

1 **On the Evolution of Extreme Structures: Static Scaling and the Function of Sexually**

2 **Selected Signals**

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31 **Introduction**

32 Understanding how morphology scales with body size is one of the most
33 pervasive topics in organismal biology (Dial, Greene, & Irschick, 2008; Gould, 1966,
34 1974b, 1974a; J. Huxley, 1932; Schmidt-Nielsen, 1984; Templeton, Greene, & Davis,
35 2005; Thompson, 1917; Voje, 2016; West & Brown, 2005; West, Brown, & Enquist,
36 1997). The reason for this is simple - virtually every measurable aspect of an organism
37 scales with body size. Some relationships hold across hundreds of species, spanning
38 multiple orders of magnitude in overall size (e.g., Kleiber's Law (Kleiber, 1932);
39 Rubner's Surface Rule (Rubner, 1883; Von Bertalanffy, 1957); Cope's Rule (Stanley,
40 1973); Rensch's Rule (Abouheif & Fairbairn, 1997; Wolf U. Blanckenhorn, Meier, &
41 Teder, 2007; Fairbairn, 1997)). Others account for transformations in shape arising
42 during ontogeny (e.g., brain/body weight (Cock, 1966; Gould, 1974a, 1977); Dyar's Law
43 (Dyar, 1890)). Here we focus on 'static' allometry, scaling that occurs among individuals
44 of the same age sampled from within populations (Cheverud, 1982; sensu Cock, 1966;
45 Pélabon et al., 2013).

46 Perhaps the most striking pattern in the study of static scaling is the observation
47 that many extreme products of sexual selection – ornaments of choice and weapons of
48 intrasexual competition – scale steeply with body size (Bonduriansky & Day, 2003;
49 Eberhard, 1998; Egset et al., 2012; Emlen, 1996; Emlen & Allen, 2003; Fromhage &
50 Kokko, 2014; Gould, 1974b; Hongo, 2007; Kelly, 2005; Kodric-Brown, Sibly, & Brown,
51 2006; Miller & Emlen, 2010; Painting & Holwell, 2013; Shingleton, Frankino, Flatt,
52 Nijhout, & Emlen, 2007; Shingleton, Mirth, & Bates, 2008; L. W. Simmons & Tomkins,
53 1996; Stern & Emlen, 1999; Voje, 2016; Wilkinson, 1993). Specifically, when examined

54 on a log scale, the relationship between the size of these structures and body size is
55 greater than one ('positive allometry') (Gould, 1966; J. S. Huxley & Teissier, 1936;
56 Kerkhoff & Enquist, 2009; Shingleton & Frankino, 2013; Voje, 2016). These steep
57 scaling relationships cause ornaments and weapons to attain extraordinary proportions in
58 the largest individuals, inspiring descriptions such as 'extreme', 'exaggerated' (Darwin,
59 1871) and 'bizarre' (Gould, 1974b) (Fig. 1).

60 Early studies of static scaling often focused on the products of sexual selection,
61 including cervid antlers (Gould, 1973; J. Huxley, 1932; Thompson, 1917), fiddler crab
62 (*Uca*) chelae (J. Huxley, 1932), and beetle (Scarabaeidae) horns (Bateson & Brindley,
63 1892; Paulian, 1935). Since then, hundreds of sexually selected structures have been
64 examined, and the overwhelming majority scale steeply with body size (Emlen, 2008;
65 Emlen & Nijhout, 2000; Knell, Naish, Tomkins, & Hone, 2013b; Kodric-Brown et al.,
66 2006; e.g., Otte & Stayman, 1979; Petrie, 1988, 1992; Voje, 2016). In fact, the link
67 between steep scaling and exaggerated ornaments and weapons is so widespread that
68 many consider the steepness of static allometry indicative of the intensity of sexual
69 selection acting on a structure (e.g., stalk-eyed fly (Diopsidae) eyestalks (Baker &
70 Wilkinson, 2001); frog (Anura) forelimbs (Schulte-Hostedde, Kuula, Martin, Schank, &
71 Lesbarrères, 2011); earwig forceps (L. W. Simmons & Tomkins, 1996)), and testing of
72 this 'positive allometry' hypothesis is frequently used to infer a sexual selection function
73 when natural observation is unattainable (e.g., trilobite spines (Knell & Fortey, 2005)).

74 The positive allometry hypothesis has, however, been met with resistance.
75 Bonduriansky (2007) noted that the near universality of this pattern may be an artefact of
76 the structures researchers elect to study. That is, when studies focus on morphological

77 scaling, scientists seek the extremes, so the literature is biased in favour of steep scaling
78 relationships (Emlen, 2008; Emlen & Nijhout, 2000; Kodric-Brown et al., 2006). Some
79 extreme structures known to function as sexually selected ornaments, such as elaborate
80 plumage in birds, do not scale positively with body size (José Javier Cuervo & Møller,
81 2001), nor do many genitalic traits, despite the fact that some experience strong selection
82 for increased size (Bertin & Fairbairn, 2007; W. U. Blanckenhorn, Kraushaar, Teuschl, &
83 Reim, 2004; Voje, 2016). Indeed, considering the full range of sexually selected
84 structures, including those that are not extreme in size, reveals that slopes are frequently
85 shallow or negative (Bonduriansky, 2007).

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

92 We argue that steep static scaling relationship slopes can be powerful clues to trait
93 function, particularly when combined with other morphological measures of among-
94 individual variation (e.g., trait-specific coefficients of variation; see below). In this
95 context, we suggest much of the controversy and inconsistency in the literature stems
96 from two sources. First, the positive allometry hypothesis has been applied to all sexually
97 selected structures, when, in fact, the logic holds only for a particular subset: sexually
98 selected signal structures where the size of the structure functions as an honest signal of
99 the body size *or* resource holding potential of their bearers. Second, tests of the positive

100 allometry hypothesis often rely on demonstrating a slope significantly greater than one.
101 While rich in historical precedent, this approach fails to incorporate the signalling
102 function of these structures. We propose future studies ask not whether the slope is
103 greater than one, but rather whether the slope is relatively steeper for the focal signal
104 structure than it is for other, more typically proportioned, non-signal related body parts. It
105 is the relative increase in slope that allows these structures to function effectively as
106 signals, and appropriate tests should incorporate this into their methods.

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

113 We test these predictions by comparing the slopes of a suite of extreme
114 morphological structures (14 signal, 15 non-signal; Table 1) to slopes of more typically
115 proportioned ‘reference’ structures within the same organism (rather than the traditional
116 comparison to isometry, see below), and show that relatively steep slopes are common
117 for structures that function as sexually selected signals but not for comparably extreme
118 structures that function in other, non-signalling contexts.

119

120 **Methods**

121 *Specimen/structure selection and morphological measures*

122 All species with putatively ‘extreme’ structures – hereafter referred to as ‘focal
123 structures’ (see Appendix 1 for our classification of ‘extreme’) – and adequate sample
124 size ($n \approx 10$) were surveyed from the Phillip L. Wright Zoological Museum at the
125 University of Montana (MT, USA), the Museum of Comparative Zoology at Harvard
126 (MA, USA), and the Emlen Lab Entomological Collection (MT, USA). Surveying all
127 species that met these criteria allowed for a relatively unbiased sample of both taxa and
128 structure type. However, since most sexually selected structures in insects are beetle
129 horns (reviewed in Emlen, 2008), the invertebrates surveyed here appear somewhat
130 Coleoptera-biased. Six additional datasets were sourced specifically for this analysis –
131 Jackson’s chameleons (*Triceros jacksonii*) for the presence of both an extreme signal
132 (horns) and non-signal (tongue) structure, large bee flies (*Bombylius major*), sabre wasps
133 (*Rhyssa persuasoria*), and peacock moths (*Saturnia pyri*), for the presence of sexually
134 selected non-signal structures, and ceratopsids (*Protoceratops andrewsi*) and pterosaurs
135 (*Rhamphorhynchus muensteri*) to test the described methods on fossil datasets. Finally, it
136 should be noted that while the species/structures surveyed here were unbiased relative to
137 the sampled collections, the collections may have been biased either in taxa or in favour
138 of particularly exaggerated structures. If true, then the results presented here, and their
139 interpretation, may be limited to a particular subset of extreme morphology.

140 Focal structures of extant species were categorized as a ‘sexually selected
141 signals’(i.e., structures used by potential mates *or* competitive rivals as visual signals of
142 the bearer’s overall condition/quality (M. B. Andersson, 1994; Bradbury & Vehrencamp,
143 1998)) or ‘non-signal’ structures using relevant behavioural studies from the literature
144 (see Table 1). When literature on the focal species was unavailable, studies in closely

145 related species were used to infer trait function. Bill function in the American pelican
146 (*Pelecanus erythrorhynchos*) was inferred from its sister species, *P. occidentalis* (Bels et
147 al., 2012; Kennedy, Taylor, Nádvorník, & Spencer, 2013; Orians, 1969; Schreiber,
148 Woolfenden, & Curtsinger, 1975). Lantern function in the Malagasy lantern bug (*Zanna*
149 *madagascariensis*) was inferred from several other Fulgoridae species with similar head
150 morphology (Hogue, 1984; Urban & Cryan, 2009). Snout function in the elephant shrew
151 (*Elephantulus fuscus*) was inferred from two species of the same genus with similar
152 rostral morphology, *E. brachyrhynchus* and *E. myurus* (Kingdon, 1974; Kratzing &
153 Woodall, 1988). Horn function in dung beetles (*Sulcophanaeus menelas*, *Phanaeus*
154 *saphirinus*, *Othophagus lanista*) was inferred from both a comprehensive review of horn
155 function in beetles (Eberhard, 1980) and empirical studies of dung beetle mating systems
156 (e.g., Emlen, Marangelo, Ball, & Cunningham, 2005; Moczek & Emlen, 2000). Hindleg
157 function in frog legged beetles (*Sagra buqueti*) was inferred from a closely related
158 species with similar leg morphology and mating behaviour (Katsuki, Yokoi, Funakoshi,
159 & Oota, 2014; O'Brien, Katsuki, & Emlen, 2017). Finally, the function of focal traits in
160 extinct species were inferred from key publications focused on 'bizarre' morphology in
161 the fossil record (Knell & Sampson, 2011; Knell, Naish, Tomkins, & Hone, 2013a; D. W.
162 Hone, Wood, & Knell, 2016; but see Padian & Horner, 2011, 2013, 2014).

163 Reference structures were then chosen for each species as structures that could be
164 consistently measured across all samples and lacked obvious functional connection with
165 the focal structure. These criteria appear adequate in choosing reference structures.
166 However, the authors recognize the limitation of using a single reference structure and
167 encourage the use of multiple reference structures per organism in future application of

168 the described methods. Doing so will better capture the scaling relationship of ‘typical’
169 (i.e., non-signal) traits and help mitigate impact of choosing inappropriate reference
170 structures.

171 Measures of overall body size were based on established, taxon specific methods
172 for estimating body size. For species where established estimates of body size were
173 unavailable, methods were adopted from closely related taxa. A summary of study
174 species names, sample sizes, relevant morphological information (e.g., focal structure,
175 reference structure, body size measures), and literature used to establish sexually selected
176 signal/naturally selected non-signal function is provided in Table 1.

177 Dung beetles (*Sulcophanaeus menelas*), earwigs, mantidflies (*Climaciella*
178 *brunnea*), large bee flies, sabre wasps, and wildebeest (*Connochaetes tourinus*) were
179 measured using photographs (including scale bars) and ImageJ 1.50i software (NIH,
180 USA). *S. menelas*, earwigs, and mantidflies, large bee flies, and sabre wasps were
181 photographed using a 16.2 megapixel Nikon D5100 DSLR camera mounted on a
182 binocular stereo microscope (Leica S6D) set at a fixed distance. Wildebeest were
183 photographed using a 14.2 megapixel Nikon D3100 DSLR camera set at a fixed distance
184 designated to minimize perspective effects (i.e., approximating orthographic projection).
185 All other extant species were measured using digital callipers.

186 Measures of ceratopsians (*Protoceratops andrewsi*) and pterosaurs
187 (*Rhamphorhynchus muensteri*) were collected directly using digital callipers, from
188 photographs of specimens including scale bars, or from the literature when appropriate, to
189 maximize the number of available specimens (see Appendices 2 and 3).

190

191 *Statistical analyses*

192 Statistical analyses were performed in R 3.3.2 (R Core Development Team 2016).
193 Measurements were \log_{10} transformed and mean standardized prior to analysis. Ordinary
194 least squares (OLS) regression was used to assess scaling relationship slope (Kilmer &
195 Rodríguez, 2016; Smith, 2009; Warton, Duursma, Falster, & Taskinen, 2012; Warton,
196 Wright, Falster, & Westoby, 2006). For every species, focal structure size and reference
197 structure size were regressed on body size in separate models. Analyses of covariance
198 (ANCOVA) were then used to compare regression slopes of focal structure size on body
199 size (β_{focal}) to regression slopes of reference structure size on body size ($\beta_{\text{reference}}$) within
200 the same species (i.e., to determine whether or not there was a significant interaction
201 between body size and trait group (focal/reference) in explaining trait size). (Differences
202 in intercept were not analysed, since all data were mean-standardized prior to analysis.)
203 In addition, slope estimates (β_{focal} and $\beta_{\text{reference}}$) were collected from each model and 95%
204 confidence intervals constructed. These 95% confidence intervals were then compared
205 between focal and reference structures within the same species.

