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Horn scaling relationships in three species of *Bledius* Leach 1819 (Insecta: Coleoptera: Staphylinidae) show no indication of fitting non-linear allometric models

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Abstract

The males of some species of the rove beetle genus *Bledius* Leach (1918) have a pronounced horn protruding from the anterior margin of the pronotum. Their function is not known, however in many other horn-bearing beetles, these structures are implicated in male-male combat over females. In this study, scaling relationships are investigated for three species; *B. spectabilis* Kraatz 1857, *B. frisius* Lohse, 1978 and *B. tricornis* (Herbst, 1784). Based on data collected from museum specimens, we fitted and compared different allometric models on pronotal width versus horn length in each species. A simple linear allometric model best describes the scaling relationship of horns in all three species. The horn allometry in the three *Bledius* species do accordingly not follow a 'switch point' model or a curved allometric relationship, models that are commonly reported to explain the scaling relationship of horns in many other beetle species. We therefore found no evidence of male dimorphism (minor/major phenotypes) in the species examined. The potential function of the horn in *Bledius* is discussed in light of similar studies.

Keywords: *Bledius,* Coleoptera, horns, allometry

Introduction

Beetles (Coleoptera) exhibit a range of exaggerated traits, across many different lineages. Exaggerated traits manifest themselves as enlarged appendages, e.g. legs, lengthened mandibles and horns, particularly in males (e.g. Arrow 1951; Emlen and Nijhout 2000; Kawano 2002, 2004). These exaggerated traits are typically used in male-male combat, in order to gain reproductive opportunities with females, or access to a desired resource, e.g. dung, carrion, etc. Spectacular horns or remarkably enlarged mandibles are particularly prevalent in the beetle families Scarabaeidae and Lucanidae. In fact, the concepts of relative growth and allometry particularly relevant for exaggerated traits were originally described partly based on the study of beetle horns (Huxley 1932). Ever since, those concepts have been developed extensively, especially in insects (for a review, see Emlen and Nijhout 2000).

Allometries are usually described by power functions on the form $Y = aX^b$ (Huxley 1932), where b is the scaling exponent that describes how the trait Y relates to changes in the overall size variable X. In a positive allometric relationship ($b>1$) smaller individuals are associated with proportionally smaller traits compared to larger individuals. In a negative allometric relationship ($b<1$) larger individuals possess traits that are proportionately smaller than in smaller individuals. In an isometric relationship ($b=1$) body parts scale proportionately with overall body size. On a log–log scale, a power law yields a linear model with intercept $\log(a)$ and exponent b. The value of the scaling exponent has attracted a lot of attention and has often been interpreted as indicating the type of selection acting on the trait. For example, if individuals with a larger relative trait size obtains an increased mating success compared to individuals with smaller relative traits, a steep allometric exponent will be the result (due to sexual selection) according to the positive allometry hypothesis (e.g., Green 1992; Petrie 1992). However, there are many examples of sexually selected traits that are not following the prediction of having a static slope larger than 1 (Bonduriansky 2007; Voje 2016).

Rove beetles (Coleoptera: Staphylinidae) exhibit an extraordinary diversity with more that 64,000 described species (Newton, 2019), however few studies have investigated exaggerated traits or allometry in the family. In relation to the rove beetle genus *Siagonium* (Piestinae), Darwin (1871; page 374) stated that "...we have a case of dimorphism for the males can be divided into two sets, differing greatly in the size of their bodies, and in the development of their horns, without any intermediate gradations". Hanley (2001) analysed mandibular allometry in seven species of *Oxyporus* (Oxyporinae). Five of the seven species of *Oxyporus* studied exhibited bimodality of mandible length. Hanley (2001) suggested this was due to differential male mating strategies. Similarly, Forsyth and Alcock (1990) found mandibular dimorphism in males of *Leistotrophus versicolor* (Staphylininae), a neotropical rove beetle with an interesting mating system. They suggested an allometric relationship in mandible length in this species but did not fully investigate it statistically. Major males of *L. versicolor* have enlarged mandibles used for fighting rival males in order to secure desired mating sites such as dung and carrion. Minor males have smaller mandibles, resembling those of females. Minor males can therefore evade aggression from major males and remain at dung or carrion sites where they feed and obtain reproductive opportunities with females.

