn length and horn number proved to be significantly
33 correlated with increases in population density, apparently contradicting the
34 conclusion from Moczek's work.

35 Additional analysis showed that the increase in horn number with density was due
36 to an increased probability of gaining thoracic horns in the most abundant lineages.
37 Emlen *et al.* (2005b) suggested that this might arise because of resource allocation
38 trade-offs between horns and nearby organs and structures, occurring in the
39 individual animal during metamorphosis. It might be the case that thoracic horns
40 trade-off against wings more than other parts of the animal because these two
41 structures are physically close (Emlen, 2001). If this so, then because male beetles in
42 these abundant lineages are likely to have to fly less in order to find mates, they
43 might gain less fitness from large wings than they do from thoracic horns.

44 Emlen *et al.*'s study compared beetles from all over the world and from a variety
45 of habitats. Pomfret & Knell (2008) studied a single community of Onthophagine
46 beetles in a single savannah habitat in South Africa over two years. Rather than a
47 simple measure of population density, they calculated Lloyd's mean crowding

(Lloyd, 1967) for each species of beetle, a measure that takes into account not only numbers but also aggregation, to give an estimate of the number of conspecifics that an individual is likely to encounter at a particular patch.

Of 14 Onthophagini species that were present in both years, five were hornless. Analysis using a generalized least-squares model, incorporating a phylogeny derived from sequences of the mitochondrial COX1 gene, indicated that both mean crowding and OSR were correlated with the presence or absence of horns. Males from beetle species that had female-biased sex ratios were less likely to carry horns, while males from species that had lower estimates for mean crowding were more likely to carry horns (Figure 3.5).

These two interspecific studies that have considered the role of density or crowding in the evolution of beetle horns have thus returned contradictory results. As discussed above, it has been proposed that the selective advantage of weaponry should first increase and then decrease as population density increases (Knell, 2009). One possibility therefore, is that these two studies have captured two different parts of the overall picture, with the evolutionary gains of horns associated with increasing density described by Emlen *et al.* (2007) being a reflection of increases from low to moderate densities, and the losses of horns at high densities described by Pomfret & Knell (2008) reflecting increases from moderate to high densities. This simple explanation can, however, be discounted, because most of the relevant gains of horns in the Emlen study were associated with increases from moderate to high population densities rather than with increases from low to moderate.

It must also be remembered that these are studies operating at very different scales: the Pomfret & Knell study considered animals coexisting in a single habitat and used a direct measure of population density, whereas the Emlen study used animals from a range of habitats and used a rather indirect measure of density.

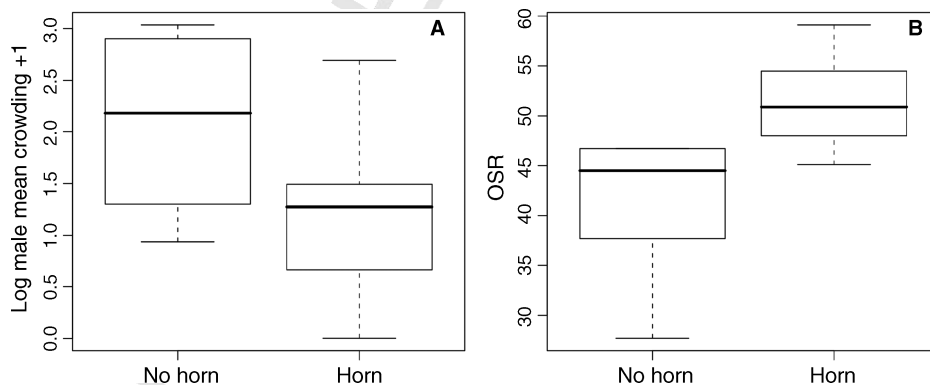


Fig. 3.5 Density and operational sex ratio (OSR) compared between horned (9 species) and hornless (5 species) of Onthophagini sampled at one location in South Africa. **A:** Log mean crowding + 1 of males, a measure of population density. **B:** OSR. For both plots, the bold line is the median, the box is the interquartile range, and the whiskers extend to the furthest data point less than 1.5 times the interquartile range from the box. Originally published in Pomfret & Knell (2008).

1 A further point to note is that the gains of horns that Emlen *et al.* found to be
2 associated with high densities were almost all gains of thoracic horns, while none of
3 the species included in the South African study carried horns of any size on the
4 thorax. This makes direct comparison of the results difficult.

5 For the moment, it is probably best to conclude that interspecific studies support
6 an important role for population density in the evolutionary gains and losses of
7 horns in this genus, but that this role might be complex and dependent on other
8 environmental variables as well.
9

10 11 **3.8 The evolution of horns: sex ratio**

12
13 The operational sex ratio (OSR), calculated by dividing the number of sexually
14 active males by the sum of the number of sexually active males and the number of
15 receptive females, is well known as an important determinant of the strength of
16 sexual selection and has been shown to be influential in mating system evolution in a
17 variety of taxa (Emlen & Oring, 1977; Kvarnemo & Ahnesjö, 1996; 2002). This is
18 because a skewed OSR will increase competition for mates among the more
19 common sex. Female fitness is not strongly correlated with the number of matings
20 achieved but male fitness is; therefore, a female-biased OSR is expected to lead to a
21 general relaxation of sexual selection unless males are extremely rare (Jiggins *et al.*,
22 2000) but a male-biased OSR will lead to increased competition between males and
23 an increase in the strength of sexual selection.