206 Mean β_{focal} was calculated for sexually selected signal structures and compared to
207 mean β_{focal} calculated for non-signal structures using Welch's t test. Mean $\beta_{\text{reference}}$ was
208 calculated for species with sexually selected signal structures and compared to mean
209 $\beta_{\text{reference}}$ for species with exaggerated non-signal structures using Welch's t-test. 95%
210 confidence intervals were constructed around mean $\beta_{\text{reference}}$ for species with sexually
211 selected signal structures and mean $\beta_{\text{reference}}$ for species with non-signal structures and
212 compared. The difference between β_{focal} and $\beta_{\text{reference}}$ ($\Delta\beta_{\text{focal-reference}}$) was calculated for
213 each species. Mean $\Delta\beta_{\text{focal-reference}}$ for species with sexually selected signal structures was

214 compared to mean $\Delta\beta_{\text{focal-reference}}$ for species with non-signal structures using Welch's t-
215 test. 95% confidence intervals were constructed around mean $\Delta\beta_{\text{focal-reference}}$ for sexually
216 selected signal structures and mean $\Delta\beta_{\text{focal-reference}}$ for non-signal structures and compared.

217 Coefficients of variation were calculated for every structure. Mean coefficient of
218 variation was calculated across all signal structures and compared to the mean coefficient
219 of variation compared across all non-signal structures using 95% confidence intervals and
220 Welch's t test.

221

222 **Results**

223 Results of species-level analyses are summarized in Table 1, including slope
224 estimates (β_{focal} and $\beta_{\text{reference}}$) and adjusted R^2 values for all models, differences between
225 β_{focal} and $\beta_{\text{reference}}$ ($\Delta\beta_{\text{focal-reference}}$), ANCOVA results, 95% confidence intervals
226 surrounding β_{focal} , $\beta_{\text{reference}}$, and $\Delta\beta_{\text{focal-reference}}$, and coefficients of variation. For the
227 majority of species with sexually selected signal structures, β_{focal} was significantly greater
228 than $\beta_{\text{reference}}$ (Table 1; Appendix 4). For two of these species, whitetail deer and
229 wildebeest, β_{focal} was greater than $\beta_{\text{reference}}$, but 95% confidence intervals surrounding
230 these estimates were overlapping and the ANCOVA showed no significant difference
231 between β_{focal} and $\beta_{\text{reference}}$. In pronghorn antelope, 95% confidence intervals surrounding
232 β_{focal} and $\beta_{\text{reference}}$ were overlapping, but ANCOVA showed a (slightly) significant
233 difference between β_{focal} and $\beta_{\text{reference}}$. Earwigs, on the other hand, displayed non-
234 overlapping 95% confidence intervals surrounding β_{focal} and $\beta_{\text{reference}}$, but the ANCOVA
235 showed no significant difference between β_{focal} and $\beta_{\text{reference}}$. For all species with

236 exaggerated, non-signal structures, β_{focal} and $\beta_{\text{reference}}$ were either not significantly
237 different, or $\beta_{\text{reference}}$ was significantly higher than β_{focal} (Table 1; Appendix 5). Unlike
238 extreme sexually selected signal structures, extreme non-signal structures appear to scale
239 similarly to reference structures within the same organism. Mean slope (β_{focal}) of all
240 exaggerated sexually selected signal structures was greater than the mean slope (β_{focal}) of
241 all non-signal structures ($t_{13.543} = -3.835, p < 0.01$) and 95% confidence intervals were
242 non-overlapping (95% CI mean β_{focal} for sexually selected signal structures [1.709, 4.56];
243 95% CI mean β_{focal} for non-signal structures [0.374, 0.783]). Mean $\Delta\beta_{\text{focal-reference}}$ for
244 sexually selected signal structures was greater than mean $\Delta\beta_{\text{focal-reference}}$ for non-signal
245 structures ($t_{14.164} = 4.079, p = 0.001$; Appendix 6) and 95% confidence intervals did not
246 overlap (95% CI mean $\Delta\beta_{\text{focal-reference}}$ for sexually selected signal structures [1.072, 3.831];
247 95% CI mean $\Delta\beta_{\text{focal-reference}}$ for non-signal structures [-0.501, 0.078]).

248 Coefficients of variation were significantly higher for extreme, sexually selected
249 signal structures (mean = 15.444, 95% CI [9.325, 21.562]) than for non-signal structures
250 (mean = 5.351, 95% CI [3.263, 7.438]) ($t_{16.043} = 3.37, p < 0.01$; Appendix 7).

251

252 **Discussion**

253 Within species, sexually selected signal structures scaled steeply with body size
254 (Table 1; Appendix 4). In the majority of sexually selected species surveyed here, the
255 scaling relationship of the signal (β_{focal}) was significantly steeper than that of the
256 reference structure ($\beta_{\text{reference}}$). Surprisingly, this pattern did not hold for whitetail deer
257 (*Odocoileus virginianus*) or wildebeest. In these species, β_{focal} was greater than $\beta_{\text{reference}}$,
258 but there was no significant difference between β_{focal} and $\beta_{\text{reference}}$. Similarly, for earwigs,

259 the ANCOVA showed no significant difference between β_{focal} and $\beta_{\text{reference}}$, but β_{focal} was
260 greater than $\beta_{\text{reference}}$ and 95% confidence intervals surrounding these estimates were non-
261 overlapping (Table 1; Appendix 4). These results may be an artefact of relatively small
262 sample size (e.g., $n < 18$ for whitetail deer) and/or biased sampling (e.g., hunters
263 favouring largest antlered males in sampled populations), since previous work has shown
264 positive allometry and/or strong selection for these, and similar, weapons (e.g., Kruuk et
265 al., 2002; Melnycky, Weladji, Holand, & Nieminen, 2013; Lundrigan, 1996; L. W.
266 Simmons & Tomkins, 1996). Alternatively, these structures may function strictly as
267 weapons (i.e., tools) of intrasexual competition, not as visual signals of quality. If true,
268 then steep scaling between weapon and body size is not expected (McCullough, Miller, &
269 Emlen, 2016, see below). Overall, our results for sexually selected signal structures are
270 consistent with previous work showing that these types of extreme structures tend to be
271 positively allometric (Bonduriansky & Day, 2003; Emlen, 2008; Green, 1992; Kodric-
272 Brown & Brown, 1984; Kodric-Brown et al., 2006; Petrie, 1988, 1992; L. W. Simmons
273 & Tomkins, 1996; Voje, 2016).

274 Every exaggerated non-signal structure measured scaled with a slope that was
275 either less than, or not significantly different from, that of the reference structure (Table
276 1; Appendix 5). In addition, across species, the scaling relationship (β_{focal}) of sexually
277 selected signal structures was significantly steeper than that of non-signal structures
278 ($t_{11.902} = -3.23, p < 0.01$). Even within the same organism, non-signal structures scaled at
279 a shallower rate than sexually selected signals. In Jackson's chameleon, for example,
280 where both an extreme sexually selected signal, horn length, and an extreme non-signal

281 prey capture structure, tongue length, were surveyed, horn size scaled at a much steeper
282 rate compared to the reference structure than did tongue size (Table 1; Fig. 2).

283

284 *Why signals should scale more steeply than other body parts*

285 Many studies have considered what makes a good signal (reviewed in Bradbury &
286 Vehrencamp, 1998; Maynard Smith & Harper, 2003; Searcy & Nowicki, 2006). In the
287 context of sexual selection, receivers are often females who use variation in signal
288 expression as a basis for mate choice, or males who use these signals to determine the
289 resource holding potential (i.e., fighting ability) of rival males (M. B. Andersson, 1994;
290 Bradbury & Vehrencamp, 1998; Hardy & Briffa, 2013). In both cases, information
291 encoded in the signal pertains to the overall genetic quality and/or condition of the bearer
292 (reviewed in Neff & Pitcher, 2005).

293 Although any phenotype could, in principle, be used as a signal (provided it is
294 detectable and variable across individuals), some make more effective signals than
295 others. The best signals are conspicuous – bigger or brighter than other body parts
296 (Bradbury & Vehrencamp, 1998). However, it is not just the structure that must be
297 conspicuous. *Variation* in the expression of that structure is key to mate and rival
298 assessment, and the more pronounced the differences, the better. For this reason, signal
299 structures are often selected to be more variable in their expression than other,
300 surrounding, non-signal structures (Alatalo, Höglund, & Lundberg, 1988; José Javier
301 Cuervo & Møller, 2001; Emlen, Warren, Johns, Dworkin, & Lavine, 2012; Fitzpatrick,
302 1997; Petrie, 1992; Pomiankowski & Moller, 1995; Rowe & Houle, 1996; L. W.
303 Simmons & Tomkins, 1996; Tazzyman, Iwasa, & Pomiankowski, 2014; Wallace, 1987).

304 Hypervariability in trait size amplifies associated variation in male quality, making these
305 otherwise subtle differences easier to see (Hasson, 1991; Tazzyman et al., 2014; Wallace,
306 1987).

307 Effective signals must also be honest. If poor quality males can cheat by
308 producing effective signals, then reliability of the signal plummets and receivers should
309 focus on other traits. One form of honesty arises when the growth of signal traits is
310 condition-sensitive (Biernaskie, Grafen, & Perry, 2014; Bonduriansky, 2006;
311 Bonduriansky & Day, 2003; Grafen, 1990; Iwasa, Pomiankowski, & Nee, 1991;
312 Johnstone, 1997; Kodric-Brown et al., 2006; Nur & Hasson, 1984; Pomiankowski, 1987;
313 Zeh & Zeh, 1988). Condition-sensitive growth of signal structures may ‘capture’ genetic
314 or environmental variation underlying overall quality, making these signals virtually
315 impossible to fake (Miller & Moore, 2007; Rowe & Houle, 1996; Wilkinson & Taper,
316 1999). Indeed, sexually selected signal structures are notoriously sensitive to stress,
317 parasite load, and nutrition (Cotton, Fowler, & Pomiankowski, 2004; Ezenwa & Jolles,
318 2008; Gosden & Chenoweth, 2011; Hamilton & Zuk, 1982; Izzo & Tibbetts, 2015; Knell
319 & Simmons, 2010; Kruuk et al., 2002; Skarstein & Folstad, 1996).

320 Hypervariability through heightened condition sensitivity causes structures to be
321 reliable and informative as signals of quality (M. B. Andersson, 1994; M. Andersson &
322 Iwasa, 1996; M. Andersson & Simmons, 2006; Bradbury & Vehrencamp, 1998), and
323 these basic characteristics are shared by a wealth of sexually selected signals (reviewed in
324 Bradbury & Vehrencamp, 1998). When information contained in a sexually selected
325 signal involves individual differences in the size of a structure, and when among-
326 individual variation in condition or genetic quality manifests as differences in overall

327 body size, then selection for increasingly effective signals should lead to the evolution of
328 not just higher trait-specific coefficients of variation, but also to a relatively steeper
329 scaling relationship slope (Biernaskie et al., 2014; Green, 1992; Kodric-Brown & Brown,
330 1984; Kodric-Brown et al., 2006; Petrie, 1988). The steeper the slope, the more variable
331 the focal structure will be relative to surrounding body parts. Mechanistically, when
332 variation in condition is driven by differential access to nutrition, then the evolution of
333 heightened condition-sensitive growth in a particular structure, relative to others, will
334 also manifest as an increase in the steepness of the slope for that structure (Emlen et al.,
335 2012; Lavine, Gotoh, Brent, Dworkin, & Emlen, 2015; Mirth, Frankino, & Shingleton,
336 2016; Shingleton & Frankino, 2013). Thus, for this particular subset of signal structures,
337 the positive allometry hypothesis should hold. Indeed, the steeper the scaling relationship
338 slope, the better the signal will be, leading to the evolution of larger and larger structures
339 with steeper and steeper patterns of static scaling.