The pronotal horns in the rove beetle genus *Bledius* Leach 1819 have been known to the biological community for a long time. At least 100 species of *Bledius* bear cephalic and/or pronotal horns (Herman 1986). Despite this, investigators of beetle horns have overlooked these structures in this relatively species-rich genus. Sexual dimorphism, in horn-bearing *Bledius* was noted by Darwin (1871) where he illustrated male and female *Bledius taurus* (=*Bledius furcatus* (Olivier, 1811)). Arrow (1951) mentions *Bledius* once in his work on beetle horns, merely to draw attention to the fact that some species bear horns. It is relevant to note that only males have pronotal horns except in *Bledius susae* Herman from Texas in which the female bears a pronotal horn but lacks cephalic horns (Herman 1986).

Observations relating to the function of the horns in *Bledius* are scant at best. Haworth (1812; page 314) suggested that *Bledius tricornis* males may use their horns ". . . to overcome his reluctant female, in her subterranean retreats". Burrell (1812) observed a male *B. tricornis* insert its head into a hole and attempt to draw something out of it. Soon after, the male brought a female out from the hole, their maxillae appearing locked to each other. The male then moved his maxillae to the back of the female's head. The female then escaped and fled back to the hole pursued by the male. Upon digging, Haworth then reports finding them mating. Although these observations are important, they do not shed light on the function of the horn. It has also been proposed that perhaps the horns are used to push intruders out of the burrow (Howard Frank, personal communication in Herman (1986)).

Bledius are notorious for the fact that they are burrow dwelling, algae feeding (Herman 1986), and predated upon by species of *Dyschirius* (Carabidae) (e.g. Frank 1985). Wyatt (1986) studied aspects of the ecology and biology of *Bledius spectabilis* Kraatz 1857. Wyatt (1986) found that all stages of this species construct burrows in the intertidal area of coastal localities. The adult female lays eggs in chambers attached to the main burrow, where the female remains with the brood in order to prevent flooding of the chamber. The larvae disperse from the maternal burrow at the end of the first larval instar (Wyatt & Foster 1989).

In this paper we characterise scaling relationships of an exaggerated trait (the pronotal horn) in the genus *Bledius* for the first time. The specific function of the horns remains unknown. We discuss the possible function of this exaggerated trait in the light of our findings and other well studied, horn-bearing beetles.

Material and methods

Taxonomy of the studied Bledius

The genus *Bledius* was first described by Leach (1819) based on a single European species. According to Herman (1986) there are 439 extant, valid species worldwide. In the British Isles (Britain, Ireland and the Isle of Man but not including the Channel Islands), there are 28 species grouped into seven subgenera as follows [the number of species within each subgenus is given in brackets]; *Astycops* (1), *Bargus* (10), *Bledius s. str.* (4), *Dicarenus* (2), *Elbidius* (3), *Euceratobledius* (1), *Hesperophilus* (7).

During the course of this study the following species were observed and measured: *Bledius spectabilis* Kraatz 1857 (Fig. 1), *Bledius frisius* Lohse, 1978 and *Bledius tricornis* (Herbst, 1784). The three species belong to the nominative subgenus *Bledius* that contains 4 species in the British Isles. In all three species males are characterised by a straight horn protruding from the anterior of the pronotum, which passes over the dorsum of the head (Lott 2009) (Fig. 1). Females lack the pronotal horns.

For the purposes of consistency, the names referred to in this manuscript follow the most recent checklist of Beetles of the British Isles (Duff 2012). An extensive four-part monograph of the genus was produced by Herman (1972, 1976, 1983 and 1986). In addition, Schülke (2010) synonymized *Bledius limicola* Tottenham 1940 with *B. spectabilis* Kraatz 1857, and elevated *Bledius frisius* Lohse, 1978 from subspecies to

species level. Hammond (2000) had previously referred to *Bledius frisius* Lohse, 1978 as a subspecies of *B. spectabilis* Kraatz 1857.

