Variation in the allometry of exaggerated rhinoceros beetle horns

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ARTICLE INFO

Exaggerated horns are a characteristic feature of many male rhinoceros beetles. We surveyed and compared the scaling relationships of these sexually selected weapons for 31 Dynastinae species with different degrees of horn exaggeration. We found that nearly all rhinoceros beetle species were male dimorphic, that the allometric slope of major males was consistently shallower than the slope of minor males, and that the decrease in slope was greatest among species with the most exaggerated horns. These patterns are consistent with the curved allometries of stag beetle mandibles and giraffe weevil rostra, and suggest that the depletion of developmental resources is a general phenomenon limiting the continued exaggeration of insect weapons. The dimorphisms in horn morphology are expected to correspond to behavioural differences between major and minor males, but little is still known about the mating tactics of most rhinoceros beetle species. Future studies on the relative benefits and performance of horns during male—male combat are needed to fully understand the diversity of horn allometries and the evolution of exaggerated structures.

Variation in organismal shape is largely characterized by differences in the relative size of body parts (Huxley, 1932; Thompson, 1942). That is, many of the gross differences in body shape among diverse animal taxa are due to differences in the proportional size of body structures (e.g. the enlarged beak of toucans, or the elongated neck of giraffes). Within species, such shape differences are typically less pronounced, because most traits scale proportionately with body size. A few traits, however, increase in size much faster than overall body size, so large individuals are not simply scaled-up versions of smaller ones. Nowhere are these patterns more pronounced, or steep scaling relationships more apparent, than in the context of sexually selected traits (Kodric-Brown, Sibly, & Brown, 2006; Shingleton & Frankino, 2013).

Ornaments and weapons are typically much more variable than other nonsexual structures (Alatalo, Hoglund, & Lundberg, 1988; Cotton, Fowler, & Pomiankowski, 2004a; Emlen, Warren, Johns, Dworkin, & Lavine, 2012; Fitzpatrick, 1997; Kawano, 2004; Pomiankowski & Møller, 1995), and they almost always exhibit positive allometries, or scaling relationships with slopes greater than 1 (Gould, 1973; Green, 1992; Kodric-Brown et al., 2006; Petrie, 1992; Simmons & Tomkins, 1996). Large individuals

therefore have disproportionately larger ornaments and weapons than small individuals, which results in extreme variation in trait size and overall body form. Sexual selection is expected to favour the evolution of these steep scaling relationships for several reasons. First, ornaments and weapons are typically used to signal a male's condition to potential mates or competitors, and the costs and benefits of signalling are expected to be size dependent. That is, large males should benefit from producing large signals by attracting more females or deterring rivals, while small males should gain very little from advertising their small size and poor condition (Green, 1992; Petrie, 1992; Simmons & Tomkins, 1996). Second, because ornaments and weapons are often expensive to produce and carry, only large, high-quality males are expected to be capable of producing them (Andersson, 1982; Kodric-Brown & Brown, 1984; Nur & Hasson, 1984; Zahavi, 1975). Third, because traits with steep scaling relationships amplify differences in body size, these traits may be particularly informative signals to choosy females and rival males in discerning otherwise subtle differences in a male's overall size and condition (Cotton, Fowler, & Pomiankowski, 2004b; Emlen et al., 2012; Kodric-Brown et al., 2006; Maynard Smith & Harper, 2003). Indeed, theoretical models indicate that, as long as males with the smallest traits can occasionally succeed at mating, sexual selection drives the evolution of ornaments and weapons with strong positive allometry (Fromhage & Kokko, 2014).

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Although simple linear allometries have received the most attention in the sexual selection literature, sexual traits can also exhibit more complex, nonlinear scaling relationships (Knell, 2009). In particular, sexual ornaments and weapons in insects exhibit a variety of nonlinear allometries, including curved, sigmoidal and discontinuous (Eberhard & Gutierrez, 1991; Emlen & Nijhout, 2000; Knell, 2009; Knell, Pomfret, & Tomkins, 2004; Nijhout & Wheeler, 1996; Pomfret & Knell, 2006). The shapes of scaling relationships are important for evolutionary biologists because they offer clues about the selective pressures acting on these traits. For example, the sigmoidal allometries of many horned dung beetles are likely to reflect alternative adaptations for obtaining mating opportunities, with large, horned 'major' males specialized for fighting, and small, hornless 'minor' males specialized for sneaking (Eberhard & Gutierrez, 1991; Emlen, 1997; Emlen & Nijhout, 2000; Moczek & Emlen, 2000; Rasmussen, 1994), and the curved allometries of exaggerated stag beetle mandibles may reflect a depletion of developmental resources that ultimately limits mandible growth (Knell et al., 2004). Previous authors have even suggested that the evolution of nonlinear allometries should favour the evolution of exaggerated structures (Emlen & Nijhout, 2000), yet, to date, little is known about how the shape of scaling relationships vary among closely related species with different degrees of trait exaggeration.