340 A few exceptions should be noted, however. First, body size is not always
341 correlated with overall genetic quality or condition, as is the case for many fishes (Bolger
342 & Connolly, 1989) and birds (José J. Cuervo & Møller, 2009). In these species, signals
343 are still expected to be condition-sensitive and hypervariable. However, because
344 condition is not correlated with body size, differences in the relative sizes of signal
345 structures may not covary with body size (e.g., Bonduriansky & Day, 2003; José J.
346 Cuervo & Møller, 2009; Fitzpatrick, 1997; Pomfret & Knell, 2006). (This was true for
347 several focal non-signal traits, and several reference traits surveyed here (indicated by
348 low adjusted R^2 values; Table 1). Indeed, future analyses may benefit from choosing
349 reference structures that more tightly covary with body size.) Similarly, signals that vary

350 in other ways besides size (e.g., colour, behaviour, chemical signals) are also not
351 expected to scale with body size. Finally, sexually selected traits that do not function as
352 signals (e.g., peacock moth antennae, measured here; Table 1; Appendix 5), are not
353 predicted to scale steeper than reference structures, since hypervariation and/or condition
354 sensitivity may actually decrease performance. This includes sexually selected weapons
355 that function only as tools of battle and not as signals of quality, condition, or resource
356 holding potential (McCullough et al., 2016). For these structures, trait expression should
357 be proportional across the entire population, even when selection favours large relative
358 trait sizes. Large structures may display especially high scaling relationship intercepts
359 compared to other traits in the body, but since there is no hypervariation and/or
360 heightened condition sensitivity, the slope should not differ from that of a reference
361 structure. Consequently, we suggest much of the confusion regarding the link between
362 positive allometry and sexual selection can be resolved by recognizing that the positive
363 allometry hypothesis applies only to those structures that act as visual signals of among-
364 individual variation in condition or genetic quality and, in fact, it applies only to a subset
365 of these, signals whose information involves differences in signal size in species where
366 quality is approximated by variation in overall size. For these structures, sexual selection
367 is predicted to drive the evolution of extreme trait size and unusually steep scaling.

368

369 *Testing the positive allometry hypothesis against reference structures, rather than*
370 *isometry*

371 We suggest three reasons for testing the positive allometry hypothesis in
372 comparison with reference structures, rather than with isometry. First, inferring signal

373 function for a structure that scales steeply only makes sense if that structure scales more
374 steeply than other body parts. Steep scaling relationship slopes are relevant because they
375 cause structures to be better signals than other, surrounding body parts. The properties
376 that make them effective signals are relative: they are more variable and more condition-
377 sensitive in their growth than other body parts. Sexual selection favours receivers who
378 pay attention to these structures because, by doing so, individuals make more informed
379 decisions than they would if they focused on other body parts. Consequently, the pattern
380 that matters for inferring a sexually selected signal function is the difference in slope
381 between the putative signal and other, non-signal, structures.

382 Second, detecting hyperallometry in a focal structure without comparing the slope
383 to a control can be misleading. It is possible for non-signal structures to scale steeply.
384 Indeed, in our sample of non-signal exaggerated structures, gaboon viper (*Bitis gabonica*)
385 fangs, elephant shrew (*Elephantulus fuscus*) snouts, and mantidfly forelegs all scaled
386 with relatively slopes (i.e., $\beta > 1$), but the reference structures were hyperallometric too
387 (Appendix 5; Table 1). Had we focused only on the absolute value of the scaling
388 relationship slope we would have erroneously inferred a signal function for these
389 structures when, in fact, their scaling relationship slopes were no different from those of
390 surrounding body parts. These structures lack the critical properties of an informative
391 signal despite being hyperallometric.

392 Finally, comparing measured slopes with isometry places undue emphasis on the
393 estimated slope *per se*. Isometry may be intuitive in principle, but actually detecting it, or
394 rejecting it, depends a lot on the particular landmarks selected, the units of measurement
395 involved, and the chosen measure of body size (Bookstein, 1989; Jungers, Falsetti, &

396 Wall, 1995; e.g., Mosimann & James, 1979). For this reason, focusing tests of the
397 positive allometry hypothesis exclusively on rejection of a slope of one may be
398 misleading, especially in the context of interspecific comparisons where landmarks and
399 measures of body size/condition often differ (e.g., Bolger & Connolly, 1989; Jakob,
400 Marshall, & Uetz, 1996, p. d; Peig & Green, 2010). Focusing instead on the slopes of
401 focal structures compared to those of reference structures delivers an internally controlled
402 assay for the properties of a structure's expression that matter. Significant increases in the
403 slope of a focal structure relative to other body parts means that the focal structure has the
404 predicted properties of a signal, and we suggest this constitutes evidence in favour of a
405 function for that structure as a sexually selected signal.

406

407 *Diversity of exaggerated morphology*

408 Not all sexually selected structures are signals, but many experience strong
409 selection for increased size. In arthropods with low population density, for example,
410 males search for receptive females and selection can lead to the evolution of elaborate
411 antennae and/or enlarged eyes (e.g., peacock moth antennae, measured here; Table 1).
412 This results in pronounced sexual dimorphism in relative trait size and, in some species,
413 exaggerated male sensory structures (M. B. Andersson, 1994; Bertin & Cezilly, 2003;
414 Lefebvre, 2000; Thornhill, 1981). Similarly, antagonistic coevolutionary arms races
415 arising from conflict between males and females can drive rapid evolution of genitalia
416 (Arnqvist & Rowe, 2002, 2005; Brennan, Clark, & Prum, 2009; Parker, 1979; Leigh W.
417 Simmons, 2014). In both contexts, sexual selection drives the evolution of extreme size,
418 but these structures do not function as signals. There is little covariance between trait

419 *variation* and fitness and, thus, no benefit in traits being hypervariable or extra condition
420 sensitive. For these traits, steep scaling slopes are not expected (e.g., Eberhard, 1998,
421 2010; Hosken & Stockley, 2004).

422 Exaggerated size can also arise through natural selection as, for example, in some
423 locomotor, prey capture, and feeding structures (reviewed in Lavine et al., 2015).
424 Appendages such as praying mantis forelimbs and antlion mandibles function like levers,
425 snapping closed to grasp prey. For these species, longer forelimbs or mandibles perform
426 better than shorter ones both because they move faster at their tips, and because they
427 sweep through a larger ‘kill zone’ (Loxton & Nicholls, 1979; Maldonado, Levin, & Pita,
428 1967). However, like sensory and genitalic structures of sexual selection, large size in
429 these naturally selected structures is not related to a signal function. There is no benefit to
430 hypervariability or heightened condition sensitivity, and steep scaling relationship slopes
431 are not expected.

432 Here, we provide measures of static allometry for 15 extreme non-signalling
433 structures (Table 1; Appendix 5). None are sexually dimorphic, and none scaled more
434 steeply than other, typically proportioned, body parts. Jackson’s chameleons provide
435 perhaps the best example of all, since males in this species have both types of extreme
436 structure: three horns on the head that function as a signal of competitive ability (Bustard,
437 1958), and an elongated tongue used to capture prey. Even though the tongue is relatively
438 larger than the horns, tongues scaled with a slope that was shallower than the reference
439 structure. Horns, in contrast, scaled disproportionately steeply (Fig. 2). Clearly, the
440 evolution of extreme structures need not entail relative increases in static allometry slope,

441 and steep slopes, when they occur, can provide valuable clues to a sexually selected
442 signal function.

443

444 *Inferring function for extreme structures in extinct taxa*

445 Unlike most organisms described above, the behaviour of extinct taxa cannot be
446 observed. Even so, lines of evidence can be drawn from static, morphological data to
447 provide testable hypotheses of behaviour (D. W. E. Hone & Faulkes, 2014). For example,
448 hypotheses surrounding mechanical function, such as those involving anchors for
449 musculature or levers that increase moment arms, can be assessed (and potentially
450 rejected) using data from fossils (e.g., D. W. Hone, Naish, & Cuthill, 2012; Knell &
451 Fortey, 2005). Similarly, we maintain the use of static scaling relationship slopes and
452 coefficients of variation may provide a means for inferring a sexually selected signal
453 function for extreme morphology in the fossil record.

454 Static scaling relationships have been used already to infer function in the fossil
455 record (Gould, 1973; D. W. Hone et al., 2016; Knell & Fortey, 2005). However, such
456 inferences remain controversial (e.g., Padian & Horner, 2011, 2013, 2014; Knell &
457 Sampson, 2011; Knell et al., 2013a; D. W. Hone & Mallon, 2017; Mallon, 2017). One
458 issue is that collecting multiple individuals from the same fossil locality and horizon (i.e.,
459 a single population) is difficult. Sample sizes are often small or gathered from animals
460 separated in space and/or time, and animals are rarely sexed (e.g., D. W. Hone & Mallon,
461 2017). As a result, detection of even fundamental patterns in morphology, such as sexual
462 dimorphism, remains elusive (Mallon, 2017; but see Sengupta, Ezcurra, &
463 Bandyopadhyay, 2017). Another issue is that distinguishing between different signal

464 functions is often difficult. Social dominance and sexually selected signals, for example,
465 are often confluent and distinguishing between them is complex. In addition, the cooption
466 of extreme structures to multiple functions, thereby exposing them to multiple patterns of
467 selection, may further confound these data (e.g., dugong tusks; Anderson, 1979;
468 Domning & Beatty, 2007).

469 Despite these limitations, we suggest behaviour can be inferred from the fossil
470 record using the methods and logic described above. We predict that when focal
471 structures act as signals of overall body size, both the slope of the static scaling
472 relationship and the coefficient of variation will be steeper/greater in the putative signal
473 structure than in reference structures used as controls. As ‘proof of concept’ for this
474 approach, we included two putative sexually selected signal structures from the fossil
475 record in our analyses, the enlarged cephalic frill of the ceratopsian dinosaur
476 *Protoceratops andrewsi* (adapted and expanded from D. W. Hone et al., 2016), and the
477 tail vane of the pterosaur, *Rhamphorhynchus*. In both cases, the focal structure scaled
478 more steeply with body size and had a higher coefficient of variation than reference
479 structures measured in the same individual (Fig. 3; Table 1), implying a signalling
480 function.

481 Overall, we believe this method useful for inferring extreme structure function in
482 the fossil record (perhaps even more useful when analysed in conjunction with other
483 patterns in morphology - e.g., changes in complexity during ontogeny, high variation in
484 trait shape and size between species lineages). Both morphological scaling relationships
485 and coefficients of variation can be reliably measured in fossil specimens, even when
486 sample size is small. We recommend the use of these methods in subsequent analyses of

487 extreme or ‘bizarre’ morphology in the fossil record, and are hopeful that they might
488 provide insight into the ongoing debate regarding sexual selection in non-avian dinosaurs.

489

490 Overall, we suggest that when applied specifically and exclusively to
491 disproportionately large animal structures that function as signals of overall body size,
492 and when assessed through comparison with surrounding, non-signal structures rather
493 than through detection of an estimated slope greater than 1, the positive allometry
494 hypothesis holds. Sexually selected signal structures are predicted to – and, in fact,
495 appear to – scale more steeply with body size than non-signal structures. For this reason,
496 we suggest that relative patterns of trait scaling offer powerful clues to trait function,
497 particularly when combined with other measures of trait expression such as trait specific
498 coefficients of variation.

499

500

501 **Data archive**

502 Datasets supporting this article will be uploaded to Dryad

503

504

505 **Competing interests**

506 The authors have no competing interests to report

507

508

509 **References**

510

511 Abouheif, E., & Fairbairn, D. J. (1997). A comparative analysis of allometry for sexual
512 size dimorphism: assessing Rensch's rule. *The American Naturalist*, 149(3), 540–
513 562.

514 Alatalo, R. V., Höglund, J., & Lundberg, A. (1988). Patterns of variation in tail ornament
515 size in birds. *Biological Journal of the Linnean Society*, 34(4), 363–374.

516 Anderson, P. K. (1979). Dugong behavior: on being a marine mammalian grazer.
517 *Biologist*, 61(4), 113–144.

518 Andersson, M. B. (1994). *Sexual selection*. Princeton University Press.

519 Andersson, M., & Iwasa, Y. (1996). Sexual selection. *Trends in Ecology & Evolution*,
520 11(2), 53–58. [https://doi.org/10.1016/0169-5347\(96\)81042-1](https://doi.org/10.1016/0169-5347(96)81042-1)

521 Andersson, M., & Simmons, L. W. (2006). Sexual selection and mate choice. *Trends in*
522 *Ecology & Evolution*, 21(6), 296–302.

523 Arnqvist, G., & Rowe, L. (2002). Correlated evolution of male and female morphologies
524 in water striders. *Evolution*, 56(5), 936–947.

525 Arnqvist, G., & Rowe, L. (2005). *Sexual conflict*. Princeton University Press,
526 Princeton, NJ.

527 Baker, R. H., & Wilkinson, G. S. (2001). Phylogenetic analysis of sexual dimorphism
528 and eye-span allometry in stalk-eyed flies (Diopsidae). *Evolution*, 55(7), 1373–
529 1385.

530 Bateson, W., & Brindley, H. H. (1892). 3. On some cases of Variation in Secondary
531 Sexual Characters, statistically examined. *Journal of Zoology*, 60(4), 585–596.

532 Bels, V. L., Aerts, P., Chardon, M., Vandewalle, P., Berkhoudt, H., Crompton, A. W., ...
533 Frazzetta, T. H. (2012). *Biomechanics of feeding in vertebrates* (Vol. 18).
534 Springer Science & Business Media.

