



Sexual selection and horn allometry in the dung beetle *Euoniticellus intermedius*

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Secondary sexual characters are often positively allometric, such that larger individuals of a species have proportionally larger traits. The sexually selected weapons found on many insect species, however, show declining allometric slopes with body size. Previous work on these curved allometric relations has focused on the role of competition for limited resources between growing body parts within pupae, but there is an alternative explanation that has received little attention: changes in the allometric slope may reflect changes in the fitness benefits associated with increases in horn size and body size change as an animal gets larger. The allometric curve of the horn of the male dung beetle *Euoniticellus intermedius* shows one of the largest declines in slope known and by setting up contests between males of similar, or different, sizes over access to females we were able to investigate the importance of horn and body size for males of different sizes and horn lengths. Both body size and horn size were important in determining contest outcome in small males, but horn size became more important as body size increased, so that in contests between large males it was by far the most important predictor of victory. These findings are consistent with theoretical predictions of how fitness functions can affect allometry and offer an alternative to some of the previous verbal arguments made to explain positive allometry.

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The way that individual organs or other parts of animals scale with body size (allometry) is a subject that has been of interest to biologists for many years. One of the more robust patterns in these scaling relationships is the positive allometry that sexually selected traits tend to show (Gould 1973; Alatalo et al. 1988; Petrie 1988, 1992; Green 1992; Simmons & Tomkins 1996; Knell et al. 1999; Emlen & Nijhout 2000; Palestini et al. 2000; Baker & Wilkinson 2001). Positive allometry, meaning that larger individuals have proportionally larger traits than smaller individuals, is defined as a value greater than one for the exponent k in the equation relating organ size to body size, $y = bx^k$, where y is organ size and x is body size (Huxley 1932; Gould 1966; Simmons & Tomkins 1996; Knell et al. 1999; Emlen & Nijhout 2000; Baker & Wilkinson 2001). Negative allometry, where the value of k is less than one means that larger individuals have proportionally smaller traits than smaller individuals and isometry means that k is equal to one and relative trait size does not change with body size.

Positive allometry has been described in many sexually selected traits from a variety of animals, including the antlers of deer (Huxley 1932), the antlers of the extinct giant deer, *Megaloceros giganteus* (Gould 1973), the tails of a number of bird species (Alatalo et al. 1988), the crest of the great crested newt, *Triturus cristatus* (Green 1992), the eye stalks of flies from the family Diopsidae (Wilkinson & Dodson 1997; Knell et al. 1999; Baker & Wilkinson 2001) and the forceps of earwigs (Dermaptera; Simmons & Tomkins 1996). Not all secondary sexual traits are positively allometric, however; Bonduriansky & Day (2003) discussed a number of examples of isometry or negative allometry in such traits, and in the insects there is a wide range of nonlinear allometries known in sexually selected traits (Emlen & Nijhout 2000).

Most explanations for the relatively large sexually selected traits carried by larger animals rely on the increasing benefits and decreasing costs of possessing an enlarged secondary sexual character as overall size increases (Petrie 1988, 1992). In the case of traits used in intrasexual contests, if the outcome of competitive interactions is dictated by body size (Otte & Stayman 1979), then larger individuals will benefit from displaying a large structure, because this could act to reduce the number and intensity of fights in which they are involved (Clutton-

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Brock 1982). Furthermore, since these traits are assumed to be costly and condition dependent small individuals that are of a lower quality may be prevented from producing large traits (Zahavi 1975). Small individuals may also invest fewer resources because there are few benefits to a structure that advertises low competitive ability (Petrie 1988).

It has been argued that traits used in female choice should be positively allometric for the same reasons; small individuals would not benefit from, and may not be able to invest in, secondary sexual characteristics (Green 1992). It has also been suggested that the steepness of the allometric slope is determined by the degree of sexual selection experienced by males, with species under more intense sexual selection having steeper allometries because it will profit the larger males to signal more where there is more competition (Simmons & Tomkins 1996).

Bonduriansky & Day (2003) attempted to give these arguments a more formal theoretical footing by using allocation trade-off models to predict the allometric slopes of sexually selected traits against body size under different selection regimes. Their model suggests that positive allometry will result only under certain restricted conditions. Specifically, positive allometry will evolve only if fitness is related to body size by an increasing function with diminishing returns, and to trait size by an increasing function without diminishing returns. This is because in this situation, smaller males will gain more from investing in body size, but larger males will enhance their fitness more by preferentially investing in trait size. This is similar to the verbal argument proposed by Green (1992). In contrast to the predictions from Green's verbal argument, however, if fitness depends on trait size alone, independent of body size (e.g. a courtship signal), or on the ratio of trait size to body size, then Bonduriansky & Day's model predicts that isometry will evolve because the optimal trait size across all body sizes is constant, and all males of all sizes should invest maximally in trait expression.