Here, we present and analyse the most comprehensive survey to date on the scaling relationships of rhinoceros beetle horns. Male rhinoceros beetles produce long horns on their head and prothorax, and use them as weapons in male—male battles over reproductive access to females (Beebe, 1944, 1947; Eberhard, 1977, 1980; Hongo, 2007; Siva-Jothy, 1987). Rhinoceros beetles exhibit a wide range of both absolute and relative horn sizes (Enrödi, 1985; Mizunuma, 1999), which makes them an ideal system for comparing the scaling relationships among species with different degrees of horn exaggeration. We use our data to test for associations between scaling relationship shape and among-species patterns of horn exaggeration, and discuss the factors that have influenced the shape of horn allometries and the evolution of exaggerated structures.

METHODS

We measured male specimens of nearly all horned Dynastinae species from collections of the Smithsonian Institute and the University of Nebraska State Museum. We focused on the scaling relationships of head horns because the head horn is used to pry and dislodge opponents from contested resource sites (Beebe, 1944; Eberhard, 1980; Hongo, 2003; McCullough, Tobalske, & Emlen, 2014), and therefore is likely to be the primary target of sexual selection. All species with at least 20 males were measured and analysed, except for species belonging to the genus Strategus, which have thoracic horns but no head horns.

Horn length and body size were measured to the nearest 0.01 mm with dial calipers. We measured head horn length (hereafter simply referred to as horn length, unless otherwise specified) as the straight-line distance from the clypeus to the horn tip (Eberhard & Gutierrez, 1991; Kawano, 1995; Knell et al., 2004), and body size as pronotum width (see Emlen, 1997, for justification). Our results were qualitatively the same when we used elytra length instead of prothorax width as the measure of overall body size (McCullough, 2012). Males with visible signs of injury were measured, but only those with intact and undamaged horns were included in the allometric analyses. Analyses were performed on log-transformed data. Our complete data set included measurements from 31 species, representing 16 genera (Supplementary Material).

Visual inspection of the log—log scatterplots suggested that the relationships between horn length and body size were nonlinear for nearly all species. We therefore followed the recommendations of Knell (2009) to characterize possible nonlinear allometries. For each species, we compared five models on the basis of their goodness of fit (using Akaike's information criterion, AIC) to determine which model gave the best description of the relationship between horn length and body size: (1) a simple linear model, (2) a quadratic model and (3) three different breakpoint models of the form: horn length = body size × morph, where morph is a factor distinguishing major and minor males. For the breakpoint models, individuals were separated into the two morphs based on either a threshold body size (following the procedure outlined in Eberhard & Gutierrez, 1991) or a threshold horn length (following the procedure outlined in Kotiaho & Tomkins, 2001), or by examining a frequency histogram of the ratio between horn length and body size to determine a threshold ratio (following the basic approach of Cook & Bean, 2006). We chose the model with the lowest AIC score as the best-fit allometric model. Models with AIC scores that differ by less than 2 are considered to be indistinguishable from each other in their explanatory power (Burnham & Anderson, 2002), but this was an issue for only two species. In both cases, the competing models were different breakpoint models, and thus equally parsimonious, so we selected the model with the lowest AIC score.

We found that 30 of the 31 species had breakpoint allometries (see Results, Fig. 1). We therefore conducted further analyses to explore the scaling relationships between horn length and body size for the major and minor morphs. The remaining species (Heterogomphus hirtus) had a quadratic allometry with a decreasing slope. We include the raw morphometric data for this species in our supplemental data file, but we excluded it from subsequent analyses on the dimorphic species.

We calculated the residuals from the least squares regression of log median horn length on log median body size as an index of horn exaggeration across species (Knell et al., 2004; Simmons & Tomkins, 1996; see Results, Fig. 2). A positive residual indicates that the species has a longer, or more exaggerated, horn than expected for its body size, while a negative residual indicates that the species has a shorter, or less exaggerated, horn than expected for its body size. We used median horn length and body size rather than means because the median is more robust to outliers and therefore less likely to be affected by potential collection biases for very large males (Knell et al., 2004).

Because most species have both a head horn and a thoracic horn, we also calculated a composite measure of horn exaggeration (i.e. an index of total horn investment) by adding the lengths of the head horn and thoracic horn. (In Chalcosoma atlas and Coelosis bicornis, we calculated total horn investment by adding head horn length and twice the thoracic horn length, because males have a pair of thoracic horns.) Thoracic horn length was measured as the straight-line distance from the base of the pronotum to the horn tip.