535 Bergmann, P. J., & Berk, C. P. (2012). The evolution of positive allometry of weaponry
536 in horned lizards (Phrynosoma). *Evolutionary Biology*, 39(3), 311–323.

537 Bertin, A., & Cezilly, F. (2003). Sexual selection, antennae length and the mating
538 advantage of large males in *Asellus aquaticus*. *Journal of Evolutionary Biology*,
539 16(4), 698–707.

540 Bertin, A., & Fairbairn, D. J. (2007). The Form of Sexual Selection on Male Genitalia
541 Cannot Be Inferred from Within-Population Variance and Allometry—a Case
542 Study in *Aquarius Remigis*. *Evolution*, 61(4), 825–837.
543 <https://doi.org/10.1111/j.1558-5646.2007.00074.x>

544 Bertram, J. E., & Biewener, A. A. (1990). Differential scaling of the long bones in the
545 terrestrial Carnivora and other mammals. *Journal of Morphology*, 204(2), 157–
546 169.

547 Biernaskie, J. M., Grafen, A., & Perry, J. C. (2014). The evolution of index signals to
548 avoid the cost of dishonesty. *Proceedings of the Royal Society of London B:*
549 *Biological Sciences*, 281(1790), 20140876.

550 Blanckenhorn, W. U., Kraushaar, U. R. S., Teuschl, Y., & Reim, C. (2004). Sexual
551 selection on morphological and physiological traits and fluctuating asymmetry in
552 the black scavenger fly *Sepsis cynipsea*. *Journal of Evolutionary Biology*, 17(3),
553 629–641. <https://doi.org/10.1111/j.1420-9101.2004.00693.x>

- 554 Blanckenhorn, W. U., Meier, R., & Teder, T. (2007). Rensch's rule in insects: patterns
555 among and within species. *Sex, Size, and Gender Roles: Evolutionary Studies of*
556 *Sexual Size Dimorphism*, 60–70.
- 557 Bolger, T., & Connolly, P. L. (1989). The selection of suitable indices for the
558 measurement and analysis of fish condition. *Journal of Fish Biology*, 34(2), 171–
559 182.
- 560 Bonduriansky, R. (2006). The evolution of condition-dependent sexual dimorphism. *The*
561 *American Naturalist*, 169(1), 9–19.
- 562 Bonduriansky, R. (2007). Sexual selection and allometry: a critical reappraisal of the
563 evidence and ideas. *Evolution*, 61(4), 838–849.
- 564 Bonduriansky, R., & Day, T. (2003). The Evolution of Static Allometry in Sexually
565 Selected Traits. *Evolution*, 57(11), 2450–2458. [https://doi.org/10.1111/j.0014-](https://doi.org/10.1111/j.0014-3820.2003.tb01490.x)
566 [3820.2003.tb01490.x](https://doi.org/10.1111/j.0014-3820.2003.tb01490.x)
- 567 Bookstein, F. L. (1989). “Size and shape”: a comment on semantics. *Systematic Zoology*,
568 38(2), 173–180.
- 569 Bradbury, J. W., & Vehrencamp, S. L. (1998). Principles of animal communication.
570 *Behavioral Ecology*, 12, 283–286.
- 571 Brennan, P. L., Clark, C. J., & Prum, R. O. (2009). Explosive eversion and functional
572 morphology of the duck penis supports sexual conflict in waterfowl genitalia.
573 *Proceedings of the Royal Society of London B: Biological Sciences*,
574 [rspb20092139](https://doi.org/10.1098/rspb.2009.2139).
- 575 Bustard, H. R. (1958). Use of horns by *Chamaeleo jacksoni*. *Brit J Herpetol*, 2, 105–107.

576 Cheverud, J. M. (1982). Relationships among ontogenetic, static, and evolutionary
577 allometry. *American Journal of Physical Anthropology*, 59(2), 139–149.

578 Christiansen, P. (1999). Scaling of the limb long bones to body mass in terrestrial
579 mammals. *Journal of Morphology*, 239(2), 167–190.
580 [https://doi.org/10.1002/\(SICI\)1097-4687\(199902\)239:2<167::AID-](https://doi.org/10.1002/(SICI)1097-4687(199902)239:2<167::AID-)
581 [JMOR5>3.0.CO;2-8](https://doi.org/10.1002/(SICI)1097-4687(199902)239:2<167::AID-JMOR5>3.0.CO;2-8)

582 Cock, A. G. (1966). Genetical aspects of metrical growth and form in animals. *The*
583 *Quarterly Review of Biology*, 41(2), 131–190.

584 Cotton, S., Fowler, K., & Pomiankowski, A. (2004). Condition dependence of sexual
585 ornament size and variation in the stalk-eyed fly *Cyrtodiopsis dalmanni* (Diptera:
586 Diopsidae). *Evolution*, 58(5), 1038–1046.

587 Cuervo, J. J., & Møller, A. P. (2001). Components of phenotypic variation in avian
588 ornamental and non-ornamental feathers. *Evolutionary Ecology*, 15(1), 53–72.

589 Cuervo, J. J., & Møller, A. P. (2009). The allometric pattern of sexually size dimorphic
590 feather ornaments and factors affecting allometry. *Journal of Evolutionary*
591 *Biology*, 22(7), 1503–1515.

592 Darwin, C. (1871). *The Descent of Man: And Selection in Relation to Sex* (Vol. 2).
593 Appleton.

594 Dial, K. P., Greene, E., & Irschick, D. J. (2008). Allometry of behavior. *Trends in*
595 *Ecology & Evolution*, 23(7), 394–401.

596 Dodson, P. (1976). Quantitative aspects of relative growth and sexual dimorphism in
597 Protoceratops. *Journal of Paleontology*, 929–940.

598 Domning, D. P., & Beatty, B. L. (2007). Use of tusks in feeding by dugongid sirenians:
599 Observations and tests of hypotheses. *The Anatomical Record: Advances in*
600 *Integrative Anatomy and Evolutionary Biology*, 290(6), 523–538.
601 <https://doi.org/10.1002/ar.20540>

602 Dyar, H. G. (1890). The number of molts of lepidopterous larvae. *Psyche: A Journal of*
603 *Entomology*, 5(175–176), 420–422.

604 Eberhard, W. G. (1980). Horned beetles. *Scientific American*, 242(3), 166–183.

605 Eberhard, W. G. (1998). Sexual behavior of *Acanthocephala declivis guatemalana*
606 (Hemiptera: Coreidae) and the allometric scaling of their modified hind legs.
607 *Annals of the Entomological Society of America*, 91(6), 863–871.

608 Eberhard, W. G. (2010). Evolution of genitalia: theories, evidence, and new directions.
609 *Genetica*, 138(1), 5–18.

610 Egset, C. K., Hansen, T. F., Le Rouzic, A., Bolstad, G. H., Rosenqvist, G., & Pélabon, C.
611 (2012). Artificial selection on allometry: change in elevation but not slope.
612 *Journal of Evolutionary Biology*, 25(5), 938–948. [https://doi.org/10.1111/j.1420-](https://doi.org/10.1111/j.1420-9101.2012.02487.x)
613 [9101.2012.02487.x](https://doi.org/10.1111/j.1420-9101.2012.02487.x)

614 Emlen, D. J. (1996). Artificial Selection on Horn Length-Body Size Allometry in the
615 Horned Beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Evolution*,
616 50(3), 1219–1230. <https://doi.org/10.2307/2410662>

617 Emlen, D. J. (2008). The evolution of animal weapons. *Annual Review of Ecology,*
618 *Evolution, and Systematics*, 39, 387–413.

619 Emlen, D. J., & Allen, C. E. (2003). Genotype to Phenotype: Physiological Control of
620 Trait Size and Scaling in Insects. *Integrative and Comparative Biology*, 43(5),
621 617–634. <https://doi.org/10.1093/icb/43.5.617>

622 Emlen, D. J., Marangelo, J., Ball, B., & Cunningham, C. W. (2005). Diversity in the
623 Weapons of Sexual Selection: Horn Evolution in the Beetle Genus *Onthophagus*
624 (coleoptera: Scarabaeidae). *Evolution*, 59(5), 1060–1084.
625 <https://doi.org/10.1111/j.0014-3820.2005.tb01044.x>

626 Emlen, D. J., & Nijhout, H. F. (2000). The development and evolution of exaggerated
627 morphologies in insects. *Annual Review of Entomology*, 45(1), 661–708.

628 Emlen, D. J., Warren, I. A., Johns, A., Dworkin, I., & Lavine, L. C. (2012). A
629 Mechanism of Extreme Growth and Reliable Signaling in Sexually Selected
630 Ornaments and Weapons. *Science*, 337(6096), 860–864.
631 <https://doi.org/10.1126/science.1224286>

632 Ezenwa, V. O., & Jolles, A. E. (2008). Horns honestly advertise parasite infection in male
633 and female African buffalo. *Animal Behaviour*, 75(6), 2013–2021.

634 Fairbairn, D. J. (1997). Allometry for sexual size dimorphism: pattern and process in the
635 coevolution of body size in males and females. *Annual Review of Ecology and*
636 *Systematics*, 28(1), 659–687.

637 Fastovsky, D. E., Weishampel, D. B., Watabe, M., Barsbold, R., Tsogtbaatar, K. H., &
638 Narmandakh, P. (2011). A nest of *Protoceratops andrewsi* (Dinosauria,
639 Ornithischia). *Journal of Paleontology*, 85(6), 1035–1041.

640 Fitzpatrick, S. (1997). Patterns of morphometric variation in birds' tails: length, shape
641 and variability. *Biological Journal of the Linnean Society*, 62(1), 145–162.

642 Fromhage, L., & Kokko, H. (2014). Sexually selected traits evolve positive allometry
643 when some matings occur irrespective of the trait. *Evolution*, 68(5), 1332–1338.

644 Gosden, T. P., & Chenoweth, S. F. (2011). On the evolution of heightened condition
645 dependence of male sexual displays. *Journal of Evolutionary Biology*, 24(3), 685–
646 692.

647 Gould, S. J. (1966). Allometry and Size in Ontogeny and Phylogeny. *Biological Reviews*,
648 41(4), 587–638. <https://doi.org/10.1111/j.1469-185X.1966.tb01624.x>

649 Gould, S. J. (1973). Positive allometry of antlers in the “Irish elk”, *Megaloceros*
650 *giganteus*. *Nature*, 244(5415), 375–376.

651 Gould, S. J. (1974a). Allometry in primates, with emphasis on scaling and the evolution
652 of the brain. *Contributions to Primatology*, 5, 244–292.

653 Gould, S. J. (1974b). The origin and function of ‘bizarre’ structures: antler size and skull
654 size in the ‘Irish Elk,’ *Megaloceros giganteus*. *Evolution*, 191–220.

655 Gould, S. J. (1977). *Ontogeny and phylogeny*. Harvard University Press.

656 Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology*,
657 144(4), 517–546.

658 Green, A. J. (1992). Positive allometry is likely with mate choice, competitive display
659 and other functions. *Animal Behaviour*, 43(1), 170–172.
660 [https://doi.org/10.1016/S0003-3472\(05\)80086-7](https://doi.org/10.1016/S0003-3472(05)80086-7)

661 Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: a role for
662 parasites? *Science*, 218(4570), 384–387.

663 Handa, N., Watabe, M., & Tsogtbaatar, K. (2012). New specimens of Protoceratops
664 (Dinosauria: Neoceratopsia) from the Upper Cretaceous in Udyn Sayr, southern
665 Gobi area, Mongolia. *Paleontological Research*, 16(3), 179–198.

666 Hardy, I. C., & Briffa, M. (2013). *Animal contests*. Cambridge University Press.

667 Hasson, O. (1991). Sexual displays as amplifiers: practical examples with an emphasis on
668 feather decorations. *Behavioral Ecology*, 2(3), 189–197.

669 Hogue, C. L. (1984). Observations on the plant hosts and possible mimicry models of
670 Lantern Bugs (*Fulgora* spp.)(Homoptera: Fulgoridae). *Rev. Biol. Trop*, 32(1),
671 145–150.

672 Hone, D. W. (2012). A new specimen of the pterosaur Rhamphorhynchus. *Historical*
673 *Biology*, 24(6), 581–585.

674 Hone, D. W. E., & Faulkes, C. G. (2014). A proposed framework for establishing and
675 evaluating hypotheses about the behaviour of extinct organisms. *Journal of*
676 *Zoology*, 292(4), 260–267.

677 Hone, D. W., Farke, A. A., Watabe, M., Shigeru, S., & Tsogtbaatar, K. (2014). A new
678 mass mortality of juvenile Protoceratops and size-segregated aggregation
679 behaviour in juvenile non-avian dinosaurs. *PloS One*, 9(11), e113306.

680 Hone, D. W., & Mallon, J. C. (2017). Protracted growth impedes the detection of sexual
681 dimorphism in non-avian dinosaurs. *Palaeontology*, 60(4), 535–545.

