

Horn size predicts physical performance in the beetle *Euoniticellus intermedius* (Coleoptera: Scarabaeidae)

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Summary

1. In many animals, the size of secondary sexual ornaments is known to be related to the probability of victory in fights between males, and hence to fighting ability. However, few studies have attempted to link fighting ability to any physical performance measures.

2. Here we show that horn size in the dung beetle *Euoniticellus intermedius* accurately predicts two types of whole-organism performance, independent of body size, that are likely to play an important role in male contests: the force required to pull a beetle out of a tunnel, and the distance the beetle was able to run before exhaustion (maximum exertion).

3. Body length is also a statistically significant predictor of pulling force, but not of exertion, suggesting that horn size is a more reliable predictor of performance than body size alone, a result that is consistent with a previous finding that horn size becomes more important in determining victory in male–male contests as body size increases.

4. This study is the first to establish direct links between whole-organism performance abilities, male armaments and fighting ability in the same species. Our findings suggest that physiological performance capacities are important factors underlying the evolution of signal expression in *E. intermedius*, and should be considered in future studies of the evolution of animal signalling.

Key-words: Dung beetles, male combat, signalling, whole-organism performance

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Introduction

Fights between competing males for access to females are common in the animal kingdom, and sexual selection has equipped the males of many species with weaponry that is used during fights. There are many striking examples of these weapons, including the antlers of cervids, the spurs carried by male pheasants, the enlarged mandibles of stag beetles and the horns carried by males of many other beetle species (Darwin 1871; Andersson 1994). These traits range from those that are used during fights to overpower and even to kill opponents (e.g. the mandibles of male fig wasps, Bean & Cook 2001), to others that do not actually play any physical role in fights, but are instead thought to be used as signals of fighting ability (e.g. the eyestalks of *Cyrtodiopsis dalmanni*, Panhuis & Wilkinson 1999). The size of these weapons and the probability of victory in male fights are correlated in several species

(Andersson 1994; Emlen 1997; Sneddon, Huntingford & Taylor 1997; Panhuis & Wilkinson 1999; Moczek & Emlen 2000), but the functional mechanisms that lead to this correlation have received little attention.

Likelihood of victory in fights is associated with larger body size in many animal taxa (e.g. Clutton-Brock, Albon & Guinness 1988; Alcock 1996; Ladich 1998), but this tells us little about the proximate functional characteristics influencing fight outcomes, as body size is frequently correlated with both functional capacities (e.g. Toro, Herrel & Irschick 2003) and armament size (Petrie 1988; Andersson 1994; Emlen & Nijhout 2000). If physical confrontations between males are influenced by individual performance capacities, such as strength or endurance, then one might predict that such capacities will be linked to signal expression independent of body size. Nonetheless, while a few studies have established links between armament size and physiological variables such as metabolic rate (Whiting, Nagy & Bateman 2003), the relationship between male armaments and physical variables that are likely to directly influence the outcome

of male contests, such as performance capacities, are seldom explored.

Whole-organism performance abilities, defined as any measurement of an organism conducting an ecologically relevant task such as locomotion, have long been the subject of investigation because of their presumed importance to Darwinian fitness (see Irschick & Garland 2001 for a review). Several recent studies have also demonstrated a relationship between various locomotor capacities and the ability to win male–male fights in lizards (Garland, Hankins & Huey 1990; Robson & Miles 2000; Perry *et al.* 2004; Lailvaux *et al.* 2004). Endurance capacity in particular has been indirectly linked to competitive success in taxa such as odonates (Marden 1989; Marden & Waage 1990; Plaistow & Siva-Jothy 1996), crabs (Thorpe, Taylor & Huntingford 1995; Sneddon, Taylor & Huntingford 1999; Briffa & Elwood 2001, 2002, 2004) and cichlid fish (Neat, Taylor & Huntingford 1998). Thus far, however, only a single study has shown that performance traits relevant to male combat can be signalled by male secondary sexual traits. In a study of Caribbean *Anolis* lizards, Vanhooydonck *et al.* (2005) found that the size of the anole dewlap (i.e. throat-fan), a secondary sexual male character, is positively correlated with bite force in several anole species following correction for body size. Given that bite force is a known determinant of male combat outcomes in some anole species (Lailvaux *et al.* 2004), males may be able to glean information about a rival's fighting ability (i.e. bite force) from the size of his dewlap. However, the role of the dewlap in resolving male conflicts in anoles is equivocal (e.g. Tokarz, Paterson & McMann 2003; S. P. Lailvaux & D. J. Irschick unpublished data), and it is therefore unclear whether information on performance capacity transmitted by secondary sexual traits is actually used by rivals. Here we examine the relationships between a known determinant of victory in male fights, horn size and two different measures of whole-organism performance ability in the Horned Dung Beetle, *Euoniticellus intermedius*.