Measurements

We measured 206 male specimens from the British Coleoptera collection of the BMNH (Natural History Museum, London). All 206 specimens were measured by the same person (J.J.S.); 106 *Bledius spectabilis* Kraatz, 1857, 54 *B. frisius* Lohse, 1978 and 46 *B. tricornis* (Herbst, 1784). Specimens were collected from various locations across the United Kingdom. For many specimens, location data was either absent entirely or restricted to counties. Geographic variation was therefore not possible to account for in downstream analyses. Specimens were photographed using a Canon EOS 700D and Canon EF 100mm Macro lens on standardized settings (Programme mode; ISO400; standard exposure; with flash) illuminated by a Meiji Techno FL-150 Fiber Optic Light Source. Measurements were obtained from images using the free software ImageJ (Schneider et al. 2012). Measurements were taken as straight-line distances between two points (Fig. 1A). Due to the pronotal horns being fused to the anterior margin of the pronotum, horn length (Fig. 1A, HL) was taken from the tip of the horn to the posterior margin of the pronotum. Width of the pronotum (Fig. 1A, PW) was taken at the widest point as an indication of overall body size, as in Miller and Wheeler (2005) and Eberhard (1998). In most cases the widest point of the pronotum was just in front of the middle. There is some variation in how authors interpret overall body size in allometric studies. For example, Miller and Wheeler (2005) and Emlen and Nijhout (1999) used pronotal width whilst Eberhard et al. (2000) used pronotal length. Hanley (2001) used elytra length and Rowland and Emlen (2009) used elytra width. Pronotal width was used in this study due to the ease of measuring this trait from photographs and because some specimens were lacking elytra.

Statistics

All statistical analyses were carried out in R version 3.2.1 (R Core Team 2015). Traits were (natural) log transformed prior to statistical analysis. Log transformation makes traits scale-independent (Kerkoff et al. 2009; Shingleton et al. 2013) and is the preferred method for studies on allometry (Voje et al. 2014). We used ordinary least-squares regression to estimate linear static allometries for each of the three species. Since a number of beetle species have been found to deviate from the linear allometric model (e.g. Elmen 1996; Pomfret and Knell 2006; Knell 2009; McCullough et al. 2015), we also fitted a quadratic model and a single break-point model (following Eberhard and Guiterrez 1991) to investigate for non-linear allometries within these species. A single breakpoint model was fitted using the package Segmented (Muggeo, 2003) using the segmented function. We used AIC to investigate the relative fit of the three models.

Results

The three species show a similar overall size based on the size of the pronotum, while the length of the horn differs substantially across the species (Table 1). The linear allometric model had a better (lower) AIC score compared to the non-linear allometric

models for all three species (Figs 2-4, Table 2). Horn length shows a positive allometric scaling relationship with overall size in all three species, albeit the slope of *Bledius tricornis* is not statistically significantly different from 1 (Table 1). The coefficient of determination (R^2) is above 0.67 for the linear allometric model for all three species (Table 1).

Discussion

The literature examining sexual dimorphism and scaling relationships of exaggerated traits in beetles is extensive (e.g. Kawano 2002; 2004; Knell et al. 2004; McCullough et al. 2015). Sexually selected traits in males, such as horns, tend to show positive allometric relationships (e.g. Kawano 2004) and many species fit non-linear allometric models (e.g. Emlen 1996; Hanley 2001; Knell et al. 2004; Miller & Wheeler 2005; Knell 2009; McCullough et al. 2015). The scaling relationships of horn versus pronotum width in the three species of *Bledius* studied here were linear rather than non-linear (Figs 1, 2, 3; Tables 1, 2). Non-linear allometries may be the result of polyphenism (one genotype may produce two or more phenotypes), which is often associated with differential reproductive strategies. This has previously been shown in the beetle *Onthophagus taurus* (Scarabaeidae) (Moczek et al. 2002). Lack of evidence for non-linear allometries within the three *Bledius* species indicates no male dimorphism in horns, which is consistent with the hypothesis of similar reproductive strategies for males independent of their horn size. Whether this is true or not must be determined by behavioural studies, which are badly needed for *Bledius*.