682 Hone, D. W., Naish, D., & Cuthill, I. C. (2012). Does mutual sexual selection explain the
683 evolution of head crests in pterosaurs and dinosaurs? *Lethaia*, 45(2), 139–156.

684 Hone, D. W., Wood, D., & Knell, R. J. (2016). Positive allometry for exaggerated
685 structures in the ceratopsian dinosaur *Protoceratops andrewsi* supports socio-
686 sexual signaling. *Palaeontologia Electronica*, *19*(1), 1–13.

687 Hongo, Y. (2007). Evolution of male dimorphic allometry in a population of the Japanese
688 horned beetle *Trypoxylus dichotomus septentrionalis*. *Behavioral Ecology and*
689 *Sociobiology*, *62*(2), 245–253. <https://doi.org/10.1007/s00265-007-0459-2>

690 Hosken, D. J., & Stockley, P. (2004). Sexual selection and genital evolution. *Trends in*
691 *Ecology & Evolution*, *19*(2), 87–93.

692 Huxley, J. (1932). Problems of relative growth. Retrieved from [http://agris.fao.org/agris-](http://agris.fao.org/agris-search/search.do?recordID=US201300287973)
693 [search/search.do?recordID=US201300287973](http://agris.fao.org/agris-search/search.do?recordID=US201300287973)

694 Huxley, J. S., & Teissier, G. (1936). Terminology of Relative Growth. *Nature*,
695 *137*(3471), 780–781. <https://doi.org/10.1038/137780b0>

696 Iwasa, Y., Pomiankowski, A., & Nee, S. (1991). The evolution of costly mate preferences
697 II. The 'handicap' principle. *Evolution*, 1431–1442.

698 Izzo, A., & Tibbetts, E. A. (2015). Heightened condition dependence of a sexually
699 selected signal in male *Polistes dominulus* paper wasps. *Ethology*, *121*(6), 586–
700 592.

701 Jakob, E. M., Marshall, S. D., & Uetz, G. W. (1996). Estimating Fitness: A Comparison
702 of Body Condition Indices. *Oikos*, *77*(1), 61–67. <https://doi.org/10.2307/3545585>

703 Johnstone, R. A. (1997). The evolution of animal signals. *Behavioural Ecology: An*
704 *Evolutionary Approach*, 155–78.

705 Jungers, W. L., Falsetti, A. B., & Wall, C. E. (1995). Shape, relative size, and size-
706 adjustments in morphometrics. *American Journal of Physical Anthropology*,
707 38(S21), 137–161.

708 Katsuki, M., Yokoi, T., Funakoshi, K., & Oota, N. (2014). Enlarged Hind Legs and
709 Sexual Behavior with Male-Male Interaction in *Sagra femorata* (Coleoptera:
710 Chrysomelidae). *Entomological News*, 124(3), 211–220.
711 <https://doi.org/10.3157/021.124.0306>

712 Kelly, C. D. (2005). Allometry and sexual selection of male weaponry in Wellington tree
713 weta, *Hemideina crassidens*. *Behavioral Ecology*, 16(1), 145–152.

714 Kennedy, M., Taylor, S. A., Nádvorník, P., & Spencer, H. G. (2013). The phylogenetic
715 relationships of the extant pelicans inferred from DNA sequence data. *Molecular*
716 *Phylogenetics and Evolution*, 66(1), 215–222.

717 Kerkhoff, A. J., & Enquist, B. J. (2009). Multiplicative by nature: why logarithmic
718 transformation is necessary in allometry. *Journal of Theoretical Biology*, 257(3),
719 519–521.

720 Kilmer, J. T., & Rodríguez, R. L. (2016). Ordinary least squares regression is indicated
721 for studies of allometry. *Journal of Evolutionary Biology*, n/a-n/a.
722 <https://doi.org/10.1111/jeb.12986>

723 Kingdon, J. (1974). *East African Mammals; an Atlas of Evolution in Africa. Volume II*
724 *Part A (Insectivores and Bats)*. Academic Press.

725 Kleiber, M. (1932). Body size and metabolism. *ENE*, 1(9). Retrieved from
726 <http://biology.unm.edu/jhbrown/Miami/Kleiber1932.pdf>

727 Knell, R. J., & Fortey, R. A. (2005). Trilobite spines and beetle horns: sexual selection in
728 the Palaeozoic? *Biology Letters*, 1(2), 196–199.

729 Knell, R. J., Naish, D., Tomkins, J. L., & Hone, D. W. (2013a). Is sexual selection
730 defined by dimorphism alone? A reply to Padian and Horner. In *Proc. Zool. Soc.*
731 *Lond* (Vol. 35, pp. 491–562). Citeseer.

732 Knell, R. J., Naish, D., Tomkins, J. L., & Hone, D. W. (2013b). Sexual selection in
733 prehistoric animals: detection and implications. *Trends in Ecology & Evolution*,
734 28(1), 38–47.

735 Knell, R. J., & Sampson, S. (2011). Bizarre structures in dinosaurs: species recognition or
736 sexual selection? A response to Padian and Horner. *Journal of Zoology*, 283(1),
737 18–22.

738 Knell, R. J., & Simmons, L. W. (2010). Mating tactics determine patterns of condition
739 dependence in a dimorphic horned beetle. *Proceedings of the Royal Society B:*
740 *Biological Sciences*, 277(1692), 2347–2353.

741 Kodric-Brown, A., & Brown, J. H. (1984). Truth in advertising: the kinds of traits
742 favored by sexual selection. *American Naturalist*, 309–323.

743 Kodric-Brown, A., Sibly, R. M., & Brown, J. H. (2006). The allometry of ornaments and
744 weapons. *Proceedings of the National Academy of Sciences*, 103(23), 8733–8738.
745 <https://doi.org/10.1073/pnas.0602994103>

746 Kratzing, J. E., & Woodall, P. F. (1988). The rostral nasal anatomy of two elephant
747 shrews. *Journal of Anatomy*, 157, 135–143.

748 Kruuk, L. E. B., Slate, J., Pemberton, J. M., Brotherstone, S., Guinness, F., & Clutton-
749 Brock, T. (2002). Antler Size in Red Deer: Heritability and Selection but No

750 Evolution. *Evolution*, 56(8), 1683–1695. <https://doi.org/10.1111/j.0014->
751 3820.2002.tb01480.x

752 Lavine, L., Gotoh, H., Brent, C. S., Dworkin, I., & Emlen, D. J. (2015). Exaggerated
753 Trait Growth in Insects. *Annual Review of Entomology*, 60, 453–472.

754 Lefebvre, H. (2000). *Everyday life in the modern world*. A&C Black.

755 Loxton, R. G., & Nicholls, I. (1979). The functional morphology of the praying mantis
756 forelimb (Dictyoptera: Mantodea). *Zoological Journal of the Linnean Society*,
757 66(2), 185–203.

758 Lundrigan, B. (1996). Morphology of horns and fighting behavior in the family Bovidae.
759 *Journal of Mammalogy*, 77(2), 462–475.

760 Maldonado, H., Levin, L., & Pita, J. C. B. (1967). Hit distance and the predatory strike of
761 the praying mantis. *Zeitschrift Für Vergleichende Physiologie*, 56(3), 237–257.
762 <https://doi.org/10.1007/BF00333669>

763 Mallon, J. C. (2017). Recognizing sexual dimorphism in the fossil record: lessons from
764 nonavian dinosaurs. *Paleobiology*, 1–13.

765 Maynard Smith, J., & Harper, D. (2003). *Animal Signals*. OUP Oxford.

766 McCullough, E. L., Miller, C. W., & Emlen, D. J. (2016). Why Sexually Selected
767 Weapons Are Not Ornaments. *Trends in Ecology & Evolution*.

768 Melnycky, N. A., Weladji, R. B., Holand, Ø., & Nieminen, M. (2013). Scaling of antler
769 size in reindeer (*Rangifer tarandus*): sexual dimorphism and variability in
770 resource allocation. *Journal of Mammalogy*, 94(6), 1371–1379.
771 <https://doi.org/10.1644/12-MAMM-A-282.1>

772 Miljutin, A. (2008). Trends of Specialisation in Rodents: the Five-toed Jerboas,
773 Subfamily Allactaginae (Dipodoidea, Rodentia). *Acta Zoologica Lituanica*, 18(4),
774 228–239. <https://doi.org/10.2478/v10043-008-0033-9>

775 Miller, C. W., & Emlen, D. J. (2010). Dynamic effects of oviposition site on offspring
776 sexually-selected traits and scaling relationships. *Evolutionary Ecology*, 24(2),
777 375–390. <https://doi.org/10.1007/s10682-009-9312-6>

778 Miller, C. W., & Moore, A. J. (2007). A potential resolution to the lek paradox through
779 indirect genetic effects. *Proceedings of the Royal Society of London B: Biological*
780 *Sciences*, 274(1615), 1279–1286.

781 Mirth, C. K., Frankino, W. A., & Shingleton, A. W. (2016). Allometry and size control:
782 what can studies of body size regulation teach us about the evolution of
783 morphological scaling relationships? *Current Opinion in Insect Science*, 13, 93–
784 98.

785 Moczek, A. P., & Emlen, D. J. (2000). Male horn dimorphism in the scarab beetle,
786 *Onthophagus taurus*: do alternative reproductive tactics favour alternative
787 phenotypes? *Animal Behaviour*, 59(2), 459–466.

788 Mosimann, J. E., & James, F. C. (1979). New statistical methods for allometry with
789 application to Florida red-winged blackbirds. *Evolution*, 33(1Part2), 444–459.

790 Neff, B. D., & Pitcher, T. E. (2005). Genetic quality and sexual selection: an integrated
791 framework for good genes and compatible genes. *Molecular Ecology*, 14(1), 19–
792 38.

793 Nijhout, H. F., & Emlen, D. J. (1998). Competition among body parts in the development
794 and evolution of insect morphology. *Proceedings of the National Academy of*
795 *Sciences*, 95(7), 3685–3689.

796 Nur, N., & Hasson, O. (1984). Phenotypic plasticity and the handicap principle. *Journal*
797 *of Theoretical Biology*, 110(2), 275–297.

798 O’Brien, D. M., Katsuki, M., & Emlen, D. J. (2017). Selection on an extreme weapon in
799 the frog-legged leaf beetle (*Sagra femorata*). *Evolution*, 71(11), 2584–2598.

800 Ohl, M., Barkalov, A. V., & Xin-Yue, C. (2004). *Annotated catalog of the Mantispidae of*
801 *the world (Neuroptera)*. Associated Publishers.

802 Orians, G. H. (1969). Age and hunting success in the brown pelican (*Pelecanus*
803 *occidentalis*). *Animal Behaviour*, 17, 316–319. [https://doi.org/10.1016/0003-](https://doi.org/10.1016/0003-3472(69)90016-5)
804 [3472\(69\)90016-5](https://doi.org/10.1016/0003-3472(69)90016-5)

805 Otte, D., & Stayman, K. (1979). BEETLE HORNS. *Sexual Selection and Reproductive*
806 *Competition in Insects*, 259.

807 Padian, K., & Horner, J. R. (2011). The evolution of “bizarre structures” in dinosaurs:
808 biomechanics, sexual selection, social selection or species recognition? *Journal of*
809 *Zoology*, 283(1), 3–17.

810 Padian, K., & Horner, J. R. (2013). Misconceptions of sexual selection and species
811 recognition: a response to Knell et al. and to Mendelson and Shaw. *Trends in*
812 *Ecology & Evolution*, 28(5), 249–250.

813 Padian, K., & Horner, J. R. (2014). The species recognition hypothesis explains
814 exaggerated structures in non-avian dinosaurs better than sexual selection does.
815 *Comptes Rendus Palevol*, 13(2), 97–107.

816 Painting, C. J., & Holwell, G. I. (2013). Exaggerated Trait Allometry, Compensation and
817 Trade-Offs in the New Zealand Giraffe Weevil (*Lasiornychus barbicornis*).
818 *PLOS ONE*, 8(11), e82467. <https://doi.org/10.1371/journal.pone.0082467>

819 Parker, G. A. (1979). Sexual selection and sexual conflict. *Sexual Selection and*
820 *Reproductive Competition in Insects*, 123–166.

821 Paulian, R. (1935). polymorphisme des males de coléoptères. Retrieved from
822 <http://agris.fao.org/agris-search/search.do?recordID=US201300400362>

823 Peig, J., & Green, A. J. (2010). The paradigm of body condition: a critical reappraisal of
824 current methods based on mass and length. *Functional Ecology*, 24(6), 1323–
825 1332. <https://doi.org/10.1111/j.1365-2435.2010.01751.x>

826 Pélabon, C., Bolstad, G. H., Egset, C. K., Cheverud, J. M., Pavlicev, M., & Rosenqvist,
827 G. (2013). On the relationship between ontogenetic and static allometry. *The*
828 *American Naturalist*, 181(2), 195–212.

