



## On the evolution of extreme structures: static scaling and the function of sexually selected signals

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The 'positive allometry hypothesis' predicts that ornaments and weapons of sexual selection will scale steeply when among-individual variation in trait size is compared with variation in overall body size. Intuitive and striking, this idea has been explored in hundreds of contemporary animal species and sparked controversy in palaeobiology over the function of exaggerated structures in dinosaurs and other extinct lineages. Recently, however, challenges to this idea have raised questions regarding the validity of the hypothesis. We address this controversy in two ways. First, we suggest the positive allometry hypothesis be applied only to morphological traits that function as visual signals of individual body size. Second, because steep scaling slopes make traits better signals than other body parts, we propose that tests of the positive allometry hypothesis compare the steepness of the scaling relationships of focal, putative signal traits to those of other body parts in the same organism (rather than to an arbitrary slope of 1). We provide data for a suite of 29 extreme structures and show that steep scaling relationships are common when structures function as signals of relative body size, but not for comparably extreme structures that function in other contexts. We discuss these results in the context of animal signalling and sexual selection, and conclude that patterns of static scaling offer powerful insight into the evolution and function of disproportionately large, or extreme, animal structures. Finally, using data from a ceratopsid dinosaur and a pterosaur, we show that our revised test can be applied to fossil assemblages, making this an exciting and powerful method for gleaning insight into the function of structures in extinct taxa.

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Understanding how morphology scales with body size is one of the most pervasive topics in organismal biology (Gould, 1966, 1974a, 1974b; Dial, Greene, & Irschick, 2008; Huxley, 1932; Schmidt-Nielsen, 1984; Templeton, Greene, & Davis, 2005; Thompson, 1917; Voje, 2016; West & Brown, 2005; West, Brown, & Enquist, 1997). The reason for this is simple – virtually every measurable aspect of an organism scales with body size. Some relationships hold across hundreds of species, spanning multiple orders of magnitude in overall size (e.g. Kleiber's law: Kleiber, 1932; Rubner's surface rule: Rubner, 1883; Von Bertalanffy, 1957; Cope's rule: Stanley, 1973; Rensch's rule: Abouheif & Fairbairn, 1997; Blanckenhorn, Meier, & Teder, 2007; Fairbairn, 1997). Others

account for transformations in shape arising during ontogeny (e.g. brain/body mass: Cock, 1966; Gould, 1974a, 1977; Dyar's law: Dyar, 1890). Here we focus on 'static' allometry, scaling that occurs among individuals of the same age sampled from within populations (Cheverud, 1982; sensu Cock, 1966; Pélabon et al., 2013).

Perhaps the most striking pattern in the study of static scaling is the observation that many extreme products of sexual selection – ornaments of choice and weapons of intrasexual competition – scale steeply with body size (Bonduriansky & Day, 2003; Eberhard, 1998; Egset et al., 2012; Emlen & Allen, 2003; Emlen, 1996; Fromhage & Kokko, 2014; Gould, 1974b; Hongo, 2007; Kelly, 2005; Kodric-Brown, Sibly, & Brown, 2006; Miller & Emlen, 2010; Painting & Holwell, 2013; Shingleton, Frankino, Flatt, Nijhout, & Emlen, 2007; Shingleton, Mirth, & Bates, 2008; Simmons & Tomkins, 1996; Stern & Emlen, 1999; Voje, 2016; Wilkinson, 1993). Specifically, when examined on a log scale, the relationship

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between the size of these structures and body size is greater than one ('positive allometry') (Gould, 1966; Huxley & Teissier, 1936; Kerkhoff & Enquist, 2009; Shingleton & Frankino, 2013; Voje, 2016). These steep scaling relationships cause ornaments and weapons to attain extraordinary proportions in the largest individuals, inspiring descriptions such as 'extreme', 'exaggerated' (Darwin, 1871) and 'bizarre' (Gould, 1974b) (Fig. 1).

Early studies of static scaling often focused on the products of sexual selection, including cervid antlers (Gould, 1973; Huxley, 1932; Thompson, 1917), fiddler crab (*Uca*) chelae (Huxley, 1932) and beetle (Scarabaeidae) horns (Bateson & Brindley, 1892; Paulian, 1935). Since then, hundreds of sexually selected structures have been examined, and the overwhelming majority scale steeply with body size (Emlen, 2008; Emlen & Nijhout, 2000; Knell, Naish, Tomkins, & Hone, 2013b; Kodric-Brown et al., 2006; e.g. Otte & Stayman, 1979; Petrie, 1988, 1992; Voje, 2016). In fact, the link between steep scaling and exaggerated ornaments and weapons is so widespread that many consider the steepness of static allometry indicative of the intensity of sexual selection acting on a structure (e.g. stalk-eyed fly (Diopsidae) eyestalks: Baker & Wilkinson, 2001;

frog (Anura) forelimbs: Schulte-Hostedde, Kuula, Martin, Schank, & Lesbarrères, 2011; earwig forceps: Simmons & Tomkins, 1996), and testing of this 'positive allometry' hypothesis is frequently used to infer a sexual selection function when natural observation is unattainable (e.g. trilobite spines: Knell & Fortey, 2005).