Work on Horned Dung Beetles over the last 15 years has provided important insights into the evolution of alternative mating strategies (Cooke 1990; Emlen 1994, 1997; Moczek & Emlen 2000; Hunt & Simmons 2001), the importance of sperm competition (Simmons, Tomkins & Hunt 1999; Tomkins & Simmons 2000; Simmons & Kotiaho 2002) and the trade-offs that ultimately determine the sizes of individual body parts (Emlen 2000). The role of horn size in determining the outcomes of male–male contests in the species *Onthophagus acuminatus* and *Onthophagus taurus* has been well described (e.g. Emlen 1997; Moczek & Emlen 2000). In both of these species males who are larger tend to win contests, but when males of similar sizes meet then the male with the longer horns tends to be the victor.

Euoniticellus intermedius is, like the *Onthophagus* species mentioned above, a small (usually < 1 cm long)

dung beetle that buries dung directly underneath the dung pad. Females dig tunnels and bury balls of dung within which they lay eggs. Females are solely responsible for digging the tunnels, and males, who carry a curved horn on the clypeus, guard and mate with females in these tunnels and will fight with other males within the tunnels for access to females (Pomfret 2004). All males will fight, using their horns either to push rival males out of the tunnels if defending a female, or, if an intruder, to push a defender backwards until the intruder is able to pass him in the tunnel (Pomfret 2004). There is no evidence of alternative tactics being used to achieve 'sneak' matings by smaller males as is common in *Onthophagus*, small males of which have been reported to avoid guarding males by digging side tunnels (Emlen 1997), by manoeuvring past the defending male, or by entering the tunnel when it is temporarily unguarded (Moczek & Emlen 2000). A beetle that is able to resist a greater force than other males, and hence prevent himself from being pushed out, will therefore have a clear advantage in fights. Also in contrast to *Onthophagus*, horn size is the most important predictor of contest outcome in *E. intermedius* especially in contests between larger males, when body size is in fact weakly negatively related to the probability of victory (Pomfret & Knell 2005). Here we test the hypothesis that relative horn size in *E. intermedius* also predicts relative whole-organism performance ability, as would be expected if performance capabilities are related to the outcome of male contests. In particular, we measure two types of whole-organism performance relevant to male contests in *E. intermedius*: net pull resisting force (hereafter 'pulling force'), which represents the force required to push a beetle out of a tunnel, and maximal exertion (also known as distance capacity) a measure of the locomotor effort expended before the onset of exhaustion. This capacity is an important deciding factor in lengthy bouts between males of other invertebrate species (e.g. Marden & Waage 1990; Marden & Rollins 1994; Briffa & Elwood 2001, 2002, 2004).

Materials and methods

CULTURE

All insects were taken from the same *E. intermedius* laboratory culture used in Pomfret & Knell (2005), originally started with >100 adult beetles collected from South Africa. Briefly, beetles were reared at 28 °C with a 12:12 h light : dark photoperiod in 1000 ml pots of mixed males and females (no more than three males and three females per pot). Each pot contained 500 ml damp sand and 200 ml cow dung. Brood masses were removed from the pots after 1 week, and the brood balls separated and placed in individual pots with moist sand. After approximately 1 month, emerging beetles were collected and placed in single-sex culture until sexually mature (about 2 weeks).