829 Petrie, M. (1988). Intraspecific variation in structures that display competitive ability:
830 large animals invest relatively more. *Animal Behaviour*, 36(4), 1174–1179.

831 Petrie, M. (1992). Are all secondary sexual display structures positively allometric and, if
832 so, why? *Animal Behaviour*, 43(1), 173–175.

833 Pomfret, J. C., & Knell, R. J. (2006). Sexual selection and horn allometry in the dung
834 beetle *Euoniticellus intermedius*. *Animal Behaviour*, 71(3), 567–576.

835 Pomiankowski, A. (1987). Sexual selection: The handicap principle does work–
836 sometimes. *Proceedings of the Royal Society of London. Series B. Biological*
837 *Sciences*, 231(1262), 123–145.

838 Pomiankowski, A., & Moller, A. P. (1995). A resolution of the lek paradox. *Proceedings*
839 *of the Royal Society of London. Series B: Biological Sciences*, 260(1357), 21–29.

840 Rowe, L., & Houle, D. (1996). The lek paradox and the capture of genetic variance by
841 condition dependent traits. *Proceedings of the Royal Society of London B:*
842 *Biological Sciences*, 263(1375), 1415–1421.

843 Rubner, M. (1883). Ueber den einfluss der korpergrosse auf stoffund kftwechsel.
844 *Zeitschrift Fur Biologie*, 19, 535–562.

845 Schmidt-Nielsen, K. (1984). *Scaling: Why is Animal Size So Important?* Cambridge
846 University Press.

847 Schreiber, R. W., Woolfenden, G. E., & Curtsinger, W. E. (1975). Prey Capture by the
848 Brown Pelican. *The Auk*, 92(4), 649–654. <https://doi.org/10.2307/4084778>

849 Schulte-Hostedde, A., Kuula, S., Martin, C., Schank, C. C. M., & Lesbarrères, D. (2011).
850 Allometry and sexually dimorphic traits in male anurans. *Journal of Evolutionary*
851 *Biology*, 24(5), 1154–1159.

852 Searcy, W. A., & Nowicki, S. (2006). Signal interception and the use of soft song in
853 aggressive interactions. *Ethology*, 112(9), 865–872.

854 Sengupta, S., Ezcurra, M. D., & Bandyopadhyay, S. (2017). A new horned and long-
855 necked herbivorous stem-archosaur from the Middle Triassic of India. *Scientific*
856 *Reports*, 7(1), 8366. <https://doi.org/10.1038/s41598-017-08658-8>

857 Shingleton, A. W., & Frankino, W. A. (2013). New perspectives on the evolution of
858 exaggerated traits. *Bioessays*, 35(2), 100–107.

859 Shingleton, A. W., Frankino, W. A., Flatt, T., Nijhout, H. F., & Emlen, D. J. (2007). Size
860 and shape: the developmental regulation of static allometry in insects. *BioEssays*,
861 29(6), 536–548. <https://doi.org/10.1002/bies.20584>

862 Shingleton, A. W., Mirth, C. K., & Bates, P. W. (2008). Developmental model of static
863 allometry in holometabolous insects. *Proceedings of the Royal Society of London*
864 *B: Biological Sciences*, 275(1645), 1875–1885.
865 <https://doi.org/10.1098/rspb.2008.0227>

866 Simmons, L. W. (2014). Sexual selection and genital evolution. *Austral Entomology*,
867 53(1), 1–17.

868 Simmons, L. W., & Tomkins, J. L. (1996). Sexual selection and the allometry of earwig
869 forceps. *Evolutionary Ecology*, 10(1), 97–104.

870 Skarstein, F., & Folstad, I. (1996). Sexual dichromatism and the immunocompetence
871 handicap: an observational approach using Arctic charr. *Oikos*, 359–367.

872 Smith, R. J. (2009). Use and misuse of the reduced major axis for line-fitting. *American*
873 *Journal of Physical Anthropology*, 140(3), 476–486.

874 Stanley, S. M. (1973). An explanation for Cope’s rule. *Evolution*, 27(1), 1–26.

875 Stern, D. L., & Emlen, D. J. (1999). The developmental basis for allometry in insects.
876 *Development*, 126(6), 1091–1101.

877 Tazzyman, S. J., Iwasa, Y., & Pomiankowski, A. (2014). Signaling Efficacy Drives the
878 Evolution of Larger Sexual Ornaments by Sexual Selection. *Evolution*, 68(1),
879 216–229. <https://doi.org/10.1111/evo.12255>

880 Templeton, C. N., Greene, E., & Davis, K. (2005). Allometry of alarm calls: black-
881 capped chickadees encode information about predator size. *Science*, 308(5730),
882 1934–1937.

883 Thompson, D. W. (1917). On growth and form. *On Growth and Form*. Retrieved from
884 <https://www.cabdirect.org/cabdirect/abstract/19431401837>

885 Thornhill, R. (1981). *Panorpa* (Mecoptera: Panorpidae) Scorpionflies: Systems for
886 Understanding Resource-Defense Polygyny and Alternative Male Reproductive
887 Efforts. *Annual Review of Ecology and Systematics*, 12, 355–386.

888 Urban, J. M., & Cryan, J. R. (2009). Entomologically famous, evolutionarily unexplored:
889 The first phylogeny of the lanternfly family Fulgoridae (Insecta: Hemiptera:
890 Fulgoroidea). *Molecular Phylogenetics and Evolution*, 50(3), 471–484.
891 <https://doi.org/10.1016/j.ympev.2008.12.004>

892 Voje, K. L. (2016). Scaling of morphological characters across trait type, sex, and
893 environment: a meta-analysis of static allometries. *The American Naturalist*,
894 187(1), 89–98.

895 Von Bertalanffy, L. (1957). Quantitative laws in metabolism and growth. *The Quarterly*
896 *Review of Biology*, 32(3), 217–231.

897 Wallace, B. (1987). Ritualistic combat and allometry. *The American Naturalist*, 129(5),
898 775–776.

899 Warton, D. I., Duursma, R. A., Falster, D. S., & Taskinen, S. (2012). smatr 3—an R
900 package for estimation and inference about allometric lines. *Methods in Ecology*
901 *and Evolution*, 3(2), 257–259.

- 902 Warton, D. I., Wright, I. J., Falster, D. S., & Westoby, M. (2006). Bivariate line-fitting
903 methods for allometry. *Biological Reviews*, *81*(2), 259–291.
- 904 Wellnhofer, P. (1975). Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke
905 S\c ddeutschlands, Teil III: Pal^kologie und Stammesgeschichte.
906 *Palaeontographica Abteilung A*, 1–30.
- 907 West, G. B., & Brown, J. H. (2005). The origin of allometric scaling laws in biology from
908 genomes to ecosystems: towards a quantitative unifying theory of biological
909 structure and organization. *Journal of Experimental Biology*, *208*(9), 1575–1592.
- 910 West, G. B., Brown, J. H., & Enquist, B. J. (1997). A General Model for the Origin of
911 Allometric Scaling Laws in Biology. *Science*, *276*(5309), 122–126.
912 <https://doi.org/10.1126/science.276.5309.122>
- 913 Wilkinson, G. S. (1993). Artificial sexual selection alters allometry in the stalk-eyed fly
914 *Cyrtodiopsis dalmanni* (Diptera: Diopsidae). *Genetics Research*, *62*(3), 213–222.
915 <https://doi.org/10.1017/S001667230003192X>
- 916 Wilkinson, G. S., & Taper, M. (1999). Evolution of genetic variation for condition-
917 dependent traits in stalk-eyed flies. *Proceedings of the Royal Society of London B:*
918 *Biological Sciences*, *266*(1429), 1685–1690.
- 919 Wu, S., Zhang, F., Edwards, S. V., Wu, W., Ye, J., Bi, S., ... Organ, C. L. (2014). The
920 evolution of bipedalism in jerboas (Rodentia: Dipodoidea): origin in humid and
921 forested environments. *Evolution*, *68*(7), 2108–2118.
- 922 Zeh, D. W., & Zeh, J. A. (1988). Condition-dependent sex ornaments and field tests of
923 sexual-selection theory. *The American Naturalist*, *132*(3), 454–459.

924 Zeh, D. W., Zeh, J. A., & Tavakilian, G. (1992). Sexual Selection and Sexual
925 Dimorphism in the Harlequin Beetle *Acrocinus longimanus*. *Biotropica*, 24(1),
926 86–96. <https://doi.org/10.2307/2388476>

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946 Figure 1: Extreme non-signal (ns) and sexually selected (ss) signal structures. Clockwise
947 from top right; bighorn sheep horns (*O. canadensis*; ss), Jackson's chameleon horns (*T.*
948 *jacsonii*; ss), praying mantis forelimbs (Mantodea; ns), ichneumon wasp ovipositor
949 (Ichneumonoidea; ss non-signal), gaboon viper fangs (*B. gabonica*; ns), and dung beetle
950 horns (Scarabaeidae, ss). Photos credited in Acknowledgments.



Fig. %

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954 Figure 2: Static scaling relationships for an extreme sexually selected signal structure
 955 (horns; red; left; n = 40) and an extreme, non-signal naturally selected structure (tongue;
 956 blue; right; n = 25) in Jackson's chameleons (*T. jacksonii*). Red and blue indicate focal
 957 structures. Grey indicates the reference structures. Lines represent ordinary least squares
 958 regression of standardized \log_{10} structure size on standardized \log_{10} body size. In
 959 Jackson's chameleon, the extreme sexually selected signal (horn length) scales at a
 960 significantly steeper rate than the reference structure (hindfoot length). The extreme non-
 961 signal structure (tongue length) does not. 95% CI for horn length [3.358, 5.159], tongue
 962 length [0.251, 0.949], and hindlimb length [1.13, 1.979].
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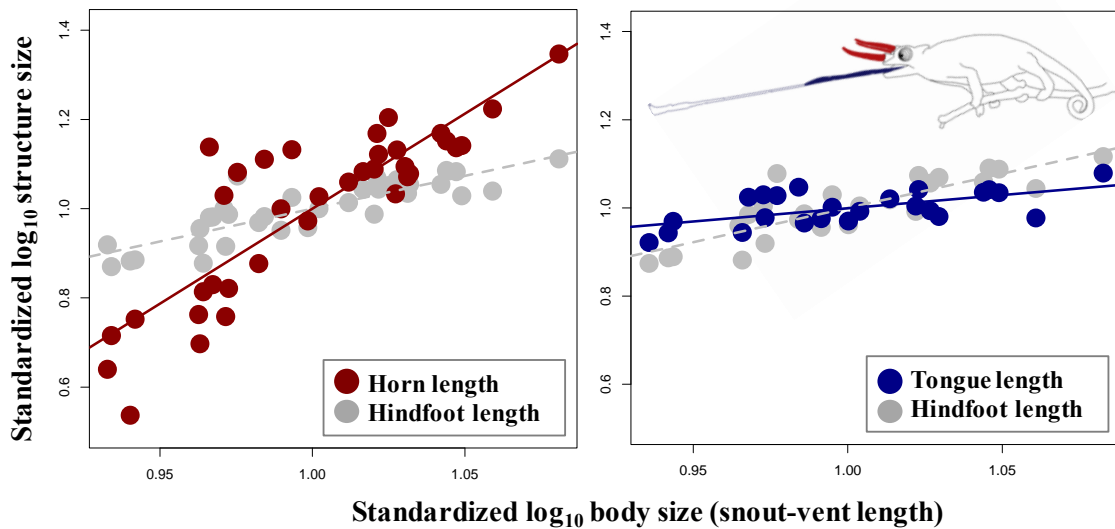


Fig. 2

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968 Figure 3: Static scaling relationships for extreme putative sexually selected signal
 969 structures in ceratopsians (*Protoceratops andrewsi*; left; n = 38) and pterosaurs
 970 (*Rhamphorhynchus muensteri*; right; n = 10). Red indicates putative signal structures.
 971 Grey indicates reference structure. Lines represent the ordinary least squares regression
 972 of standardized \log_{10} structure size on standardized \log_{10} body size. In both species, the
 973 scaling relationship of the putative signal trait is steeper than that of the reference trait (*P.*
 974 *andrewsi*: 95% CI for slope of focal structure [1.173, 1.353], 95% CI for slope of
 975 reference structure [0.925, 1.039]; *R. muensteri*: 95% CI for slope of focal structure
 976 [1.332, 2.930], 95% CI for slope of reference structure [0.871, 1.262]), consistent with a
 977 history of selection for a hypervariable sexually selected signal. Inlaid photographs
 978 display study species with focal structures highlighted in red. Photos credited in
 979 Acknowledgments.
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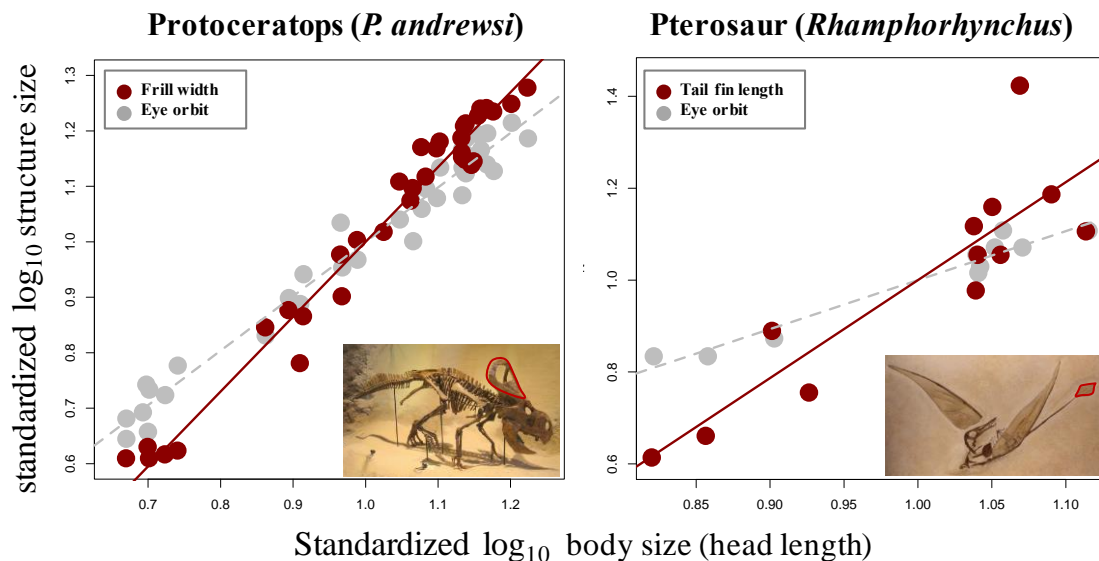


Fig. 3

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983 Table 1: Summary of study species and results.

