



**HAL**  
open science

## Evolution of morphological allometry

Christophe Pélabon, Cyril Firmat, Geir H. Bolstad, Kjetil L. Voje, David Houle, Jason Cassara, Arnaud Le Rouzic, Thomas F. Hansen

► **To cite this version:**

Christophe Pélabon, Cyril Firmat, Geir H. Bolstad, Kjetil L. Voje, David Houle, et al.. Evolution of morphological allometry. *Annals of the New York Academy of Sciences*, 2014, 1320 (1), pp.58-75. 10.1111/nyas.12470 . hal-01534649

**HAL Id: hal-01534649**

**<https://hal.science/hal-01534649>**

Submitted on 27 Mar 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Copyright

**Evolution of morphological allometry**

Journal:	<i>Annals of the New York Academy of Sciences</i>
Manuscript ID:	Draft
Manuscript Type:	Review paper
Date Submitted by the Author:	n/a
Complete List of Authors:	Pelabon, christophe; NTNU, Biology Firmat, Cyril; NTNU, Biology Bolstad, Geir; NTNU, Biology Voje, Kjetil; University of Oslo, Department of Biology Cassara, Jason; Florida State University, Department of Biological Science Le Rouzic, Arnaud; Centre National de la Recherche Scientifique, Laboratoire Evolution, Génomes, Spéciation Houle, David; Florida State University, Department of Biological Science Hansen, Thomas; University of Oslo, Department of Biology
Keywords:	allometry, adaptation, evolution

SCHOLARONE™  
Manuscripts

Manuscript

# Evolution of morphological allometry

Christophe Pélabon<sup>1</sup>, Cyril Firmat<sup>1</sup>, Geir H. Bolstad<sup>1</sup>, Kjetil L. Voje<sup>2</sup>, David Houle<sup>3</sup>, Jason  
Cassara<sup>3</sup>, Arnaud Le Rouzic<sup>4</sup>, Thomas F. Hansen<sup>2</sup>

*1 – Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of  
Science and Technology, 7491 Trondheim, Norway*

*2 – Department of Biology, Centre for Ecological and Evolutionary Synthesis, University of  
Oslo, Oslo, Norway*

*3 – Department of Biological Science, Florida State University, Tallahassee, FL, USA*

*4 – Laboratoire Evolution, Génomes, Spéciation, Centre National de la Recherche  
Scientifique UPR9034, Gif-sur-Yvette, France*

Pélabon et al.

The evolvability of allometry

23 **Abstract**

24 Allometry refers to the power-law relationship that often occurs between body parts and total  
25 body size. Whether measured during growth (ontogenetic allometry), among individuals at  
26 similar developmental stage (static allometry) or among populations or species (evolutionary  
27 allometry), allometric relationships are often surprisingly tight, and relatively invariant.  
28 Consequently, it has been suggested that allometry could constrain phenotypic evolution, that  
29 is, force evolving species along fixed trajectories. Alternatively allometric relationship may  
30 result from selection. Despite nearly a century of active research on allometry, distinguishing  
31 between these two alternatives remains difficult partly due to the use of a broad sense  
32 definition of allometry where the meaning of relative growth was lost. Focusing on the  
33 original narrow-sense definition of allometry, we review evidence for and against the  
34 “allometry as a constraint” hypothesis. Although the low evolvability of the static allometric  
35 slopes observed in some studies suggests a possible constraining effect of this parameter on  
36 phenotypic evolution, the nearly complete absence of knowledge about selection on allometry  
37 prevents any firm conclusion.

38  
39 **Keywords:** adaptation, microevolution, macroevolution, evolutionary constraint

40

41 Abstract: 166 words; Main text: 5565 words ; 1 table; 5 figures; 2 boxes

Pélabon et al.