PULLING FORCE

This experiment was carried out within horizontal artificial tunnels made from two strips of plaster of Paris separated by *c.* 4.5 mm and placed between two panes of glass. A piece of cotton thread tied at one end to a plastic pot was run over a smooth, horizontal aluminium rod, and glued to the posterior end of one elytron of a beetle with cyanoacrylate adhesive ('super-glue'), and the beetle allowed to enter the tunnel until it was completely within it. The amount of force required to pull a beetle out of a tunnel was measured by slowly filling the pot with water at a constant rate until the beetle was pulled backwards out of the tunnel. The pot and water were weighed using a Sartorius electronic balance and weights were converted to newtons (N). (Note that a small amount of force will be lost owing to the friction of the thread passing over the rod.) Each trial consistently lasted <30 s, and so we do not regard our measure of pull-resisting force as an endurance measure. Force trials were carried out three times on each individual, with a 1 h rest between trials. Of the three trials, the trial resulting in the largest pulling force was used in statistical analyses (see Losos, Creer & Schulte 2002 for justification of the use of maximal values in performance studies). Beetles were observed closely to ensure that no trials resulted in obviously submaximal results, and no individuals were eliminated for consistent submaximal performance. Our results indicate pull-resisting force is a real aspect of physiological performance rather than a consequence of morphology (see Discussion below). All trials were carried out in a constant temperature room at 25 °C.

MAXIMAL EXERTION

We carried out all exertion trials using methods consistent with those that have been successfully applied to vertebrates by previous researchers (see Cullum 1998; Lailvaux, Alexander & Whiting 2003 for recent examples). Maximal exertion was measured as the distance an individual walked at maximum speed before the onset of exhaustion when chased around a circular raceway 0.5 m in circumference. Individual beetles were forced to walk in the same direction around the track at all times, and were motivated to run by lightly tapping their abdomens with a paintbrush. Beetles were forced to move continuously in this manner, as intermittent locomotion is known to increase distance capacity in other invertebrates (e.g. Weinstein & Full 1992, 1998). The track was marked in such a way that distance run could be measured to the nearest 0.1 m. A beetle was considered to be exhausted when it refused to move despite repeated tapping, or was unable to right itself when placed on its back. All beetles reached this end-point, and consequently none was excluded from the analysis. As in previous studies (Cullum 1998; Lailvaux *et al.* 2003) each individual was measured

once. All trials were carried out in a constant temperature room at 25 °C.

MORPHOLOGY

Body length (tip of the abdomen to the front of the pronotum) was measured using Vernier callipers. This measure has previously been found to be a useful linear indicator of overall body size (Pomfret 2004). Measurements of horn length were made using the public domain NIH Image program (v. 1.62: developed at the U.S. National Institutes of Health and available on the Internet at <http://rsb.info.nih.gov/ni-image/>) on photographs of each beetle taken under a dissecting microscope at $\times 65$ with a Nikon Coolpix 950 digital camera (Nikon Corp., Tokyo, Japan).

STATISTICAL ANALYSES

Data were analysed using multiple regression models. To examine relationships between horn size and performance variables independent of body size, we included both body size and horn size as predictor variables in the multiple regressions. Partial regression coefficients express the correlation between two variables under the condition that all concomitantly measured variables are held constant (Kachigan 1991). Therefore, the partial correlation coefficients in the above model give us the relationship between horn size and performance with the effects of body size statistically extracted, in a manner analogous to residual analyses, but without the loss of a degree of freedom (see Darlington & Smulders 2001; Garcia-Berthou 2001). (Note that residual values are used for figures where necessary to illustrate 'size-free' relationships between variables.)