We describe here a study of allometry and sexual selection in the horned dung beetle, *Euoniticellus intermedius*. The male has a slightly curved blunt horn on its head, and the pronotum is sexually dimorphic, being enlarged into a forward-projecting hump (Blume 1984). *Euoniticellus intermedius* feeds on mammal dung. Once sexually mature a female beetle burrows into the soil beneath the dung pat, dragging dung down and creating a hollow ball of dung (the 'brood ball') into which she lays an egg. The egg hatches into a larva after about 2 days and the adult emerges after about a month (Blume 1984; J. Pomfret, personal observation). Male beetles guard and mate with females inside the tunnels dug by the latter. A male that is resident in a tunnel will fight with any intruding male competitors. Studies of other horned beetles with similar life histories have found that the males use their horns in these fights (Otte & Stayman 1979; Eberhard 1978; Rasmussen 1994; Emlen 1997; Emlen & Nijhout 2000).

The horns of *E. intermedius* show a curved allometric relationship, with positive allometry in smaller individuals but decreasing in slope as body size increases, so that in the largest beetles the horn is isometric or even negatively

allometric (Fig. 1). Similar curves are known from a variety of other insect taxa and are usually thought to arise from competition among growing traits within pupae for limited resources (Emlen & Nijhout 2000; Knell et al. 2004). Insect pupae do not feed, and within this closed environment rapidly growing parts can deplete the available pool of nutrients, reducing the growth rate of developing structures. The structures most affected by this process are likely to be the largest ones. For this reason, competition among body parts may be especially relevant for sexually selected traits (which are often very large), and for the largest individuals within populations (which produce the largest versions of these traits). In this situation, trait competition could lead to a decrease in the slope of a trait size/body size allometry as body size increases, resulting in a curved rather than a linear trait allometry (Nijhout & Wheeler 1996). Such a situation may be the cause of curved mandible allometries in stag beetles, where a recent comparative study showed a strong influence of relative mandible size on the curvature of the allometric relationship (Knell et al. 2004). It may also partly explain the decline in slope in *E. intermedius*. However, the horns of *E. intermedius* are not especially large relative to their body size, suggesting that the effects of competition for pupal nutrients may be less important. Furthermore, the amount of allometric curvature in *E. intermedius* is greater than that found in other beetles with much larger weapons (see Results and Discussion). We investigated a second possible mechanism that could lead to changes in allometric slope: a change in the fitness consequences of horn size associated with body size.

In contrast to the horn, the sexually dimorphic pronotum of these beetles is isometric. The role of the enlarged pronotum in intrasexual contests has not been documented, and we included pronotum length in our investigations to clarify this and to explore further the relationship between male competitive ability and morphology.

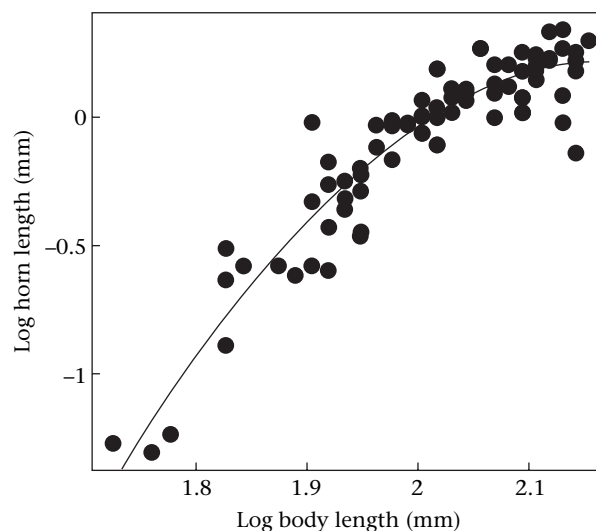


Figure 1. Allometry of horn length for male *E. intermedius*. The line is a fitted second-order polynomial ($Y = -7.96X^2 + 34.68X - 37.55$, $r^2 = 0.90$).

The models of Bonduriansky & Day (2003) predict that different patterns of allometry can arise from different functions relating trait and body size to fitness, and this may explain the changes in allometric slope seen in this beetle. Our aims in this study were therefore to determine whether horn and pronotum length are important in competitive success and, if they are, whether their importance changes as body size increases and the allometric curve for horn length changes from positive to negative allometry.

METHODS

Culture of Experimental Animals

All insects used were taken from a large laboratory colony of *E. intermedius*, originally started with 100 adults collected from South Africa. Beetles were reared at 28°C and with a 12:12 h light:dark photoperiod. Males and females were kept in 1000-ml pots (two males and two females per pot) with 500 ml of damp sand and 200 ml of cow dung. Every week the contents of the pots were sieved and brood balls removed. These were separated and placed individually in containers filled with moist sand. Emerging beetles were collected after about a month and were kept in single-sex cultures until sexually mature (about 2 weeks).

Measurements of Body Parts

Body length (tip of the elytra to the front of the pronotum), pronotum length, height and width were measured (± 0.1 mm) with Vernier callipers. All measurements were made by the same person (J.P.) and the same pair of callipers was used for all measurements. Elytra length was calculated as body length minus pronotum length to give a measure of body size that was independent of the sexually dimorphic hump. To measure horn length we photographed each beetle's head from the side under a dissecting microscope and used the NIH Image version 1.62 image analysis program (developed at the U.S. National Institutes of Health and available on the internet at <http://rsb.info.nih.gov/nih-image/>) to measure horn length. To test the repeatability of these measurements we measured the first 30 beetles from the culture, then randomly reselected each of these beetles and measured it two additional times. Repeatability (measured as r , the intraclass correlation coefficient, Lessells and Boag 1987) was high for all three measurements (elytra length: $r = 0.95$; pronotum length: $r = 0.92$; horn length: $r = 0.93$).