24 In dung beetles, sex ratio has been examined in two studies. First, Moczek (2003)
25 measured the sex ratio of the three populations of *Onthophagus taurus* mentioned
26 in the discussion of population density. The population was found to be most male-
27 biased in Western Australia, which has the lowest proportion of major males, and
28 most female-biased in the Eastern US population, which has the highest proportion
29 of majors. This might at first seem to go against the accepted wisdom that male-
30 biased sex ratios lead to stronger sexual selection but, as with population density,
31 this can be resolved if we consider that aggression might not be the optimal strategy
32 when competition is fierce. If horned males are unable to defend females effectively
33 in the presence of large numbers of competitors, then it is possible that, in the case
34 of *O. Taurus*, sex ratio is acting in concert with population density to select for
35 males that are less likely to develop into majors in the Western Australian
36 populations.

37 Pomfret & Knell (2008) measured OSR as well as crowding for the community of
38 South African beetles discussed earlier. OSR, rather than the simple sex ratio, was
39 estimated by excluding beetles that were 'callow' and therefore undergoing
40 maturation feeding. In this study, OSR was found to be an important predictor
41 of the presence or absence of horns, with female-biased sex ratios being associated
42 with the hornless condition (Figure 3.5). In this case, therefore, horned species were
43 more likely to have low levels of crowding in even or slightly male-biased sex ratios,
44 whereas hornless species were likely to have high levels of crowding and female-
45 biased sex ratios. These results are at odds with the intraspecific study of Moczek
46 (2003), so clearly more work is necessary to disentangle the effects of population
47 density and sex ratio on the evolution of dung beetle horns.

3.9 Future work

Research on horned beetles has made important contributions to our understanding of the evolution of weaponry in the animal kingdom. We have moved from asking what is the function of the horns to questions regarding their costs and benefits and their extraordinary diversity. In this review, the need for further work on questions such as the role of ecological factors in horn evolution, whether some horns are used as signals rather than weapons, and how horn size is linked to aspects of male quality, has already been highlighted. In the final section of this chapter, I will call attention to some further questions that are of interest but that have not so far received much attention from researchers.

First, what drives the evolution of elaborate horn morphology? The question of whether some of the more slender horns are used as weapons or as signals has already been raised. A separate question is how the elaborate forms of some of the more robust horns, for example those carried by male *O. imperator* (Figure 3.1E), are used and why they have evolved. Some other animal taxa, such as the cervids, carry weapons of similar diversity and complexity (Emlen, 2008), and researchers working on these groups have shown that some of this diversity can be ascribed to differences in mating systems and to the way the animals fight (Brø-Jørgensen, 2007; Caro *et al.*, 2003).

However, it has also been suggested that an advantage to novel structures in contests might also be a driving force leading to weapon diversity (Emlen, 2008; West-Eberhard, 1983). If the extra tines and notches that are often found on the horns of dung beetles give the beetle some mechanical advantage during fights with opponents who do not have them then, as pointed out by Emlen (2008), this could lead for selection for novelty, which would lead to evolution down species-specific arbitrary pathways. This is an attractive theory that could explain much about the patterns of diversity seen in animal weaponry, but it is yet to be tested. Horned dung beetles would appear to be ideal model organisms with which to investigate this issue further.

Second, a related question is why horn morphology in some taxa is so variable, while in others it is not. In *Heliocopr* and *Onthophagus*, for example, the horns are highly variable in number, morphology and location (Figures 3.1D, F and H, and Figures 3.1A, E, I, and J respectively). In genera such as *Oxysternon*, *Phanaeus* and *Copris*, by contrast, all horned males carry a single, curved cephalic horn (although pronotal structures can vary between species). Why have the horns of these latter taxa not diversified morphologically? As discussed earlier in the chapter, we have a number of good descriptions of the use of these horns, which are inserted beneath a rival and used to lift him (Beebe, 1947; Eberhard, 1977; 1979; Otronen, 1988; Rasmussen, 1994). The advantage that might be gained by the addition of novel parts to a weapon that was speculated about in the previous paragraph does not apply to this particular model of horn; the long, slender and slightly curved form could be the best design for this function, so any additions to it might detract from its usefulness.

Finally, why do beetles in some taxa tend to lose their horns while other taxa are all horned? This is exemplified by comparing *Onthophagus* with *Phanaeus* and *Copris*. As has already been noted, all male *Phanaeus* and *Copris* beetles carry a

1 single cephalic horn, whereas in *Onthophagus* a substantial minority of species are
2 hornless. Why, then, do some *Onthophagus* species lose their horns, while *Phanaeus*
3 or *Copris* species may develop smaller horns but do not seem to lose them
4 altogether?

5 A possible answer may lie in their breeding biology. Both of these genera have low
6 fecundity and high investment per offspring, possibly even more so than other
7 scarab genera such as *Onthophagus*. *Phanaeus* males can show long periods of pre-
8 copulatory mate guarding and will also cooperate with females to build nesting
9 burrows and construct brood balls (Halffter & Edmonds, 1982; Price & May,
10 2009), and *Copris* females construct nests, often with male assistance, containing
11 only a few brood balls and care for them until adult emergence (Halffter &
12 Edmonds, 1982). Given that these males need to make a substantial investment
13 in time before gaining a mating, it could be that the costs of losing a fight and
14 allowing another male to mate with a female shortly before oviposition are high in
15 comparison with genera like *Onthophagus*.

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