Results

Initial data exploration revealed collinearity in the three explanatory variables, with body weight and horn length being particularly closely related. Calculations of tolerance for the three variables gave values of 0.19 for horn length, 0.39 for body length and 0.17 for mass. The first and last values here are close to the guideline value of 0.1 given in Quinn & Keogh (2002) as the threshold beyond which collinearity in explanatory variables will seriously distort the results of multiple regressions. For this reason we did not include mass in the model. Further initial exploration revealed a degree of positive skew in the maximum force variable, which was log-transformed to ensure normality. Our two measures of performance, endurance and maximum force, were correlated with each other both before ($df = 30$, $P < 0.001$, $r^2 = 0.539$) (Fig. 1a) and after statistically accounting for body size ($df = 30$, $P < 0.001$, $r^2 = 0.293$) (Fig. 1b). Table 1 gives summary statistics for the two measures of beetle morphology retained and for the two measures of performance used.

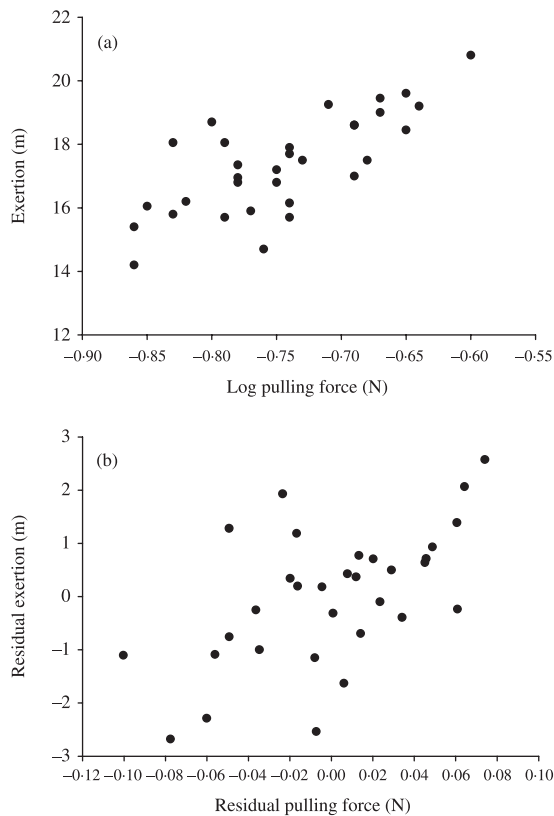


Fig. 1. Maximal exertion vs log pulling force: (a) absolute data; (b) residual (body length corrected) data.

MAXIMUM FORCE

Table 2a gives the result of fitting a linear model with body length and horn length as the explanatory variables, and Fig. 2 shows the relationships between relative and absolute values for body length, horn length

Table 1. Summary statistics for morphology, exertion and pulling performance for male *E. intermedius* beetles ($N = 32$)

	Mean	Range	Standard deviation
Body length (mm)	6.556	5.2–8.4	0.937
Horn length (mm)	0.711	0.56–0.96	0.112
Endurance (m)	17.383	14.2–20.8	1.553
Pulling force (N)	0.182	0.128–0.35	0.029

and maximum force. Both variables were statistically significant predictors of maximum force, and in particular horn length was significantly correlated with maximum force when the influence of body size was partialled out (as in this analysis). Between them, body length and horn size explained some 65% of the variance in the maximum force data (Table 2).

The standardized partial regression coefficients for the two explanatory variables allow us to assess their relative importance in the model. These were 0.406 and 0.466 for body length and horn length, respectively, with the standard error for both being 0.161. Thus both body length and horn length were of roughly equal importance in this model.

EXERTION

When both body length and horn length were included as explanatory variables in a model, neither was a statistically significant predictor (Table 2b), although horn length was only marginally non-significant. On inspection of diagnostic plots for the model one data point was found to be an important outlier, with by far the highest Cook's distance (0.36, as opposed to 0.12 and <0.1 for the other points). Excluding this data