We examined the relationships between horn exaggeration, total horn investment and allometric slopes using general linear models. As yet, there is no complete phylogeny for the Dynastinae, so we were unable to use robust comparative analyses that take into account tree topologies and branch lengths. We therefore used taxonomy to account for shared evolutionary history, which is preferable to ignoring evolutionary history altogether (Freckleton, 2009; Sunday, Bates, & Dulvy, 2011). Specifically, we controlled for the nonindependence of the data due to phylogenetic relatedness by using linear mixed effects models with genus as a random effect using the lme function in R (Blackburn & Duncan, 2001; Sodhi et al., 2008; Sunday et al., 2011; Woods & Smith, 2010).
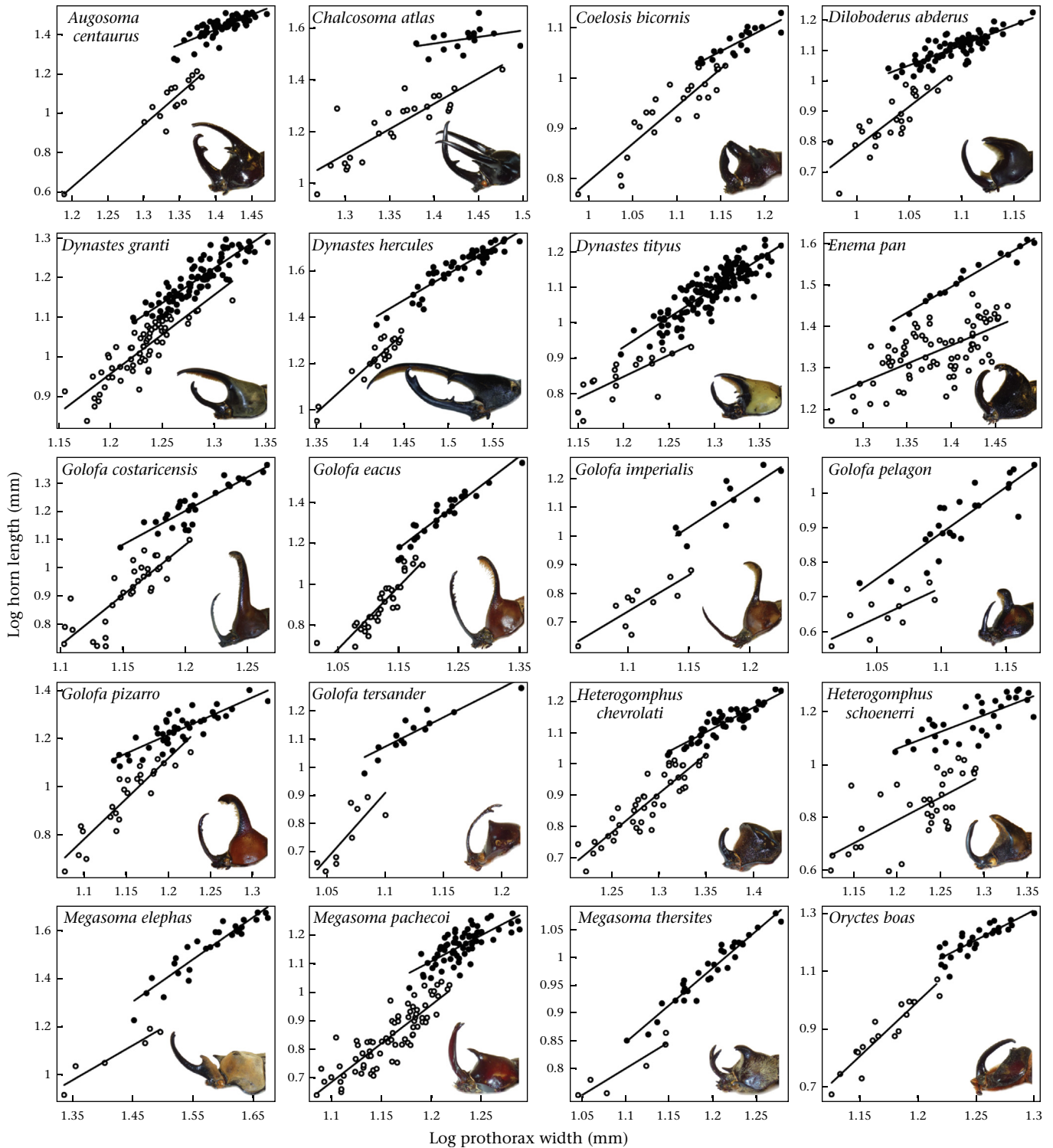
Figure 1. Variation in the allometric relationships between horn length and body size among the 30 dimorphic species. Closed circles represent major males, and open circles represent minor males.