Two previous allometric studies on Staphylinidae (Forsyth & Alcock 1990; Hanley 2001) discovered the presence of male dimorphism in the rove beetles they studied: *Leistotrophus versicolor* (Staphylininae) and the genus *Oxyporus* (Oxyporinae), respectively. Thayer (1992) also reported sexual dimorphism in the wings of *Omalium flavidum* (Omaliinae). Both Forsyth and Alcock (1990) and Hanley (2001) suggested that differential reproductive strategies might explain the presence of male dimorphism in the species they studied. The allometric scaling relationships found here lacked 'switch points' when analysed using regression models (Figs 2-4, Tables 1, 2). This suggests a lack of male dimorphism, and perhaps, therefore, a lack of differential reproductive strategies. Additionally, and in line with the results of the current study, Marlowe et al. (2015) reported positive linear allometric relationships in both sexes of the rove beetle *Triacrus dilatus* Nordmann, 1837 (Staphylininae), and found no evidence of dimorphism in either sex.

Similarities may be observed in the ecology of *Onthophagus* (Scarabaeidae) and *Bledius*. All species in both genera, as far as is known, are tunnel-builders. In *Onthophagus*, females dig tunnels under dung and males guard tunnels from rival males to obtain mating opportunities (Emlen 2011). In *Bledius*, the sex that digs tunnels seems to be unknown. Females lay eggs in chambers attached to the main burrow, where the female will remain during the development of her offspring (Wyatt 1986). It is possible that, like *Onthophagus*, horn-bearing male *Bledius* may guard burrows from rivals and engage in male-male combat in order to gain access to a female within the burrow and therefore obtain reproductive opportunities. Like species of *Bledius*, females of *Oxyporus japonicus* studied in Hanley (2001) remain with eggs in a chamber in order to protect them from conspecifics and other predatory beetles. This behaviour was termed

subsocial (Setsuda 1994) and also applies to *B. spectabilis* (Wyatt 1986; Wyatt & Foster 1989). This subsocial behaviour is possibly an adaptation to ephemeral environments; fungi in the case of *Oxyporus* and the intertidal zone in the case of *Bledius spectabilis*.

It is best to infer causes of scaling relationships in the context of ethological observations. Unfortunately, however, behavioural data with regards to the horns in *Bledius* is sparse and embedded in historic literature. The addition of behavioural observations in the wild or in a laboratory would assist in explaining the scaling relationships discovered here. Further studies on *Bledius*, perhaps taking into account geographical location, would be particularly interesting. It was not within the scope of this study to obtain specimens of *Bledius susae* Herman, 1983 as the collection of the BMNH has no specimens of this species (Roger Booth, personal communication). In this species both males and females bear a pronotal horn (Herman 1986), and therefore it would be interesting to see if there is any evidence for dimorphism in horns and allometric relationships both within and between males and females.

This manuscript represents the first estimated allometric scaling relationships in the genus *Bledius* Leach (1819). The lack of male dimorphism suggests that the three species studied do not have alternative strategies, if indeed the horns are implicated in male-male combat. Despite males of many species in the genus bearing horns, they have remained un-investigated in an allometric context. This paper may provide a basis for future studies, which will perhaps incorporate behavioural, physiological or phylogenetic data to provide a more detailed picture of what the horns are used for, and their evolution within the genus.

Declaration of interest statement

The authors declare that there is no conflict of interest.

Data availability statement

The data that support the findings of this study are openly available in Dryad at http://doi.org/[doi], reference number [reference number].

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Tables

Table 1. Allometric parameter estimates and mean trait size for the three *Bledius* species studied. SE = Standard error; SD = Standard deviation.

	intercept (SE)	slope (SE)	R^2	mean horn length (cm) (SD)	mean pronotum length (cm) (SD)
Bledius spectabilis	1.455 (0.203)	1.447 (0.096)	0.68	0.203 (0.020)	0.121 (0.007)
Bledius tricornis	0.707 (0.197)	1.166 (0.093)	0.78	0.174 (0.014)	0.121 (0.008)
Bledius frisius	2.191 (0.277)	1.816 (0.136)	0.78	0.224 (0.032)	0.131 (0.009)

Table 2. The difference in AIC score (ΔAIC) between the best model (score = 0) and the other candidate models. The linear allometric model has a better AIC score for the horn-pronotum relationship in all three species.