Table 2. (a) Results of fitting a linear model with predictors horn length and body length to the log of the maximum force required to pull each beetle from a hole. Adjusted r^2 for the model is 0.648. (b) Results of fitting a linear model with the same predictors to our measure of the endurance of each beetle (distance walked before exhaustion). Adjusted r^2 for the model is 0.349. (c) Results of refitting the model fitted in Table 2b with the outlying data point (Fig. 3) removed. Adjusted r^2 for the model is now 0.487. (d) Simplified final model for endurance, with body length removed as a predictor variable. Adjusted r^2 for the model is now 0.463

Performance measure	Variable	Coefficient	SE	<i>t</i>	<i>P</i>
(a) Log maximum force (N)	Intercept	-2.621	0.121		
	Body length	0.068	0.027	2.481	0.019
	Horn length	0.650	0.228	2.847	0.008
(b) Distance walked to exhaustion (m)	Intercept	10.59	1.629		
	Body length	0.419	0.369	1.138	0.265
	Horn length	5.677	3.079	1.184	0.075
(c) Distance walked to exhaustion (m)	Intercept	9.263	1.525		
	Body length	0.506	0.331	1.530	0.137
	Horn length	6.907	2.780	2.484	0.019
(d) Distance walked to exhaustion (m)	Intercept	10.36	1.378		
	Horn length	10.03	1.933	5.817	<0.001

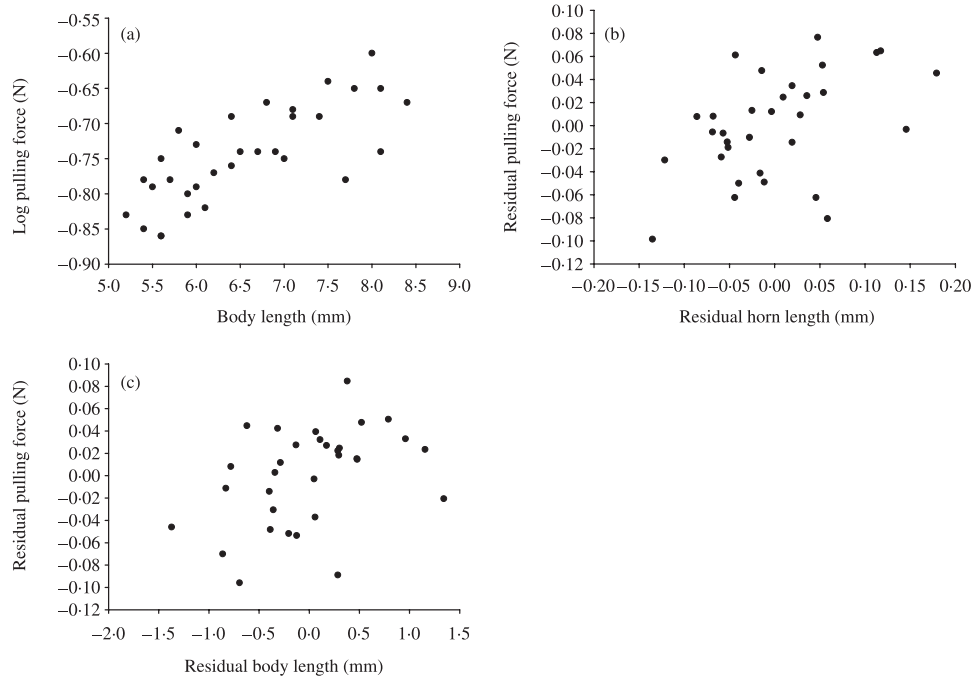


Fig. 2. (a) Log maximum pulling force plotted against body length. Note that force and body size are always positively related. (b) Residual pulling force against residual horn length (following linear regression of log pulling force vs body length and horn length vs body length). (c) Residual force vs residual body length, i.e. body length with variation attributable to horn size removed (following linear regression of log pulling force vs horn length and body length vs horn length).