RESULTS

Nearly all of the rhinoceros beetles that we measured and analysed were male dimorphic; 30 of the 31 species had a discontinuous breakpoint allometry, with different lines describing the relationship between horn length and body size for major and minor morphs (Fig. 1). The two morphs overlapped considerably in both horn length and body size in most species (22 species, 73%), so the morphs were best separated by calculating the ratio of horn length to body size. Of the remaining species (Fig. 2), there were seven (23%) in which the two morphs were best separated by a threshold horn length, and one (3%) in which the two morphs were best separated by a threshold body size.
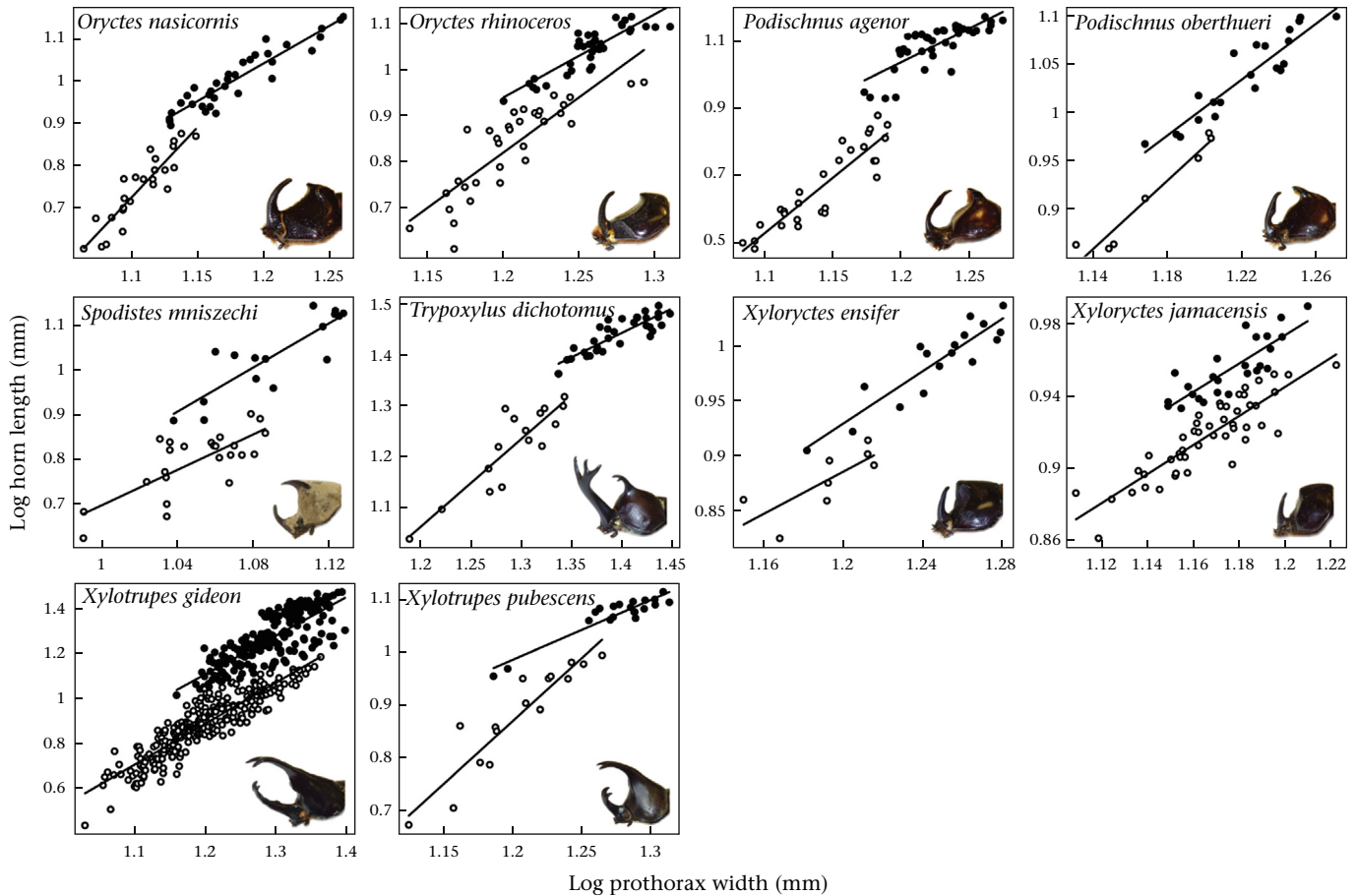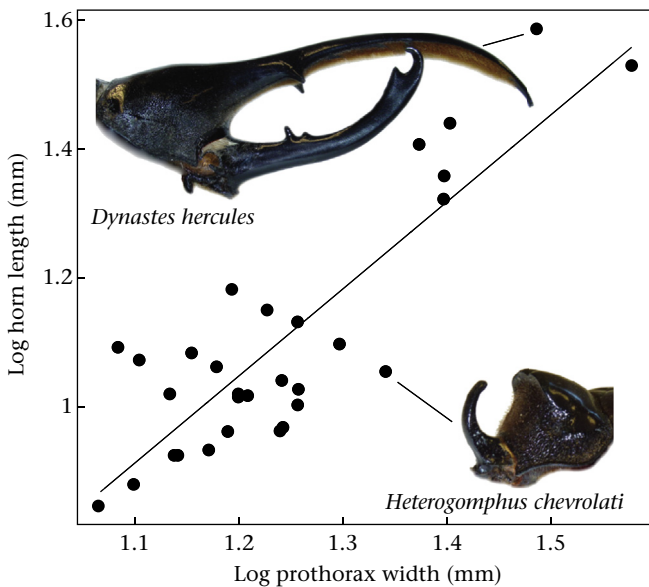
Figure 1. (continued).