Behavioural Experiments

In many species of *Onthophagus* beetles, males use alternative mating strategies, with small males 'sneaking' and large males guarding females (Cook 1990; Emlen 1994, 1997, 2000; Hunt & Simmons 1997; Moczek & Emlen 1999). These alternative strategies are associated with a morphological dimorphism in horn length that manifests itself as a change in the allometric slope. To test

whether male *E. intermedius* use such a range of strategies we constructed glass observation chambers, similar to those described by Emlen (1997). These consisted of two parallel panes of glass (25 × 35 cm) separated by a 5-mm-wide wooden U-frame, filled two-thirds with sand, with cow dung on top. A female was added to the observation chamber for 24 h, giving her time to build tunnels and to start manufacturing brood balls. Since the majority of interactions between beetles take place inside these tunnels, males were added only after the female had successfully dug a tunnel.

Because reproductive behaviour in these beetles had not been examined previously, and because establishing precisely where the switchpoint between tactics occurs is often problematic, we excluded intermediate-sized males from our behavioural trials. We focused instead on the behaviour of the largest (>7.9 mm body length) and smallest (<7.4 mm body length) thirds of the population body size distribution. To see how beetles behave without competition, we placed large and small males singly in a chamber with a female and recorded their behaviour for 1 h.

To test whether males show alternative behavioural strategies depending on the presence and size of a competitor, we added two males in the following combinations: large versus large, small versus small and large versus small. We recorded whether the males entered the tunnel, whether there were fights between males, which male retreated, whether the male successfully mated with the female and, after copulation, whether the male guarded the female. Guarding was when a male remained at the entrance of the female's tunnel, thus preventing other males from entering the tunnel. We also recorded whether males dug side tunnels or sneaked past the guarding male without entering into an aggressive encounter. Males that were with the female in the tunnel after 24 h were declared the winner. We chose 24 h because after this period one male was invariably with the female and the other had left the competitive arena and did not try to attempt to enter the female's tunnel again. All beetles were measured as above. Each combination was replicated 10 times.

Morphological Correlates of Contest Success

To determine the effect of horn size, body size and pronotum length on male success in contests we did a further set of experiments, as described above but without the detailed behavioural observations. Two combinations of males were used: large with large and small with small. We did not test large versus small males because the results from the previous experiment were conclusive: large males always beat small males. The male in the tunnel guarding the female after 24 h was classed as the winner. The beetles were then measured as before. Each combination was replicated 30 times.

Costs of Size

To determine how the manoeuvrability of males is affected by body size, pronotum length or horn length

(see the Discussion for justification), we timed males ($N = 54$) as they ran down a plaster tunnel that was 5 mm wide and 15 cm long. This is approximately the dimensions of the tunnels that female *E. intermedius* dig.

Data Analysis

To analyse the effects of elytra length (an independent measure of body size), horn length and pronotum length differences on obtaining a female in mate competition experiments, we selected one of the two males in each contest at random as the focal male. If the focal male was the loser, the outcome of the contest was coded as a 0, and if the focal male was the winner the outcome was coded as a 1. This coding was then entered into a generalized linear model with binomial errors and a logit link as a binary dependent variable (Hardy & Field 1998). The independent variables were the differences in the elytra length, horn length and pronotum length between the focal male and the other competitor and a factor representing the particular combination of males used in that replicate (large versus large or small versus small, referred to as 'size class' from now on), plus the interactions between each variable. Sequential removal of nonsignificant terms allowed the creation of a 'minimum adequate model' to describe the data (Crawley 1993; Hardy & Field 1998).

RESULTS

Horn Allometry

Figure 1 shows the allometric relation between horn length and elytra length. A second-order polynomial gives a significantly better fit to these data than a straight line (partial F test: $F_{3,77} = 397$, $P < 0.001$). A fitted 'breakpoint' regression whereby two straight lines are fitted with a breakpoint (Eberhard & Gutierrez 1991) gives a very similar fit to the polynomial ($r^2 = 0.89$) but we show the polynomial for two reasons: it is the simplest adequate model to explain the data, and we have no evidence for a behavioural dimorphism in this species (see below). Note that in this case, with a declining slope, the Eberhard & Gutierrez model is better than the alternative suggested by Kotiaho & Tomkins (2001). At small body sizes the horns showed positive allometry (at the smallest body length of 6 mm, or log body length of 1.79, the slope of the line is 5.36) but at larger body sizes the horns showed isometry tending to negative allometry (the line has a slope of 1 at a body size of 8.29 mm, log body length 2.11).

Behavioural Experiments

When males were alone with the female, both small and large males entered the tunnel and met the female head on. Small and large males were equally likely to guard and mate with the female (6/10 in both cases). When two large males were introduced, both males entered the tunnel and aggressive interactions occurred in most cases (9/10), with one male being pushed out and the other male remaining.