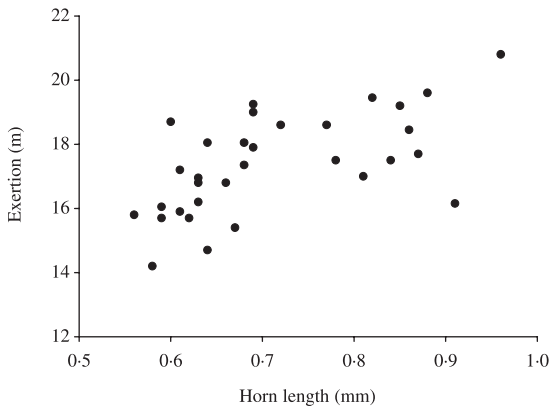


Fig. 3. Maximal exertion vs horn length.

point from the model gave the results in Table 2c, with horn length now having a statistically significant partial regression coefficient, but body length remaining non-significant.

Simplification of the model to give the ‘minimum adequate model’ (Crawley 1993) was done by fitting a model with only horn length as a predictor (Table 2d). Following simplification, horn length was a highly significant predictor of endurance performance (Fig. 3). We note that although this model was fitted with the previously identified outlier removed, this remains the case whether the outlier identified earlier is included or not (model with outlier included gives $P < 0.001$).

Examination of Fig. 3 suggests that a curvilinear, rather than a linear relationship may be the most

appropriate way to describe how exertion capacity depends on horn size. Residual plots of the linear model do not show a particularly strong deviation from randomness, however, and fitting a model with a quadratic term does not give a significantly better fit than the simple linear model.

Discussion

Many previous studies have shown that quantifiable aspects of secondary sexual characters influence the outcomes of male–male contests, but few studies have provided a rationale for this relationship. Understanding *why* males expressing large armaments win fights is important both for comprehending mechanisms that lead to armament expression itself, and because knowledge of how males win fights may yield important information on what constitutes fighting ability or ‘resource holding potential’ in males (Parker 1974). Although Vanhooydonck *et al.* (2005) showed that a whole-organism performance ability (bite force) is linked to the size of male dewlaps independent of body size in *Anolis* lizards, the role of the dewlap in resolving male contests in anoles is unknown. Here we show that horn length in *E. intermedius*, a known predictor of victory in male fights (Pomfret & Knell 2005), is strongly correlated with two measures of whole-organism performance independent of body size, namely the force required to pull a beetle out of a hole and the distance a beetle is able to walk before reaching exhaustion (Figs 2 and 3). Horn length is as important as body length in the model relating maximum force to our two

morphological variables, and in the case of maximum exertion horn length emerges as the only significant predictor variable. These findings strongly suggest that the connection between horn length and victory in intrasexual contests described by Pomfret & Knell (2005) is mediated by physical performance; male beetles with relatively long horns are stronger and have greater exertion capacities, and consequently win fights. Given the opportunities for assessment of rivals' horn lengths during male fights in this species (R. Knell, unpublished data), our results indicate that horn size probably acts as an honest index of male performance ability, signalling exertion and pulling force abilities to other males.

The finding that horn length is a better predictor of maximal exertion than body size (Fig. 3) is particularly interesting because Pomfret & Knell (2005) found that in larger male *E. intermedius* horn length alone predicted victory in contests, possibly because the size of the tunnels dug by females places a constraint on how large males can be, such that the horns of larger males signal aspects of morphology or physiology other than body size. We excluded mass from our analysis because our main aim was to investigate how body length and horn size affect physical performance, and the inclusion of mass would have made it difficult to interpret our data in this way, but we should remember that both variables, and especially horn length, were strongly correlated with body mass. The beetles used here had eclosed 2 weeks before being used, and had been allowed to undergo maturation feeding on excess food during this period. The close relationship between mass and horn length suggests a physiological link between horn length, which is set during the prepupal and pupal stage of development, and the ability of the beetle to assimilate food. Thus, our results are potentially consistent with previous studies of fighting in invertebrates showing that victory in contests is related to energetic reserves, such as fat content (Marden & Waage 1990; Marden & Rollins 1994; Briffa & Elwood 2004). These results raise the possibility that horn length and performance capacities are dependent on the same energetic resource 'pool'.