The evolvability of allometry

## 42 Introduction

43 Allometry is the study of the relationship between body size and other organismal traits.  
44 Allometry is important because variation in a wide variety of morphological, physiological  
45 and life history traits are highly correlated with organism size [1,2,3]. These relationships  
46 generate intuitive hypotheses for understanding trait variation; for example, the fact that  
47 humans are larger than mice can be used to explain why the basal metabolic rate of a human  
48 is much higher than the basal metabolic rate of a mouse. In most cases, traits show a non-  
49 linear relationship with size that is accurately captured by a power relationship of the form  $z =$   
50  $ax^b$ , where the trait value is  $z$ , the organism size is  $x$ , and  $a$  and  $b$  are parameters of the  
51 relationship. If  $b = 1$ , the relationship between the trait and size is linear, a condition referred  
52 to as isometry. When  $b \neq 1$ , the relationship is non-linear on the arithmetic scale. For  
53 example, the basal metabolic rate in mammals scales with body mass with a coefficient  $b \approx$   
54  $0.71$  [4]; as a result, for every unit increase in mass, a larger organism will have a smaller  
55 increase in basal metabolic rate than a smaller organism. Consequently, humans have a basal  
56 metabolic rate 5 to 10 times smaller than a mouse when corrected for body size. The ubiquity  
57 of these power-law relationships has led biologists to refer to them as allometric relationships.

58 Analyzed on log-transformed data these relationships become linear:  $\log(z) = \log(a) +$   
59  $b \times \log(x)$ , where  $\log(a)$  and  $b$  represent the allometric intercept and slope, respectively.  
60 Because size varies during growth, among individuals of similar age, or among populations or  
61 species, three types of allometry have been defined. Ontogenetic allometry refers to the  
62 allometric relationship when size varies during growth. Static allometry refers to the  
63 relationship when size varies among individuals measured at a similar developmental stage  
64 and evolutionary allometry refers to the allometric relationship when size varies among  
65 population or species means.

66 Allometric relationships often fit very precisely when the range of sizes is large, which

Pélabon et al.

The evolvability of allometry

1  
2  
3 67 is usually the case at the ontogenetic and evolutionary levels. Furthermore, ontogenetic and  
4  
5 68 static allometric slopes usually vary little among closely related species. These observations  
6  
7 69 have led several authors to suggest that allometric slopes most likely reflect strong physical,  
8  
9 70 physiological or biological mechanisms that somehow constrain the rate and direction of  
10  
11 71 evolution [5,6,7]. For example, the scaling of metabolism with body size, referred to above,  
12  
13 72 may be explained by the limits of diffusion through the limited surface area per volume of the  
14  
15 73 larger human than the smaller mouse [8]. Accordingly, allometric relationships have been  
16  
17 74 taken as prime evidence against the dominance of natural selection as an evolutionary force  
18  
19 75 [9]. This constraint hypothesis has been widely accepted for physiological and life history  
20  
21 76 traits [10,11], but has become more controversial for morphological traits.  
22  
23  
24

25 77 The alternative to the constraint hypothesis of allometry is that natural selection  
26  
27 78 persistently favors the particular power relationships between traits and size that are observed.  
28  
29 79 This hypothesis is at least implicitly widely accepted in the traditional studies of functional  
30  
31 80 allometry [2]. For example, the relationship between the cross-sectional area of the skeleton  
32  
33 81 with body mass may be explained in terms of optimal allocation, balancing the chances of  
34  
35 82 breakage – favoring a robust skeleton – with the costs of locomotion – favoring a lighter  
36  
37 83 skeleton. Accordingly, several authors have suggested that allometric slope could evolve  
38  
39 84 under selection [12,13,14,15]. In this context, the evolution of the static allometry of sexually  
40  
41 85 selected traits has been a particularly popular topic. Secondary sexual displays have been  
42  
43 86 predicted to evolve particularly steep slopes (i.e. positive allometry:  $b > 1$ ) under handicap  
44  
45 87 models [12,13,16,17,18], while genitalia are expected to show negative allometry ( $b < 1$ ) due  
46  
47 88 to stabilizing selection on trait size [14, 19, 20].  
48  
49  
50

51 89 Optimally, it should be possible to distinguish between the constraint and selective  
52  
53 90 explanations for allometry by quantifying both the selection forces and the evolvability of  
54  
55 91 allometry (i.e. its capacity to evolve) and compare the predicted and observed patterns of  
56  
57  
58  
59  
60

Pélabon et al.