The competing males used their horns during fights, hooking them under their opponents' heads and using them to push the other males out of the tunnel. Males would also hook their horns under the heads of females in attempts to manoeuvre them. The losing males often tried to enter the tunnel again (12/20), but only directly through the entrance. No males sneaked past the guarding male without being engaged in an aggressive interaction.

In similar competitions between small males, both males again fought within the tunnel, with one male being pushed out of the tunnel after which the displaced male either left the arena or, in two cases, attempted aggressively to gain access to the female. When the competition was between a large male and a small male, aggressive interactions occurred once again in the majority of cases (9/10); in the remaining case the small male retreated immediately on contact with the large male. The small male retreated more often from aggressive interactions (7/9, but note that this is not significantly different from an equal distribution: binomial test: $P = 0.18$), but on two occasions both males retreated. When there was a winner it was always the large male (8/8; binomial test: $P = 0.004$, or $P = 0.043$ for all contests, including the two with no clear winners). Once the smaller males had retreated from the tunnel they again either left the arena or tried directly to enter the tunnel and were again involved in aggressive interactions with the guarding male (2/10). No sneaking behaviour by smaller males was seen. In all cases the males that won after 1 h were still with the female after 24 h.

Morphological Correlates of Contest Success

Table 1 gives the fitted minimal adequate model for contests between males. Four interaction terms were significant, and the presence of the size class factor in three of these indicates that the importance of the three morphological parameters involved in determining victory in contests with other males of a similar size changes depending on whether the males in question are from the smaller or the larger thirds of the population.

The elytra length difference * size class interaction term is the simplest to interpret. When small males competed, there was a strong effect of elytra length, with males with longer elytra (i.e. larger males) being considerably more likely to win contests (Fig. 2a). When large males competed, on the other hand, there was a weaker effect in the opposite direction: males with longer elytra were somewhat less likely to win contests (Fig. 2b).

The relations between contest victory and pronotum length, horn length and size class are more complex. The three significant two-way interactions between these variables are best visualized by plotting the fitted response surface from the model for pronotum and horn length differences separately for the two size classes. Victory in contests between small males was determined by a combination of both horn length and pronotum length, with the highest probability of victory being predicted for beetles with both longer horns and longer pronotums (Fig. 3a). This contrasts with the surface shown in Fig. 3b: in contests between large beetles the difference in horn

Table 1. Results of fitting a generalized linear model with binomial errors and a logit link to predict success in contests between small males and between large males

Variable	Estimated coefficient	SE	df	Change in deviance when variable removed	P
Intercept	-1.49	0.73			
Difference in elytra length (E, mm)	-5.38	3.26			
Difference in horn length (H, mm)	31.26	12.30			
Difference in pronotum length (P, mm)	-3.63	3.32			
Size class (S)	1.28	0.95			
P*H interaction	43.99	18.17	1	6.47	0.011
H*S interaction	-23.55	12.37	1	4.95	0.026
P*S interaction	14.90	6.48	1	6.88	0.009
E*S interaction	15.57	5.51	1	11.98	<0.001
E*H interaction			1	0.19	0.66
P*E interaction			1	0.07	0.79
E*H*S interaction			1	3.15	0.076
E*P*S interaction			1	3.41	0.065
H*P*S interaction			1	0.58	0.45
E*P*H interaction			1	0.07	0.80

The full model in each case consisted of the three continuous main effects (elytra length difference, horn length difference and pronotum length difference), plus a factor indicating the type of contest (large versus small or small versus small, referred to here as size class), plus all interaction terms. All main effects and significant interaction terms are shown, and the change in deviance used to determine statistical significance represents the change in the fit of the model when the variable in question was removed, as described in Crawley (1993). Significance tests for main effects that already feature in a significant interaction term are not given (Crawley 1993), and the estimated coefficients for terms containing the size class factor are those for the small beetle class. The deviance of the final minimal adequate model was 41.77. Number of contests in each size class was 30.

length between the two combatants was by far the most important predictor of victory. Relative pronotum length changed the steepness of the relationship, such that the benefit of a longer horn was greater when the beetle also had a longer pronotum, but horn length was clearly the principal morphological predictor of victory. In contests between large males, the probability of winning increased with the difference in horn length (Fig. 4).