Figure 2. Interspecific relationship between median horn length and median pronotum width ($F_{1,28} = 76.6$, $R^2 = 0.73$, $P < 0.001$). Insets show examples of species with a positive residual horn length (i.e. high degree of horn exaggeration, *Dynastes hercules*) and a negative residual horn length (i.e. low degree of horn exaggeration, *Heterogomphus chevrolati*).

Table 1 reports the median horn length, median body size and horn allometry of major and minor males for all dimorphic species. There was a significant positive relationship between residual horn length and median head horn length among species ($F_{1,28} = 10.24$, $R^2 = 0.27$, $P < 0.001$), indicating that species with relatively longer horns also had absolutely longer horns. There was also a significant positive relationship between residual horn length and total investment in horns ($F_{2,20} = 7.54$, $R^2 = 0.43$, $P < 0.001$; with prothorax width included as a covariate to remove the effect of body size), which is attributed, at least in part, to the positive correlation between median head horn length and median thoracic horn length ($F_{1,21} = 13.59$, $R^2 = 0.39$, $P = 0.001$). These results indicate that males do not invest in head horns at the expense of thoracic horns (or vice versa).

The allometric slopes were significantly steeper for minor males than for major males ($t_{29} = 3.56$, $P = 0.001$). The mean ± SD slope was 2.32 ± 0.98 for minor males and 1.67 ± 0.56 for major males. Both morphs had allometric slopes that were significantly greater than 1 (minor males: $t_{29} = 7.36$, $P < 0.001$; major males: $t_{29} = 6.59$, $P < 0.001$). There was a significant positive relationship between the allometric slope of minor males and residual horn length ($F_{1,28} = 9.18$, $R^2 = 0.25$, $P < 0.01$), but there was no relationship between the allometric slope of major males and residual horn length ($F_{1,28} = 0.22$, $R^2 = 0.01$, $P = 0.64$; Fig. 3). These results indicate that minor males exhibit steeper scaling relationships in species with more exaggerated horns. There was also a significant positive relationship between residual horn length and the difference in slopes between minor and major males ($F_{1,28} = 17.28$, $R^2 = 0.38$, $P < 0.001$; Fig. 4), indicating that species with more

Table 1
Sample size, median body size, median horn length and allometric slope of minor and major males of all dimorphic rhinoceros beetle species included in the study

Species	N	Body size (mm)	Horn length (mm)	Minor slope	Major slope
Augosoma centaurus	83	25.29	27.57	3.18	1.50
Chalcosoma atlas	42	24.93	21.02	1.95	0.51
Coelosis bicornis	44	13.61	10.48	1.50	0.91
Diloboderus abderus	106	12.13	12.37	2.66	1.33
Dynastes granti	158	18.05	13.54	1.99	1.76
Dynastes hercules	71	30.63	38.63	3.45	2.24
Dynastes tityus	172	19.79	12.53	1.23	1.66
Enema pan	95	24.97	22.82	0.90	1.25
Golofa costaricensis	63	15.08	11.54	3.56	2.40
Golofa eacus	58	14.28	12.13	3.07	2.26
Golofa imperialis	22	13.84	8.41	2.55	2.79
Golofa pelagon	34	12.55	7.57	1.74	2.65
Golofa pizarro	70	15.62	15.22	3.38	1.57
Golofa tersander	24	12.71	11.83	4.67	2.09
Heterogomphus chevrolati	94	21.91	11.36	2.50	1.57
Heterogomphus schoenherri	68	18.06	10.06	1.72	1.25
Megasoma elephas	35	37.79	33.87	1.45	1.76
Megasoma pachecoi	144	15.83	10.47	2.71	1.83
Megasoma thersites	38	15.46	9.16	0.95	1.33
Oryctes boas	47	16.87	14.14	3.79	2.07
Oryctes nasicornis	59	13.73	8.40	3.33	1.79
Oryctes rhinoceros	70	17.43	9.27	2.41	1.82
Podischnus agenor	68	15.84	10.36	3.31	2.02
Podischnus oberthueri	29	16.17	10.40	1.78	1.45
Spodistes mniszechi	40	11.62	7.01	2.00	2.49
Trypoxylus dichotomus	49	23.62	25.55	1.73	0.96
Xyloryctes ensifer	25	17.36	9.18	0.97	1.20
Xyloryctes jamaicensis	73	14.82	8.58	0.80	0.79
Xylotrupes gideon	480	17.43	11.00	1.82	1.72
Xylotrupes pubescens	36	18.08	10.64	2.39	1.14