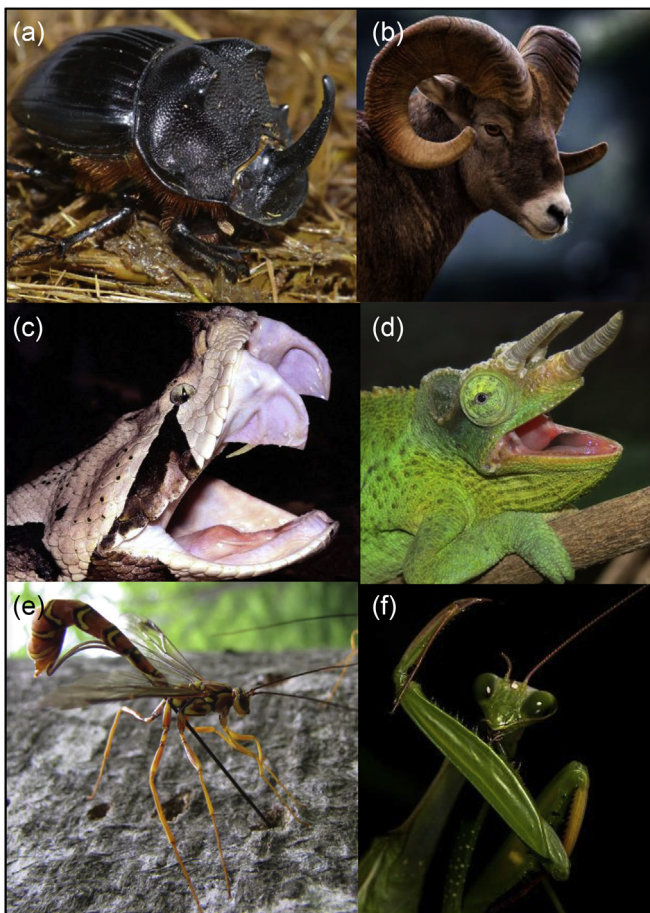
The positive allometry hypothesis has, however, been met with resistance. Bonduriansky (2007) noted that the near universality of this pattern may be an artefact of the structures researchers elect to study. That is, when studies focus on morphological scaling, scientists seek the extremes, so the literature is biased in favour of steep scaling relationships (Emlen & Nijhout, 2000; Emlen, 2008; Kodric-Brown et al., 2006). Some extreme structures known to function as sexually selected ornaments, such as elaborate plumage in birds, do not scale positively with body size (Cuervo & Møller, 2001), nor do many genitalic traits, despite the fact that some experience strong selection for increased size (Bertin & Fairbairn, 2007; Blanckenhorn, Kraushaar, Teuschl, & Reim, 2004; Voje, 2016). Indeed, considering the full range of sexually selected structures, including those that are not extreme in size, reveals that slopes are frequently shallow or negative (Bonduriansky, 2007).

Furthermore, at least a few naturally selected structures, such as long bones in large mammals (Bertram & Biewener, 1990; Christiansen, 1999) and cranial horns in lizards (Bergmann & Berk, 2012), also scale positively with body size (Voje, 2016). Clearly, sexual selection need not lead to the evolution of steep scaling, and other agents of selection, such as locomotion and predator defence, occasionally lead to positive static scaling. Where, then, does this leave the positive allometry hypothesis?

We argue that steep static-scaling relationship slopes can be powerful clues to trait function, particularly when combined with other morphological measures of among-individual variation (e.g. trait-specific coefficients of variation; see below). In this context, we suggest much of the controversy and inconsistency in the literature stems from two sources. First, the positive allometry hypothesis has been applied to all sexually selected structures, when, in fact, the logic holds only for a particular subset: sexually selected signal structures where the size of the structure functions as an honest signal of the body size or resource-holding potential of their bearers. Second, tests of the positive allometry hypothesis often rely on demonstrating a slope significantly greater than one. While rich in historical precedent, this approach fails to incorporate the signalling function of these structures. We propose future studies ask not whether the slope is greater than one, but rather whether the slope is relatively steeper for the focal signal structure than it is for other, more typically proportioned, nonsignal-related body parts. It is the relative increase in slope that allows these structures to function effectively as signals, and appropriate tests should incorporate this into their methods.

We summarize literature on animal signalling to show why positive allometry is likely when structures evolve as signals of body size, and why these structures are predicted to scale more steeply with body size than other, nonsignal structures measured in the same individuals. By the same logic, we explain why other types of extreme structures, such as those used in prey capture or locomotion, should not scale more steeply than other body parts.

We test these predictions by comparing the slopes of a suite of extreme morphological structures (14 signal, 15 nonsignal; Supplementary Table S1) to slopes of more typically proportioned 'reference' structures within the same organism (rather than the traditional comparison to isometry, see below), and show that relatively steep slopes are common for structures that function as sexually selected signals but not for comparably extreme structures that function in other, nonsignalling contexts.



**Figure 1.** Extreme nonsignal (ns) and sexually selected (ss) signal structures: (a) dung beetle horns (Scarabaeidae, ss; photo credit: Bernard Dupont); (b) bighorn sheep horns (*Ovis canadensis*; ss; photo credit: Jeremy Weber); (c) gaboon viper fangs (*Bitis gabonica*; ns; photo credit: Brimac the 2nd); (d) Jackson's chameleon horns (*Triceros jacksonii*; ss; photo credit: Bengimint444); (e) ichneumon wasp ovipositor (Ichneumonoidea; ns; photo credit: Seney Natural History Association); (f) praying mantis forelimbs (Mantodea; ns; photo credit: Oliver Koemmerling (creativecommons.org/licenses/by-sa/3.0/deed.en)). Photographs licenced under creativecommons.org/licenses/by/2.0/deed.en unless otherwise specified.

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