To determine the relative importance of the three morphological variables in contest resolution and to explore further the differences between the size classes, we fitted the model to the data for the two combinations of males separately, with the three morphological parameters standardized by subtracting the mean and dividing by the standard deviation. For contests between large males this gave estimated regression coefficients \pm SE of 2.16 ± 1.11 for horn length difference, -0.957 ± 0.645 for elytra length difference, -0.033 ± 0.867 for pronotum length difference and -0.11 ± 1.22 for the pronotum * horn length difference interaction. This shows that of the variables that we measured, horn length difference was by far the most important determinant of contest

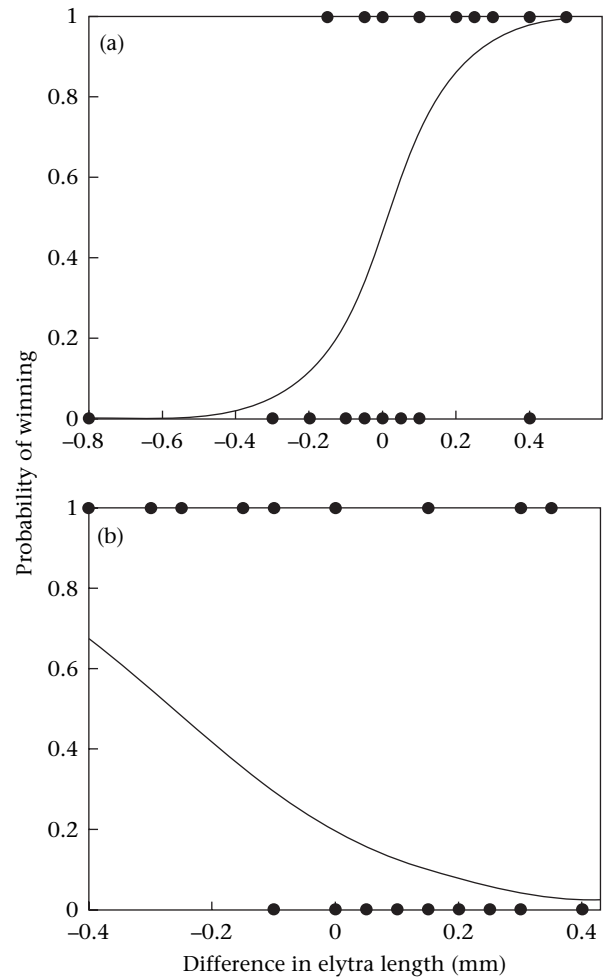


Figure 2. The relation between the difference in elytra length between competing males and their probability of victory. (a) Contests between small males; (b) contests between large males. The line is the fitted probability of winning from the model given in Table 1 with all variables apart from size class and elytra length difference set to zero.

outcome among large males. This is also shown by the significance levels for these variables in this analysis: only horn length difference was significant when the results for large males alone were analysed separately.

In contrast, both elytra length difference and the pronotum * horn length difference interaction remained highly statistically significant when the data for contests between small males were analysed separately. The estimated regression coefficients for the various parameters \pm SE are: horn length difference: 2.41 ± 1.77 ; elytra length difference: 3.20 ± 1.38 ; pronotum length difference: 4.29 ± 1.97 ; pronotum * horn length difference interaction: 4.05 ± 1.80 . For contests between small males, therefore, the combination of pronotum length and horn length was the most important determinant of contest outcome, but body size, as indicated by elytra length, also made an important contribution to victory.

The difference in the importance of elytra length between contests involving large males and contests involving small males is not a consequence of the

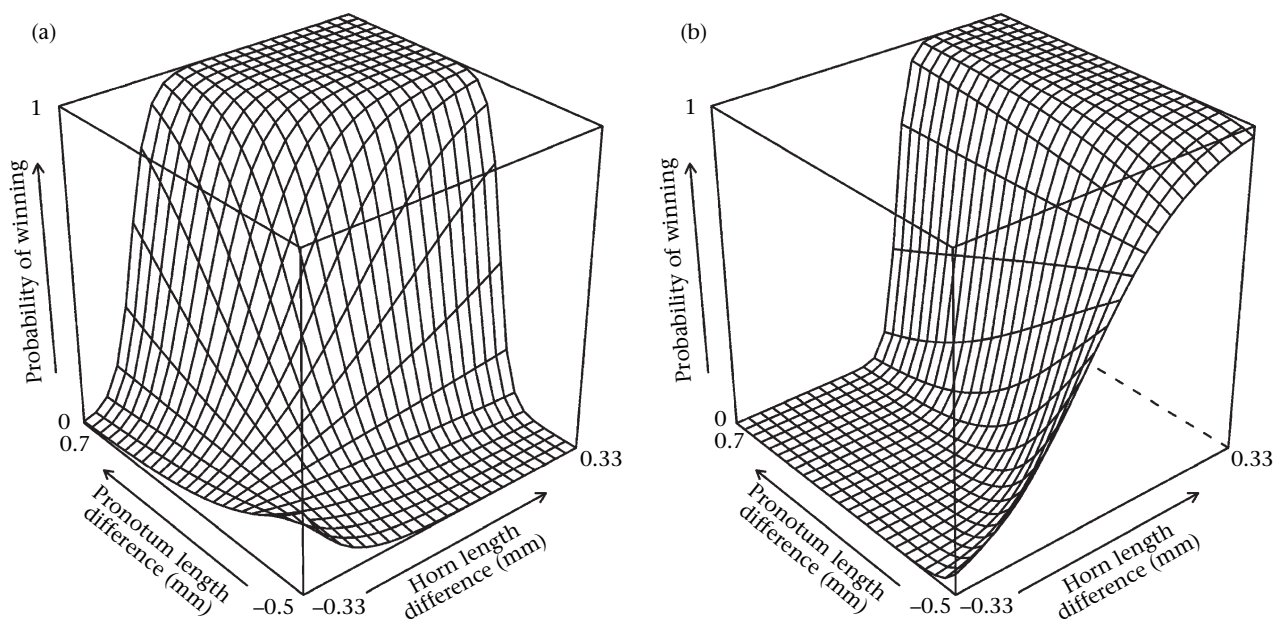


Figure 3. The response surface for the fitted minimal adequate model. We set elytra length differences to zero before calculating the response, so these graphs show the relation between differences in pronotum length, differences in horn length and the probability of victory plotted for contests between (a) small and (b) large males.