Physiological and biomechanical theory predicts that there should be trade-offs between certain pairs of performance traits (Van Damme *et al.* 2002). This process is illustrated by the general lack of correlation among vertebrates between maximum speed, which is supported anaerobically, and endurance, which is an aerobic performance trait (e.g. Dohm, Hayes & Garland 1996; Reidy, Kerr & Nelson 2000; Vanhooydonck, Van Damme & Aerts 2001; see also Bennett 1989 for a discussion of activity capacities in animals). In the case of vertebrates, the explanation for this trade-off lies partly in muscle physiology and organization; for example, human athletes relying on burst performance, such as sprinters or weightlifters, are known to have higher proportions of rapidly contracting, anaerobic (fast-twitch) muscle fibres which fatigue quickly,

while endurance athletes have higher proportions of aerobic (slow-twitch) fibres, which contract less quickly but are more resistant to fatigue (Esbjörnsson *et al.* 1993). The apparent lack of trade-off between exertion and pulling force in *E. intermedius* (Fig. 1) is therefore surprising (but see Garland 1988 who found no evidence for trade-offs between speed and stamina in Garter Snakes). By contrast with vertebrates, however, studies of comparable relationships between performance traits in insects are lacking, making it difficult to evaluate this result in a comparative context. One possibility may be that both exertion and pulling force draw on the same resource 'pool'. Given that beetles had unlimited access to food for 2 weeks of posteclosional maturation feeding, and that trade-offs are more pronounced under resource-limited conditions (Zera & Harshman 2001), the abundance of food might have ameliorated any resource-allocation trade-offs. The mechanism by which *E. intermedius* is able to seemingly maximize both strength and exertion simultaneously is therefore not readily apparent from our current dataset, but clearly warrants further study.

Studies of terrestrial performance capabilities in beetles (e.g. Kram 1996) are few, and to our knowledge only one other published study has examined the relationship between performance and horn size in dung beetles. Moczek & Emlen (2000) showed that, contrary to our results, *Onthophagus taurus* males with long horns suffered significant decrease in running speed within tunnels. In the case of *O. taurus*, however, this was due to the horns impeding the beetles' movement within the narrow tunnel confines, rather than to any intrinsic physiological capabilities. While male *E. intermedius* horns are not large enough to restrict movement within tunnels (S. Lailvaux, personal observation), Moczek & Emlen's (2000) finding raises the possibility that, at larger body sizes, the force required to pull *E. intermedius* beetles out of a tunnel is a function of beetle morphology (i.e. large beetles are more likely to become 'stuck' in a tunnel owing to their greater width), rather than strength. If this were the case, one would expect pulling force to become independent of body size above a certain beetle length. However, examination of the plot between maximum force and body length (Fig. 2a) reveals a positive relationship between these two variables at all body sizes. Furthermore, maximum force and exertion are also positively related (Fig. 1), meaning that beetles exhibiting larger pulling forces also take longer to become exhausted. Finally, our results show that individual *E. intermedius* beetles can support weights ranging from 228 to 425 times their own body weight. Similarly impressive results have been reported for Rhinoceros Beetles, *Xylocortes thestalus*, measured using a different protocol (Kram 1996). Thus, we argue that our force data are not simply a result of beetle size or shape.

In conclusion, we show here that horn size is an accurate indicator of both pulling force and exertion in *E. intermedius* even after controlling for body size. This

is the first study to relate whole-organism performance abilities to a male secondary sexual trait that is a known predictor of fight outcomes. Interestingly, no trade-offs were found between pulling force and exertion. This result, together with the positive relationship between horn size and body weight, suggests that both horn expression and physical performance may be dependent on the same resource 'pool', although further investigations, perhaps involving limiting resource conditions, are required to test this possibility. Physiological state in general, and endurance capabilities in particular, appear to be important factors influencing signal expression in nature. Our results here, in conjunction with those reported by previous researchers, constitute justification for relevant whole organism performance variables, such as endurance or exertion abilities, to be included amongst parasite load and body condition (or, ideally, combined into an integrative approach) in future investigations of the evolution of animal signalling.

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