The evolvability of allometry

1  
2  
3 92 evolution in allometry. The general prediction is that a constrained slope will either be  
4  
5 93 incapable of evolving (an absolute constraint, [21]), or that fitness will decrease so rapidly  
6  
7 94 when moved away from the optimal value that the possible advantages of the altered slope  
8  
9 95 would not outweigh the fitness costs. Unfortunately, despite renewed interest in allometry in  
10  
11 96 the last two decades, progress in understanding the evolution of morphological allometry has  
12  
13 97 been slow. A key reason for this is the rise of a ‘broad sense’ definition of allometry as any  
14  
15 98 monotonic relationship between trait size and body size [22, 23] (Box 1). This divorces the  
16  
17 99 study of scaling from the prevalence of power relationships (Box 2), and in particular from  
18  
19 100 the centrality of the slope as the essence of allometry [24]. The result is a body of literature  
20  
21 101 that has measured quantities that cannot be interpreted as parameters of a power relationship.  
22  
23

24  
25 102 Our aim in the current contribution is therefore to define clear predictions concerning  
26  
27 103 the constraint and selection hypotheses on morphological allometries and review the recent  
28  
29 104 literature in the light of these predictions.  
30  
31

32 105

### 33 34 106 Evolutionary constraint and allometry

35  
36 107 Evolutionary constraints are defined as any processes that preclude a trait from reaching a  
37  
38 108 phenotypic optimum, or slow down its evolution towards this optimum [25]. Depending on  
39  
40 109 the perspective and processes involved, many types of constraint have been defined [25,26].  
41  
42 110 Initially, allometry has been classified as developmental constraint, that is, constraint imposed  
43  
44 111 by the developmental architecture in the production of variant phenotypes [27]. Although  
45  
46 112 developmental constraints may themselves result from selection [28,29], they may still limit  
47  
48 113 the direction of phenotypic evolution. Such perspective of allometry as developmental  
49  
50 114 constraint corresponds to the view defended by early students of allometry and heterochrony  
51  
52 115 [5, 6, 7, 30, 31], who explained patterns of species divergence by changes in timing or rate of  
53  
54 116 development along constant ontogenetic processes.  
55  
56  
57  
58  
59  
60

Pélabon et al.

The evolvability of allometry

1  
2  
3 117 The introduction of the quantitative genetics framework in the study of allometry [32,  
4  
5 118 33, 34, 35] has shifted the hypothesis of allometry as a constraint from a developmental to a  
6  
7 119 genetic perspective. Genetic constraints occur when the amount or pattern of genetic variation  
8  
9 120 limits or channels the response to selection. Although these two perspectives are intimately  
10  
11 121 linked because genetic constraints often result from developmental constraints, this change in  
12  
13 122 perspective may have weakened the constraint hypothesis, given the ubiquity of genetic  
14  
15 123 variation generally found [36]. But more recently, the hypothesis of constraint due to low  
16  
17 124 genetic variation has been refueled by the realization that genetic correlations among traits  
18  
19 125 due to pleiotropy could seriously influence the direction of phenotypic evolution [21, 37, 38,  
20  
21 126 39, 40, 41, 42, 43], allometry being a perfect example of such a constraint.  
22  
23  
24