differences in elytra length being greater in contests between small males: the differences in elytra lengths in contests between large males and in contests between small males were not significantly different (t test: $t_{58} = 0.36$, $P = 0.71$).

Morphology and Male Mobility

Elytra length was the only significant morphological correlate of the time beetles took to run down a plaster of Paris tunnel, large males taking significantly longer than small males (Table 2, Fig. 5). There was no clear effect of horn or pronotum length.

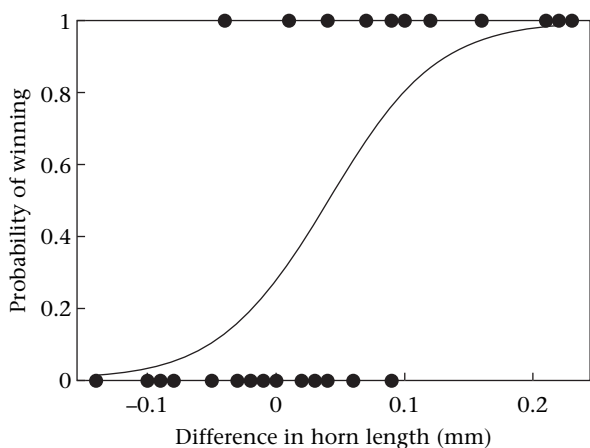


Figure 4. The effect of horn length on victory in contests between large males: differences in horn length are plotted against whether the focal male won or lost the contest. The line is the fitted probability of victory from the model detailed in Table 1, with the values of all parameters other than horn length difference set to zero.

DISCUSSION

Previous investigations of the nonlinear allometries of sexually selected traits that are common in holometabolous insects (Emlen & Nijhout 2000) have focused either on increases in slope related to changes in behavioural strategy (Cook 1990; Emlen 1997) or on the relation between decreases in slope and competition for resources between rapidly growing parts of the adult insect within the pupa (Huxley 1932; Nijhout 1994; Nijhout & Wheeler 1996; Knell et al. 2004; Moczek & Nijhout 2004). The extent to which the allometric slope declines in *E. intermedius* seems disproportionate to the size of the horn, however; the allometric curvature, as defined by the value of a from the fitted second-order polynomial $y = ax^2 + bx + c$ (Knell et al. 2004: more negative values indicate a greater decrease in slope) is -7.92 (Fig. 1). This indicates that the change in slope in this allometric relationship is substantially greater than was found in any of the stag beetles

Table 2. Relation between three morphological variables and the log time taken by a male beetle to run down an artificial tunnel, as shown by fitting a general linear model to the data

Variable	Estimated coefficient	SE	df	Mean square	F	P
Elytra length (mm)	0.663	0.268	1	0.963	6.13	0.017
Horn length (mm)	-0.008	0.470	1	<0.001	0.003	0.987
Pronotum length (mm)	0.251	1.22	1	0.107	0.681	0.413
Error			50	0.157		

All main effects are shown (no interaction terms were significant).

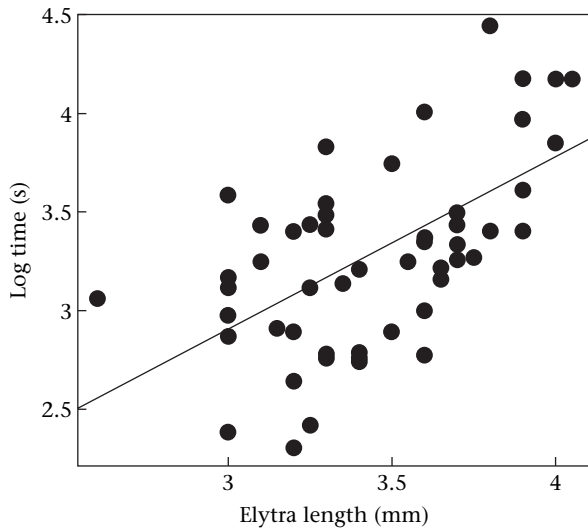


Figure 5. The relation between speed (represented by the time taken to traverse an artificial tunnel) and body size. The fitted line is $Y = 0.8691X + 0.2964$.

studied by Knell et al. (2004); the lowest value in that study was -5.26 from *Lucanus laminifer*, large males of which have mandibles that are longer than their bodies. The horn of *E. intermedius*, by contrast, is rarely longer than a fifth of body length in even the largest males. It seems, therefore, that competition for pupal resources is unlikely to explain all of the observed allometric curvature in this species.