exaggerated horns exhibit a greater decrease in allometric slope between minor and major males. This relationship remained significant even after controlling for phylogenetic relatedness ($t_{14} = 4.26$, $P < 0.001$).

Many specimens showed signs of injury from fights, including scratches and punctures on their elytra or pronota, and chipped or broken horns. On average, 7% (maximum = 17%) of the specimens for a given species showed some sign of injury, and 3% (maximum = 9%) of the specimens had broken horns. There was a weak, positive relationship among species between residual horn length and the frequency of injuries ($F_{1,28} = 3.72$, $R^2 = 0.12$, $P = 0.06$), suggesting that species with more exaggerated horns suffer higher rates of damage from fights.

DISCUSSION

We found strong evidence for male dimorphism in the rhinoceros beetles. Nearly all of the species surveyed had discontinuous, breakpoint allometries, indicating the presence of two male morphs. The two morphs, however, were relatively cryptic (sensu Cook & Bean, 2006), because there was substantial overlap in both horn length and body size. These results contrast with the patterns observed in horned dung beetles and other dimorphic insects in which males transition from having no horns to having fully sized horns over a narrow range of body size (Cook, 1987; Eberhard & Gutierrez, 1991; Emlen, 1997; Moczek, 1998). Previous authors have argued that the ability to developmentally switch from minimal to maximal trait expression may have facilitated the evolution of exaggerated morphologies by uncoupling the phenotypes of large and small individuals, thereby allowing the two size classes to evolve relatively independently (Emlen & Nijhout, 2000; West-Eberhard, 1989, 1992). Our results do not support this hypothesis. Despite the impressive size of rhinoceros beetle horns, there were no species that transitioned abruptly from minimal to complete horn expression, which indicates that the developmental capacity

to prevent horn growth in small individuals is not necessary for the evolution of exaggerated morphologies.