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985 **INCLUDED SEPARATELY AS EXCEL TABLE**

986

987 *Table 1 footnotes*

988 (f) = focal trait, (r) = reference trait, CV = coefficient of variation, β = slope of scaling

989 relationship between trait size and body size, $\Delta\beta$ = difference between $\beta_{(f)}$ and $\beta_{(r)}$, † =

990 extinct species, $R^2_{(f)}$ = adjusted R^2 of scaling relationship between focal trait size and

991 body size, $R^2_{(r)}$ = adjusted R^2 of scaling relationship between reference trait and body

992 size, * = sexual dimorphism may be impossible to detect (see D. W. Hone & Mallon,

993 2017). F and p value from ANCOVA comparing $\beta_{(f)}$ and $\beta_{(r)}$ within the same species.

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1006 **Appendix 1: Identifying extreme morphology**

1007 Many extreme structures appear self-evident. Some, like beetle horns, are massive
1008 in absolute and relative size and few would contest their designation as extreme. Others
1009 are more ambiguous. Butterfly wings, for example, rarely earn the title of extreme yet,
1010 their ontogenetic growth and relative size are more akin to that of beetle horns than other
1011 insect wings (Nijhout & Emlen, 1998). Examples like this highlight the ambiguity
1012 surrounding extreme morphology and the subjective nature of categorizing structures as
1013 extreme. This uncertainty, in part, stems from the lack of established criteria for
1014 designating a structure as extreme. For over a century, researches have explored the
1015 evolution of extreme morphology (M. B. Andersson, 1994; reviewed in Darwin, 1871;
1016 Emlen, 2008). Yet, to our knowledge, not once has the term ‘extreme’ been defined.

1017 Recognizing and limiting bias is a vital component of biological research and,
1018 given the large body of work dedicated toward putatively extreme structures, we believe
1019 a consistent method for identifying these structures is needed. Here we suggest three
1020 (potentially overlapping) categories of extreme - ontogenetically, statically, and
1021 evolutionarily extreme – and provide guidelines for assigning structures to each category.

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1023 ***Ontogenetically Extreme:*** Ontogenetically extreme structures are those displaying rates
1024 of growth, often occurring in bursts close to reproductive maturity, that outpace other
1025 surrounding structures. Examples include the horns of beetles and the wings of
1026 lepidopterans, both of which grow to drastic proportions during the same timeframe as
1027 other, more typically proportioned structures (Nijhout & Emlen, 1998). Ontogenetically

1028 extreme should be distinguished by rates of growth that are faster than those of reference
1029 structures within the same organism.

1030

1031 ***Statically Extreme:*** Statically extreme structures are disproportionately larger than other
1032 structures when sampled across same stage (generally adult) individuals within a
1033 population. Relative size of a focal trait can be assessed by comparing the size of the
1034 focal trait to other, analogous traits in the same sex (e.g., harlequin beetle (*Acrocinus*
1035 *longimanus*) forelegs are relatively larger than midlegs or hindlegs (Zeh, Zeh, &
1036 Tavakilian, 1992)) or by comparing the size of the same trait across sexes (e.g., harlequin
1037 beetle forelegs are disproportionately larger in males than they are in females (Zeh et al.,
1038 1992)). Statically extreme structures should be distinguished by comparing slopes and/or
1039 intercepts of the static scaling relationships (trait size versus body size) of the focal and
1040 reference traits.

1041

1042 ***Evolutionarily Extreme:*** Evolutionarily extreme structures are extreme when compared
1043 with homologous structures in closely related organisms. Examples include the hindlegs
1044 of jerboas, which are relatively longer than the hindlegs of their quadrupedal ancestors
1045 (Miljutin, 2008; Dipodidae; Wu et al., 2014) and the raptorial forelimbs of mantidflies
1046 (mantispidae; Ohl, Barkalov, & Xin-Yue, 2004). Evolutionarily extreme structures can be
1047 distinguished by a) comparing static scaling relationships (slopes and/or intercepts) of
1048 individuals sampled from populations of ancestral and derived species; b) comparing
1049 mean relative trait size of ancestral and derived species (e.g., Wu et al., 2014); and/or c)

1050 by mapping changes in trait size onto a phylogeny and testing for lineage specific
1051 changes in relative trait size (Wu et al., 2014).

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1073 **Appendix 2: Sources for *Protoceratops andrewsi* data.** AMNH = American Museum of
 1074 Natural History (New York, USA); MPC = Mongolian Palaeontological Centre
 1075 (Ulaanbaatar, MN); IVPP = Institute of Vertebrate Palaeontology and
 1076 Palaeoanthropology (Beijing, CN); ZPAL = Zoological Institute of Paleobiology, Polish
 1077 Academy of Sciences (Warsaw, PL); CMNH/CM = Carnegie Museum of Natural History
 1078 (Pittsburgh, USA); NHM = Natural History Museum (London, UK).

1079

Protoceratops andrewsi

	Source	Specimen	Number
1080	Dodson (1976)	AMNH	6419
	Dodson (1976)	AMNH	6434
	Dodson (1976)	AMNH	6430
1081	Dodson (1976)	AMNH	6251
	Dodson (1976)	AMNH	6431
	Dodson (1976)	AMNH	6486
1082	Dodson (1976)	AMNH	6432
	Dodson (1976)	AMNH	6428
	Dodson (1976)	AMNH	6409
1083	Dodson (1976)	AMNH	6480
	Dodson (1976)	AMNH	6444
	Dodson (1976)	AMNH	6485
1084	Dodson (1976)	AMNH	6408
	Dodson (1976)	AMNH	6433
	Dodson (1976)	AMNH	6429
1085	Dodson (1976)	AMNH	6439
	Dodson (1976)	AMNH	6441
	Dodson (1976)	AMNH	6477
1086	Dodson (1976)	AMNH	6417
	Dodson (1976)	AMNH	6425
	Dodson (1976)	AMNH	6413
1087	Dodson (1976)	AMNH	6414
	Dodson (1976)	AMNH	6438
	Dodson (1976)	AMNH	6466
1088	Dodson (1976)	AMNH	6467
	Handa et al. (2012)	MPC	100/539
	Hone et al. (2014)	MPC	100/534
1089	Hone et al. (2014)	MPC	100/526 B
	Hone et al. (2014)	MPC	100/526 C
	Fastovsky et al. (2011)	MPC	100/530 A
1090	Fastovsky et al. (2011)	MPC	100/530 B
	Fastovsky et al. (2011)	MPC	100/530 C
	Fastovsky et al. (2011)	MPC	100/530 D
1091	Fastovsky et al. (2011)	MPC	100/530 E
	Fastovsky et al. (2011)	MPC	100/530 F
	Fastovsky et al. (2011)	MPC	100/530 G
1092	Fastovsky et al. (2011)	MPC	100/530 H
	Unpublished photos	IVPP	23899
	Unpublished photos	IVPP	Unnumbered Medium
1093	Unpublished photos	IVPP	Unnumbered Small
	Unpublished photos	ZPAL	MgD-II/2b
	Unpublished photos	ZPAL	MgD-II/5
1094	Unpublished photos	CMNH	9185
	Unpublished photos	NHM	5134
	Unpublished photos	NHM	6442
	Unpublished photos	NHM	6440
1095	Unpublished photos	AMNH	6418
	Unpublished photos	AMNH	6637
	Unpublished photos	AMNH	6422
	Unpublished photos	AMNH	6485

1096 **Appendix 3: Sources for *Rhamphorhynchus muensteri* data.** BSP = Palaeontological
 1097 Museum, Munich (Munich, DE); YPM = Yale Peabody Museum (CT, USA) ;SMF =
 1098 Forschungsinstitut und Naturmuseum Senckenberg (Frankfurt, DE); CMNH/CM =
 1099 Carnegie Museum of Natural History (Pittsburgh, USA); SOS = Jura Museum (Eichstätt
 1100 DE); NHM = Natural History Museum (London, UK); TMP = Royal Tyrell Museum of
 1101 Palaeontology (Alberta, CA); MBR = Museo Argentino de Ciencias Naturales (Buenos
 1102 Aires, AR); BMNS = Brazoport Museum of Natural Science (TX, USA); NMS =
 1103 National Museums of Scotland (Edinburgh, UK); TPI = Thanksgiving Point Institute
 1104 (North American Museum of Ancient Life, UT, USA).

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Rhamphorhynchus muensteri

	Specimen	Specimen	Number	Wellnhofer number
1107	Wellnhofer (1975)	BSP	1960.I.470	9
	Wellnhofer (1975)	BSP	1938.I.503	11
1108	Wellnhofer (1975)	Eichstaett		28
	Wellnhofer (1975)	YPM	1778	33
1109	Wellnhofer (1975)	SMF	R 4128	43
	Wellnhofer (1975)	CM	11429	53
1110	Wellnhofer (1975)	BSP	1907 I 37	60
	Wellnhofer (1975)	SOS	3558	77
	Wellnhofer (1975)	NA	NA	102
1111	Hone (2012)	NHM	W1198z0077/0001	
	Direct Measurement	TMP	2008.041.0001	
1112	Direct Measurement	MBR	3650.3	
	Direct Measurement	BMNS	21	
1113	Measured from photo	NMS	G.1994.13.1.	
	Measured from Photo	TPI	1012	

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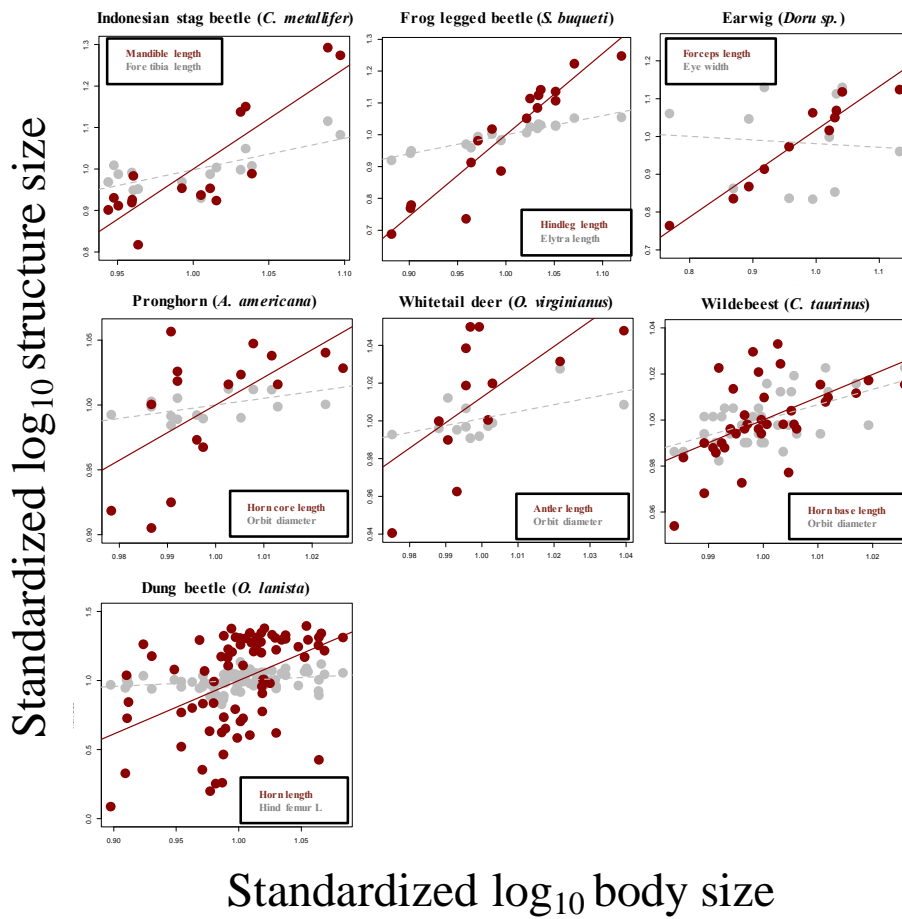
1120 **Appendix 4: Scaling relationships for extreme sexually selected signal structures.**

1121 Lines represent ordinary least squares regression of \log_{10} standardized structure size on

1122 \log_{10} standardized body size (slope estimates and sample sizes reported in Table 1). Red

1123 points and lines represent focal traits. Grey points and lines represent reference traits.