	B. frisius	*B. tricornis*	*B. spectabilis*
ΔAIC linear model	0	0	0
ΔAIC quadratic model	1.162	1.649	1.661
ΔAIC break-point model	1.333	3.177	1.247

Figure captions

Figure 1. A. *Bledius spectabilis* Kraatz, 1857 schematic diagram of pronotal measurements taken and habitus. B. *Bledius spectabilis* at Chesil Fleet, Dorset, UK (photograph by Steve Trewhella). HL = horn length; PW = pronotum width.

Figure 2. Scaling relationship between log pronotum width and log horn length in *Bledius spectabilis* Kraatz, 1857. The slope is 1.447 (SE = 0.096) and the linear model has an R^2 of 0.68.

Figure 3. Scaling relationship between log pronotum width and log horn length in *Bledius frisius* Lohse, 1978. The slope is 1.816 (0.136) and the linear model has an R^2 of 0.78.

Figure 4. Scaling relationship between log pronotum width and log horn length in *Bledius tricornis* (Herbst, 1784). The slope is 1.166 (0.093) and the linear model has an R^2 of 0.78.

Data

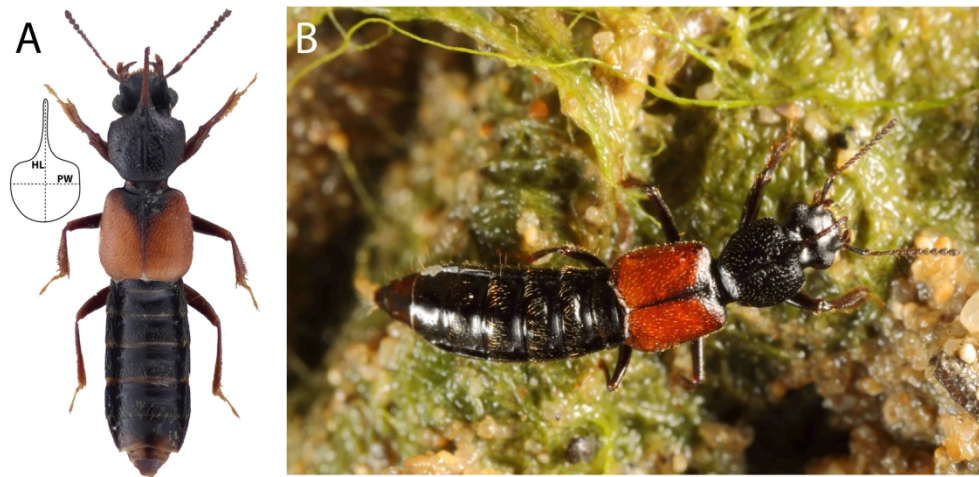The data that support the findings of this study are openly available in figshare at 10.6084/m9.figshare.12168177

Figure 1. A. Bledius spectabilis Kraatz, 1857 schematic diagram of pronotal measurements taken and habitus. B. Bledius spectabilis at Chesil Fleet, Dorset, UK (photograph by Steve Trewhella). HL = horn length; PW = pronotum width.