Male dimorphisms are common among insects and are typically associated with alternative reproductive tactics (Gross, 1996; Oliveira, Taborsky, & Brockmann, 2008). For example, in many horned dung beetles, large 'major' males use their horns as weapons to guard the entrances of tunnels and fight with rival males over access to females, while small hornless 'minor' males rely on sneaking behaviours to gain matings inside the tunnels guarded by larger males (Cook, 1987; Emlen, 1997; Moczek & Emlen, 2000; Rasmussen, 1994). Unfortunately, very few rhinoceros beetle species have been studied rigorously in the field, so it is largely unknown whether the two morphs identified by our allometric analyses use different tactics to gain matings. In the South American rhinoceros beetle *Podischnus agenor*, there is evidence that minor males emerge earlier in the season and have a greater tendency to disperse than major males, which may represent a nonaggressive satellite tactic to reduce the probability of direct combat with major males (Eberhard, 1982). However, in the Asian rhinoceros beetle *Trypoxylus dichotomus*, there are no apparent differences in behaviour between morphs: both minor and major males use their horns to fight with rivals, and both have been found using sneaking behaviours (Hongo, 2003, 2007). These observations highlight the need for more behavioural studies on natural populations of rhinoceros beetles, because discrete morphological morphs do not necessarily correspond to discrete behavioural morphs (Knell, 2009).
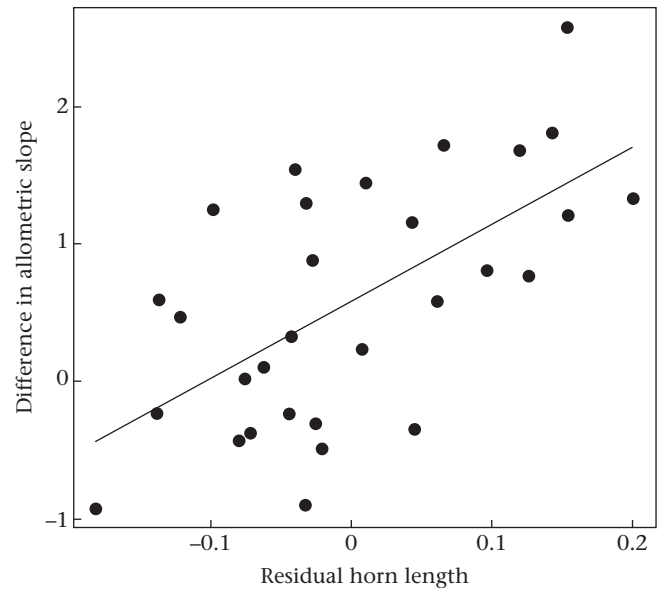
Both major and minor males showed steep positive allometries, and there was a positive correlation between the allometric slope of minor males and residual horn length. These results are consistent with the patterns found in the scaling relationships of earwig forceps and stalk-eyed fly eyespans, in which species with the most intense sexual selection also have the steepest allometric slopes (Baker & Wilkinson, 2001; Simmons & Tomkins, 1996). Although we recognize that not all traits exhibiting positive allometries are
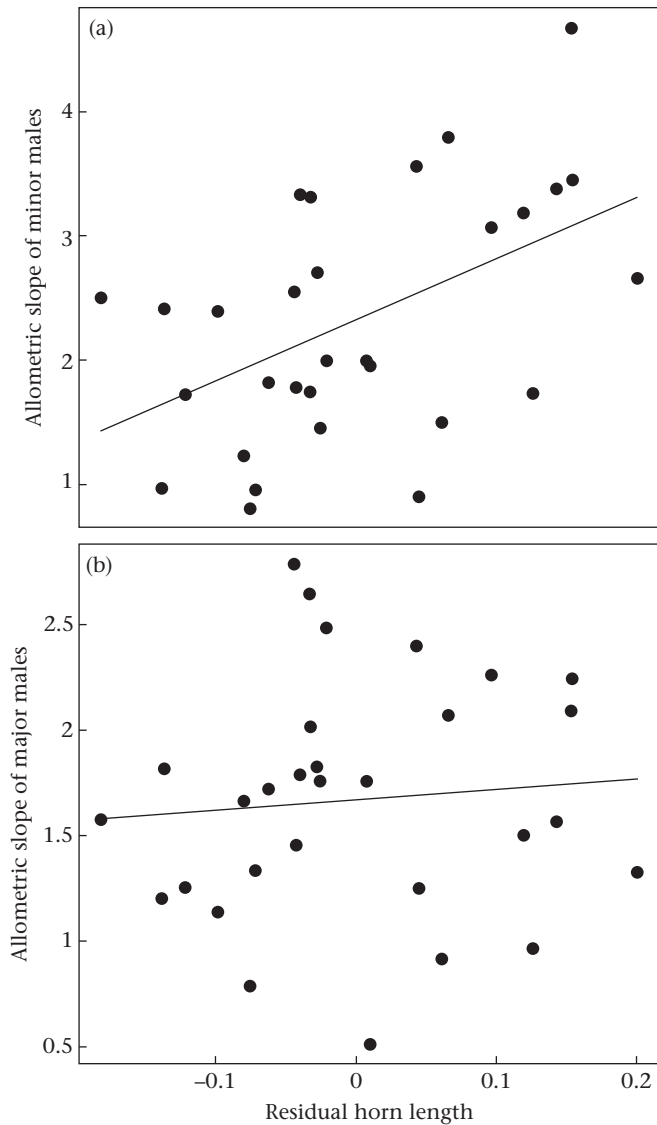
Figure 3. Relationships between residual horn length and allometric slope for (a) minor males ($R^2 = 0.25$, $F_{1,28} = 9.18$, $P < 0.01$) and (b) major males ($R^2 = 0.01$, $F_{1,28} = 0.22$, $P = 0.64$).

Figure 4. Relationship between residual horn length and the difference in allometric slope between minor and major males ($F_{1,28} = 17.3$, $R^2 = 0.38$, $P < 0.001$).

sexually selected, and not all sexually selected traits are positively allometric (Bonduriansky, 2007), we expect sexual selection to be the primary force driving the positive allometry of rhinoceros beetle horns. Theoretical models predict sexual selection to favour the evolution of traits with particularly steep allometries when male–male competition is intense and trait differences decisively determine the outcomes of competitive interactions (Fromhage & Kokko, 2014). These conditions are characteristic of rhinoceros beetle mating systems; in all species studied to date, horns are used exclusively in the context of intense male–male battles, horn length is the determining factor in the outcome of fights, and males with the longest horns win (Beebe, 1944; Eberhard, 1980; Hongo, 2003, 2007; Karino, Niiyama, & Chiba, 2005; Siva-Jothy, 1987).

In contrast to the positive correlation between residual horn length and the allometric slope of minor males, there was no relationship between residual horn length and the allometric slope of major males. Major males generally had shallower slopes than minor males, and the difference in slope depended on residual horn length: species with relatively long horns showed a greater

decrease in slope between major and minor males than did species with relatively short horns. These patterns mirror the curved allometries of stag beetle mandibles (Huxley, 1932; Knell et al., 2004) and the tapered allometries of giraffe weevil rostra (Painting & Holwell, 2013), and suggest that asymptotes in maximum trait size are common among beetles and other holometabolous insects with exaggerated weapons.