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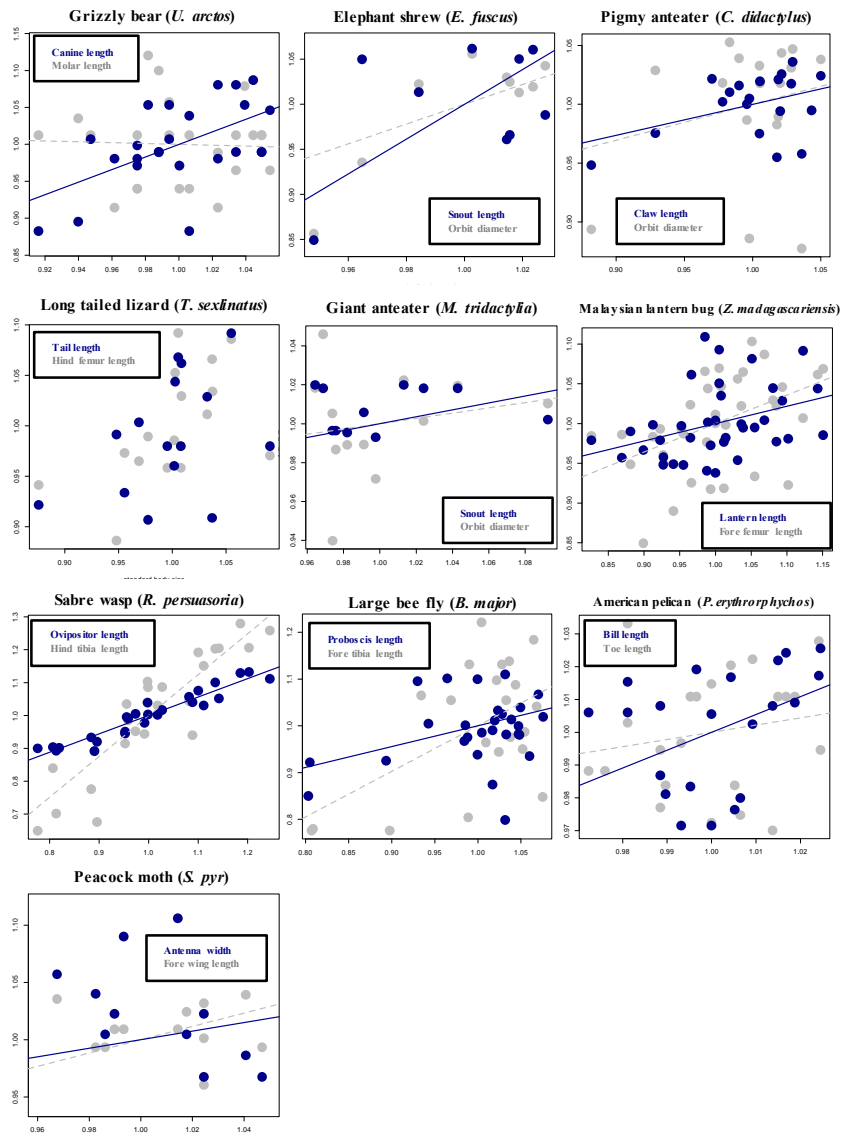
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1130 **Appendix 5: Scaling relationships for extreme naturally selected/non-signal**
 1131 **structures.** Lines represent ordinary least squares regression of \log_{10} standardized
 1132 structure size on \log_{10} standardized body size (slope estimates and sample sizes reported
 1133 in Table 1). Blue points and lines represent focal traits. Grey points and lines represent
 1134 reference traits.
 1135



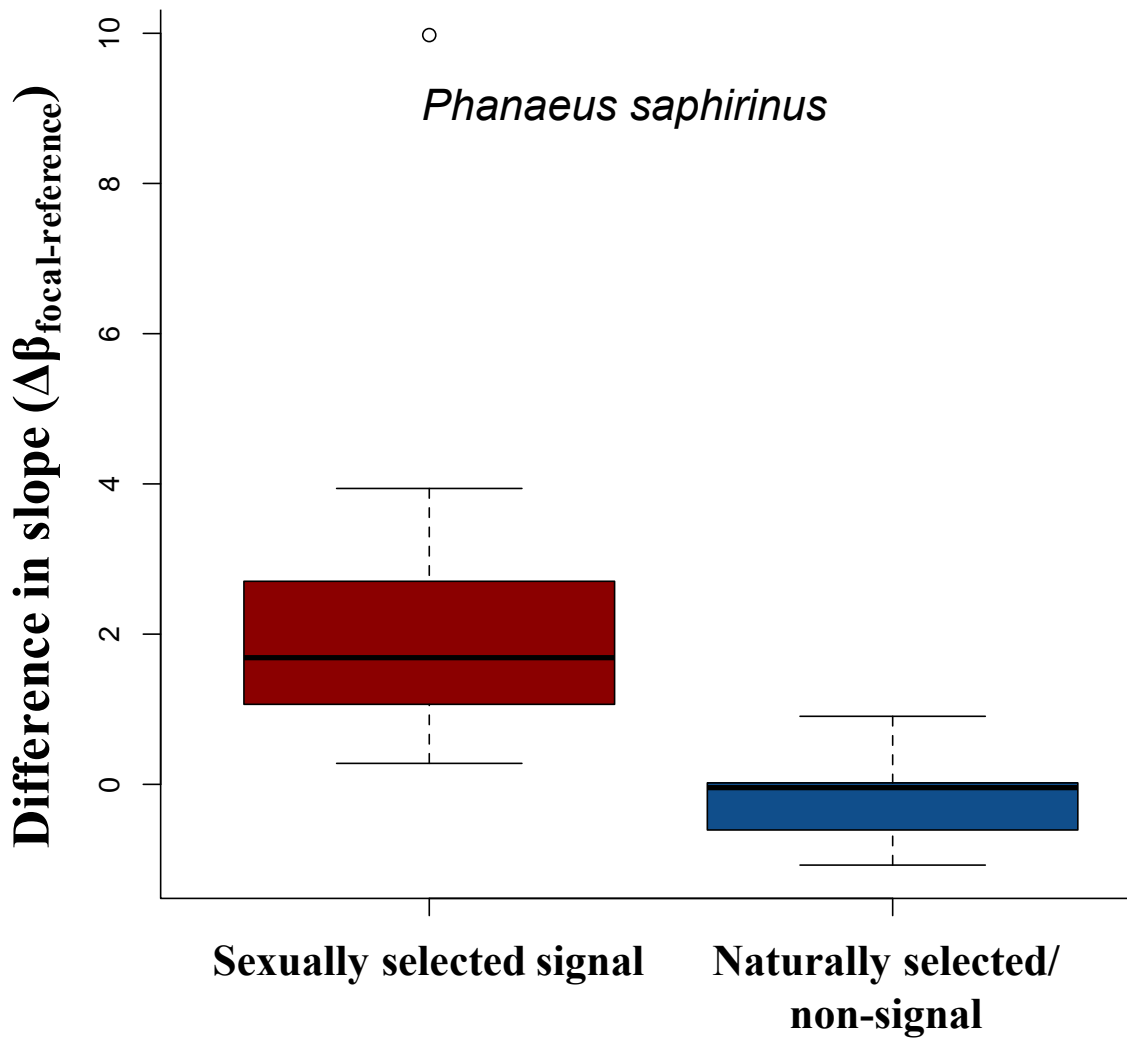
Standardized \log_{10} body size

1136

1137 **Appendix 6: Comparison of $\Delta\beta_{\text{focal-reference}}$ (difference between the scaling**
1138 **relationship slope of focal traits and reference traits) between extreme sexually**
1139 **selected signal traits (n = 14) and extreme non-signal selected traits (n = 15). $\Delta\beta_{\text{focal-}}$**
1140 **reference of extreme sexually selected signal structures is significantly greater than $\Delta\beta_{\text{focal-}}$**
1141 **reference of extreme non-signal structures ($t_{15,616} = 4.153$ $p < 0.001$).**

1142

1143



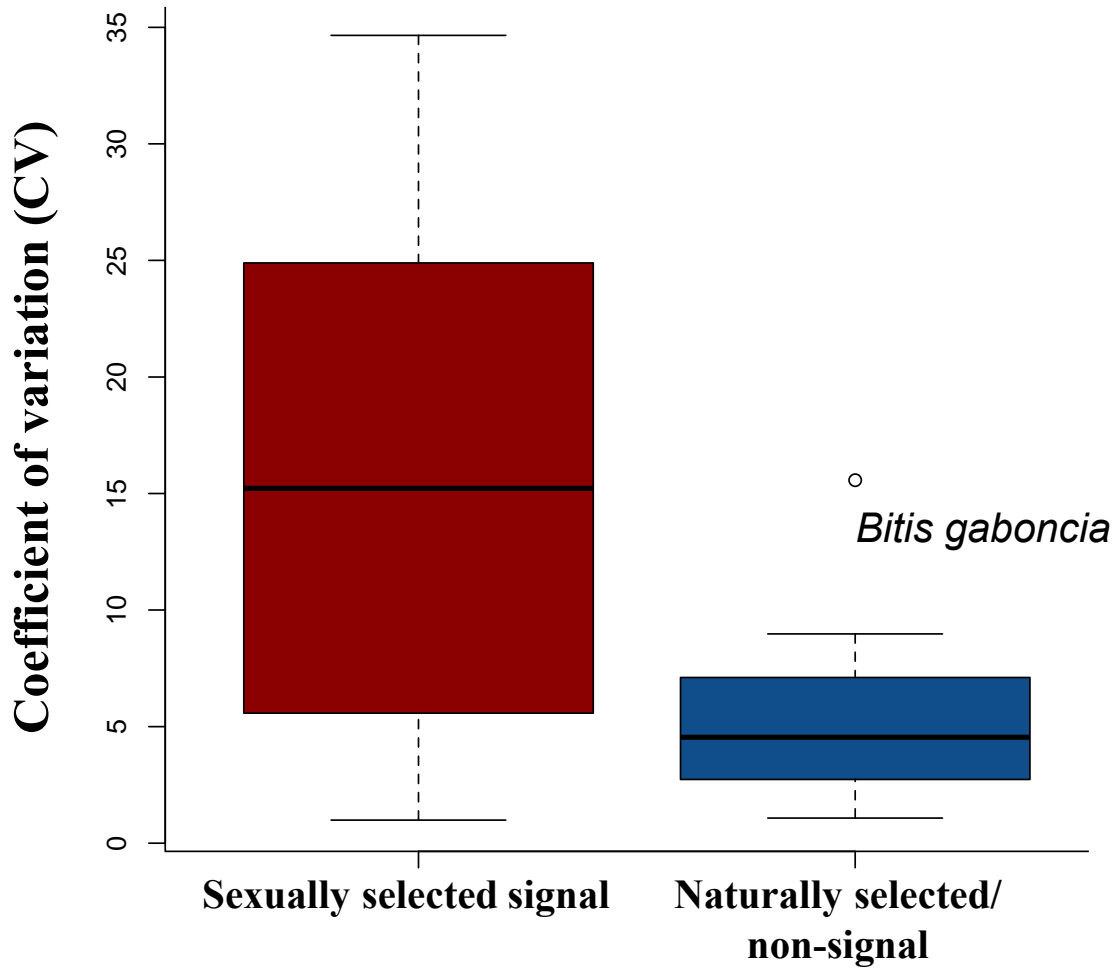
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1147 **Appendix 7: Comparison of coefficients of variation (CV) between extreme sexually**
1148 **selected signal traits (n = 14) and extreme non-signal selected traits (n = 15). CVs of**
1149 extreme sexually selected signal structures is significantly greater than CVs of extreme
1150 non-signal structures ($t_{16,043} = 3.37, p < 0.01$).

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