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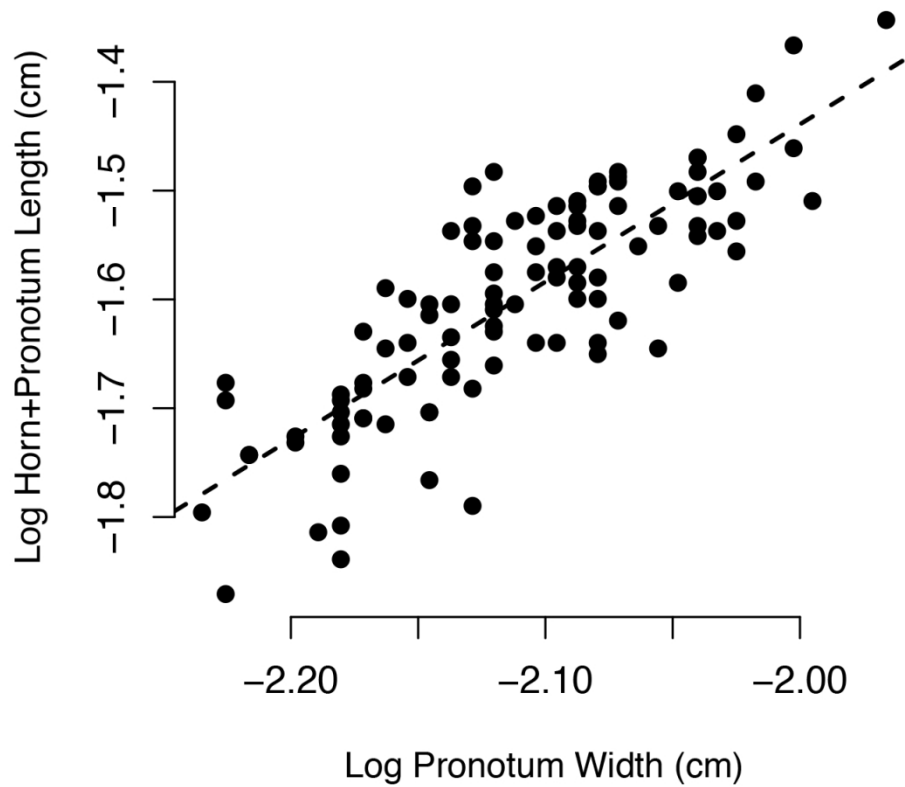42
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Figure 2. Scaling relationship between log pronotum width and log horn length in Bledius spectabilis Kraatz, 1857. The slope is 1.447 (SE = 0.096) and the linear model has an R^2 of 0.68.

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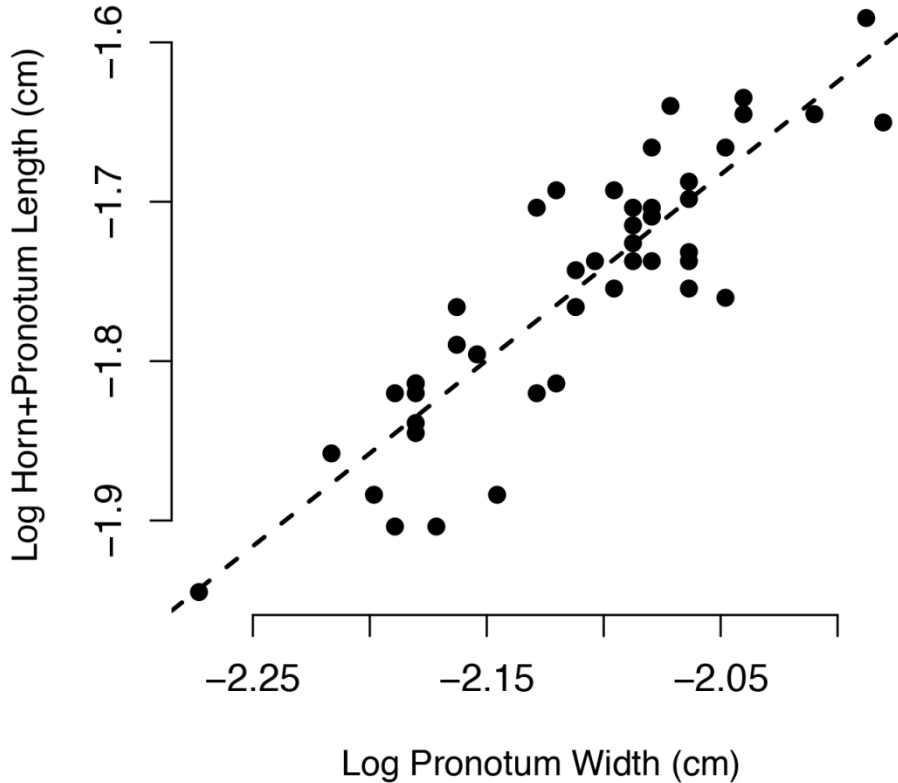41
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Figure 4. Scaling relationship between log pronotum width and log horn length in Bledius tricornis (Herbst, 1784). The slope is 1.166 (0.093) and the linear model has an R2 of 0.78.