The decrease in the allometric slope of the horn of *E. intermedius* that occurs with increasing body size appears to be associated with changes in the horn's importance during intrasexual contests. In contests between small males, elytra length difference (a measure of body size) and the interaction between pronotum length difference and horn length difference all contributed towards determining the winning male. In contests between large males, however, horn length difference was the main predictor of victory, indicating that the importance of the horn in intrasexual contests increases with the body size of the contestants, and the sign of the relationship between elytra length and victory is reversed: it appears that the larger male is disadvantaged when competing with another male from the largest third of the population. Furthermore, we found no evidence of alternative mating strategies; both large and small males guarded the females and male beetles of whatever size did not attempt to achieve 'sneak' matings.

Petrie's (1998) argument would lead us to expect that the horns of smaller males should be important in determining contest outcome because they show positive allometry, but the isometric horns of the large males should not influence contest outcome. However, we found that the isometric horns of the larger males were more important in contest resolution than the positively allometric horns of the smaller males. These data seem to be best explained by reference to Bonduriansky & Day's recent (2003) mathematical models of allometric slopes. We did not measure the fitness functions for horn and body size directly (and, given the interactions between

size class, pronotum length and horn length, simple fitness functions would be difficult to justify for these beetles), but it is possible to estimate that the function relating horn size and body size to fitness for small beetles is similar to Bonduriansky & Day's fitness function 5, with diminishing fitness returns for increases in body size but an equal, or even an increasing, fitness return for increases in horn size with body size. This fitness function leads to positively allometric traits in the model, and in *E. intermedius* the horns of small beetles are indeed positively allometric. In contests between large male *E. intermedius*, on the other hand, horn size mainly determines victory, whereas body size is weakly negatively related to the probability of winning. Bonduriansky & Day did not explicitly model this situation, with directional selection for larger trait size and stabilizing selection or directional selection for smaller size acting on body size, but given the relatively weak effect of body size the closest approximation is their fitness function 1, whereby trait size alone is related to fitness. This model predicts trait isometry, and this is approximately what we see in large male *E. intermedius*: the fitted polynomial has a slope of 1 at a body length of 8.29 mm (Fig. 1).

The means by which these beetles achieve these changes in allometry are likely to be associated with the various peptides (such as insulin and insulin-like peptides) and hormones (for example, juvenile hormone and ecdysone) that regulate the growth and metamorphosis of the animal (e.g. Goberdhan & Wilson 2003; Nijhout 2003; Emlen & Allen 2004). Allometric relationships in holometabolous insects are believed to be determined by the sensitivity of the proliferating cells to these signals (Emlen & Allen 2004), so it may be that these beetles invest relatively more in horn length when resources are abundant, but less in horn length and more in overall body size when resources are scarce by modifying the relative sensitivity of their growing tissues to these growth hormones depending on nutrient availability. Both this mechanism for generating curved allometry and the alternative of competition for pupal resources are dependent on the resource trade-offs that operate in the metamorphosing insect, and they are not mutually exclusive; indeed, both may operate simultaneously.

The mechanism the beetles use to modify the sensitivity of the growing body parts to growth signals is likely to be similar to that described in the related species *Onthophagus taurus*; here, the change in horn allometry that leads to males developing into horned 'major' males or hornless 'minor' males is brought about by a pulse of the hormone ecdysone towards the end of the larval feeding period that, combined with a lower juvenile hormone concentration in small males, 'reprograms' the development of the animal's horns (Emlen & Nijhout 1999, 2001; Emlen & Allen 2004).

This explanation for the change in allometric slope relies on a number of assumptions, in particular that there is genetic variability on which size-dependent selection can operate, allowing males to follow different developmental pathways. Given the well-known evidence for such processes in the dimorphic *Onthophagus* species (e.g. Emlen 1997; Moczek & Emlen 1999, 2000; Hunt &

Simmons 2001) this seems a reasonable assumption to make for *E. intermedius*. A further assumption is that increasing body size does not contribute to fitness in ways other than those measured here. It is of course possible that body size could contribute towards, for example, foraging or flight ability, and we have no data available to allow us to explore this possibility. None the less, the *E. intermedius* males in this study had a negatively skewed frequency distribution of size (Fig. 6), suggesting that there is a constraint on male body size.

These beetles show sexual size dimorphism, with smaller females than males. The females dig the tunnels in which the males compete and mate, and so the size of these tunnels will place an upper limit on male body size. This idea is supported by our data on male manoeuvrability in artificial tunnels, which showed that body size, but not horn size, appears to limit a male beetle's speed. This decreased manoeuvrability may explain at least part of the change in the relation between elytra length and contest victory between small and large beetles. This result for *E. intermedius* contrasts with the findings of Moczek & Emlen (2000), who showed that *O. taurus* males with long horns suffered significant decreases in running speed within tunnels. This discrepancy is likely to arise from the lack of sexual size dimorphism of *O. taurus*, which means that the tunnels that the females dig will be relatively large in comparison with male body size in this species.

