



## Variation in the allometry of exaggerated rhinoceros beetle horns



Erin L. McCullough<sup>a, b, \*</sup>, Kimberly J. Ledger<sup>a</sup>, Devin M. O'Brien<sup>a</sup>, Douglas J. Emlen<sup>a</sup>

<sup>a</sup> Division of Biological Sciences, University of Montana, Missoula, MT, U.S.A.

<sup>b</sup> Centre for Evolutionary Biology, University of Western Australia, Crawley, Western Australia, Australia

### ARTICLE INFO

#### Article history:

Received 1 June 2015

Initial acceptance 8 July 2015

Final acceptance 27 July 2015

Available online

MS. number: A15-00468R

#### Keywords:

allometry  
dimorphism  
Dynastinae  
horn  
rhinoceros beetle  
scaling  
sexual selection

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.

© 2015 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

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).

\* Correspondence: E. L. McCullough, Centre for Evolutionary Biology, M092, University of Western Australia, Crawley, WA 6009, Australia.

E-mail address: [mccullough.e@gmail.com](mailto:mccullough.e@gmail.com) (E. L. McCullough).

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  $\times$  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).

Download English Version:

<https://daneshyari.com/en/article/8489591>

Download Persian Version:

<https://daneshyari.com/article/8489591>

[Daneshyari.com](https://daneshyari.com)