We predict that the decline in slope from minor to major males reflects a limitation in resource allocation during horn growth (Knell et al., 2004; Nijhout & Wheeler, 1996; Tomkins, Kotiaho, & LeBas, 2005a). Because beetle horns develop from a finite resource pool after the larva has stopped feeding, the growth of very large horns may locally deplete developmental resources, and thereby limit further allometric growth (Knell et al., 2004; Tomkins et al., 2005a). In particular, large individuals of species with relatively long horns are the most likely to suffer from resource allocation constraints, which helps explain why the decline in allometric slopes between major and minor males is greatest among species with the largest residual horn lengths, and thus the most exaggerated horns (Knell et al., 2004).

There are at least three alternative explanations that could also account for the decline in slope between major and minor males. First, the fitness gain from greater investment in horns may decrease with body size. For example, if major males already have a competitive advantage over most males in the population due to their large size, they may not face strong selection to invest further in horn growth (Painting & Holwell, 2013). Future studies should therefore measure the relative benefits of horn investment across the full range of male body size to examine how different fitness functions may affect the shape of horn allometries (Bonduriansky & Day, 2003; Pomfret & Knell, 2006).

Second, resource allocation trade-offs with other fitness-enhancing traits may prevent major males from investing more in horns. Previous studies on armed insects have shown that the development of exaggerated weapons often comes at a cost to the development of other body parts, such as eyes, wings or testes (Emlen, 2001; Nijhout & Emlen, 1998; Simmons & Emlen, 2006; Yamane, Okada, Nakayama, & Miyatake, 2010), so strong selection on a male's ability to see, fly or invest heavily in sperm may

constrain the further exaggeration of horns (Emlen, 2001; Yamane et al., 2010).

Third, increasingly larger horns may be prohibitively costly if males cannot also invest more in compensatory or supportive traits. Sexually selected weapons are often accompanied by changes in morphology and physiology that either mitigate the costs of bearing these structures (Husak & Swallow, 2011; Oufiero & Garland, 2007), or enhance a male's ability to use them in mal-e−male combat (Okada & Miyatake, 2009; Tomkins, Kotiaho, & LeBas, 2005b). For example, male stalk-eyed flies have larger wings and thoraces than females, which may offset the costs of flying with their exaggerated eyespans (Husak, Ribak, Wilkinson, & Swallow, 2011; Ribak & Swallow, 2007; Swallow, Wilkinson, & Marden, 2000), and male earwigs with relatively large forceps also have relatively large hindlegs, which presumably helps them wield the weapons and improves their fighting success (Tomkins et al., 2005b). Because selection should favour individuals that can use, display and bear their weapons most effectively, male rhinoceros beetles may not benefit from developing larger horns unless there are commensurate changes in their integrated body plan.

There was a significant correlation between investment in head horns and thoracic horns, and the scaling relationships of thoracic horns were very similar to those of head horns (McCullough, 2012). These observations suggest that head and thoracic horns are developmentally coupled, but further work is needed to determine whether this link is due to the same genetic mechanism for horn growth, or similar selection on head and thoracic horns as an integrated fighting structure (Okada & Miyatake, 2009; Tomkins et al., 2005b). However, species also differ in the number and location of thoracic horns (e.g. thoracic horns can develop from the front, middle or sides of the pronotum), and future studies should examine whether these differences contribute to the variation in the size and scaling relationships of head horns among species. For example, if multiple thoracic horns constrain the development of wings and other neighbouring body parts (Emlen, 2001; Kawano, 1995; Nijhout & Emlen, 1998), then species that must fly long distances for food or mates may be selected to invest less in thoracic horns (Emlen, 2001), and concomitantly may invest less in head horns.

Finally, we note that this study only examined variation in horn length, even though species also vary dramatically in horn shape. Interspecific differences in horn morphology are likely to reflect structural adaptations to species-specific fighting styles (McCullough et al., 2014), but little is known about how horn morphology varies within species across the range of body size, and whether these changes also reflect structural adaptations to meet the mechanical demands of fighting. We recently found that, in the Asian rhinoceros beetle Trypoxylus dichotomus, the second moment of area of horns (a measure of cross-sectional shape) increased with horn length in a way that preserved the horns' performance as a stiff and strong weapon (McCullough, Ledger, & Moore, 2015). However, these relationships may differ among species depending on the style and intensity of fights (Kitchener, 1985, 1991; McCullough, 2014; McCullough et al., 2015). Studies that compare the fighting behaviours and performance of horns within and among species will be important for understanding the variation in scaling relationships of rhinoceros beetle horns and other animal weapons.

Acknowledgments

Supplementary Material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2015.08.013.

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