If there is an upper limit on male body size, 'high-quality' males may instead invest any spare resources in other ways. This would lead to horn size and body size becoming uncoupled at larger body sizes and it seems that the competitive ability of large beetles is determined not by body size but by horn size. This might be caused by longer horns allowing better removal of competitors, but horn size may also be related to competitive ability as determined by other aspects of morphology or physiology. Positive correlations between horn length, immune investment (Pomfret & Knell, in press) and physical performance (Lailvaux et al. 2005) suggest that the latter is the case. This theory that size constraints arising from

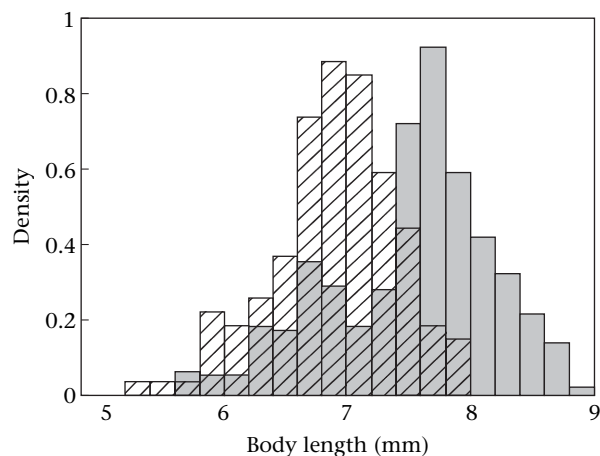


Figure 6. Frequency distributions of body length for male (■, $N = 464$) and female (▨, $N = 135$) beetles. Plotted as probability densities to allow comparisons between the two different-sized samples.

male-biased sexual size dimorphism can lead to a change in the function of a sexually selected trait remains to be investigated in detail, but we feel that this is a likely explanation for our results.

Previous detailed studies of the relation between horn length, body size and contest outcome in the Scarabaeidae have concentrated on the genus *Onthophagus*. In both *O. acuminatus* (Emlen 1997) and *O. taurus* (Moczek & Emlen 2000) body size is the most important predictor of victory, and horn size is important only when males are matched for size. Clearly this is a very different situation to that found in *E. intermedius*, but again an explanation for this difference may lie in the patterns of sexual size dimorphism found in the three species; as already discussed, *E. intermedius* males are larger than females, but neither *Onthophagus* species shows sexual size dimorphism (D. Emlen, personal communication), so the constraints on male size that we have suggested for *E. intermedius* will not operate. For both *O. taurus* and *O. acuminatus* the allometric slope of horn size declines at the largest body sizes, however, and it would be interesting to investigate whether these declines are associated with changes in the relative importance of horn and body size in the same way that they are in *E. intermedius*.

Moving beyond the Coleoptera, few studies have found instances of contests being determined by weapon size independently of body size, but Sneddon et al. (1997) found that weapon size (claw length) was a much better predictor of contest success than body size in male shore crabs, *Carcinus maenas*. Claw length is positively allometric in this species, (least-squares regression slope 1.24, significantly greater than a slope of 1 [$t_{79} = 2.13$, $P = 0.036$], reduced major axis slope 1.60, bootstrapped 95% confidence intervals 1.39–1.87, data from L. Sneddon, personal communication). In the context of the Bonduriansky & Day model, this may indicate that body size in these crabs is related to fitness via an aspect of the animal's biology that is not associated with contest success.

In our study, when small males competed, a longer horn was important only when combined with a long pronotal hump. The relation between pronotum length and body size is an isometric straight line with a slope of 1. This seems to be at odds with the change in the importance of pronotum length that we found, but it is possible that pronotum length is also important in other aspects of the male's fitness that we have not investigated here; for example, Petrie (1988) suggested that traits used in female choice should be isometric because it would pay all males to invest maximally, a situation analogous to Boduriansky & Day's first fitness function. Møller & Pomiankowski (1993) discussed the evolution of multiple sexual traits, and suggested that they can act separately to each other, signalling either different qualities or to different individuals, or can act together signalling the same quality to the same audience. In contests between small *E. intermedius* the horn and pronotum seem to be acting in combination, reinforcing each other so other competitors can gain a more accurate idea of body size-linked competitive ability (Møller & Pomiankowski 1993). This agrees with the accepted theory that secondary sexual trait size is linked to competitive ability through body size.

To conclude, our results provide a clear example of a sexually selected trait used in intrasexual contests that becomes more important in determining contest outcome as its allometric slope declines. This somewhat counterintuitive pattern is consistent with the results of recent mathematical models of the allometry of secondary sexual traits, and may well be the reason why the allometric curve shows such strong curvature. We do not rule out the possible role of competition in the pupa in causing the curved horn allometry, but we do note first that the extent of the decline of slope in this case is disproportionate to the size of the horn, and second that these two mechanisms are not mutually exclusive, and could well both be operating. It is likely that the increase in the importance of horn size in larger *E. intermedius* is associated with constraints on the body size of large males arising from male-biased sexual size dimorphism in this species. Clearly, at least in this case, the assumption that contest outcome is determined by relative body size and that weapon size reflects body size is incorrect, and it may be that horn size instead indicates other physiological or morphological determinants of victory.

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