25 127 Importantly, the quantitative genetics approach of allometry underlines the fact that  
26  
27 128 understanding the evolution of allometry, and testing whether allometry represents an  
28  
29 129 evolutionary constraint requires quantifying the evolvability of allometry and comparing the  
30  
31 130 observed evolutionary patterns with those patterns expected under specific selection  
32  
33 131 pressures. If we are to test the “allometry as a constraint” hypothesis, we should therefore  
34  
35 132 answer the following questions; 1) Is allometry evolvable? 2) Does allometry constrains  
36  
37 133 patterns of phenotypic evolution? Static allometry represents the pivotal level at which these  
38  
39 134 questions should be asked. Indeed, it is the level at which developmental constraints will be  
40  
41 135 expressed, and patterns of static allometry will allow us to make predictions about phenotypic  
42  
43 136 evolution.  
44  
45  
46

137

### 138 **Is static allometry evolvable?**

139 Testing whether a trait is evolvable or not may be achieved by quantifying either its  
140 propensity to vary (i.e. its evolvability; [44]), or its evolution, that is, quantifying the changes  
141 in the trait when selected. In the following, after considering the possible sources of constraint



Pélabon et al.

The evolvability of allometry

1  
2  
3 142 and selection acting on static allometry, we review evidence for both the evolution of static  
4  
5 143 allometry at the microevolutionary scale and its evolvability.  
6

7 144

9 145 *Sources of constraint*

10 146 Evolution of static allometry depends on the evolution of the static allometric slopes and  
11  
12 147 intercepts. One key challenge is that an individual organism expresses neither a slope nor an  
13  
14 148 intercept. Therefore, if these parameters represent quantitative traits, estimating their genetic  
15  
16 149 variation requires clonal organisms where genetically similar organisms of different size can  
17  
18 150 be measured, measurement of "allometries" across relatives in family groups, or across  
19  
20 151 modules in modular organisms. Alternatively, because ontogenetic, static and evolutionary  
21  
22 152 allometries of morphological traits all result from a single process, namely growth, testing the  
23  
24 153 evolvability of static allometry could be achieved by estimating the evolvability of the growth  
25  
26 154 processes that generate covariance among traits. Several growth models have been suggested  
27  
28 155 to explain how static allometry is generated from simple growth patterns [5, 16, 31, 45, 46].  
29  
30 156 Using these models one can identify possible constraints on the variation of static allometry.  
31  
32  
33  
34  
35

36 157 From Huxley's (1932) [5] model of relative growth (Box 1), it can be shown that when  
37  
38 158 two traits present an ontogenetic allometry such as  $z = a + bx$ , with  $x$  and  $z$  varying during  
39  
40 159 growth, the static allometric slope at any specific time  $t$  can be expressed as:  
41  
42

43 160

44  
45  
46 161 
$$b_s = \bar{b} + \frac{Cov(x_t, a) + \bar{x}_t Cov(x_t, b)}{Var(x)}, \quad (1)$$
  
47  
48

49 162

50  
51 163 where  $\bar{b}$  is the ontogenetic allometric slope averaged across all individuals, (i.e. the mean  
52  
53 164 ontogenetic allometry of the population), and  $\bar{x}_t$ , the mean body size at time  $t$  [47]. This  
54  
55 165 shows that the static allometric slope is affected by both the average slope of the ontogenetic  
56  
57  
58  
59  
60

Pélabon et al.

The evolvability of allometry

166 allometry and the covariance between the parameters of the ontogenetic allometry (slope and  
 167 intercept) and body size. Similarly, parameters of the ontogenetic allometry will affect the  
 168 average value of the trait over the entire range of sizes. This effect can be expressed in terms  
 169 of the mean trait at the population mean body size,  $\bar{x}_t$ , in the following way:

$$171 \quad \bar{z}_t = \bar{a} + E(bx_t) = \bar{a} + \bar{b}\bar{x}_t + \sigma(b, x_t), \quad (2)$$

172  
 173 where  $\bar{a}$  is the average ontogenetic intercept across all individuals. Therefore a positive  
 174 covariance between the ontogenetic slope and body size at stage  $t$  will increase the mean  
 175 value, while a negative covariance will decrease it. This model illustrates how variation in the  
 176 static allometric slope and intercept can be generated by variation of the ontogenetic  
 177 parameters. Importantly, it also shows that when ontogenetic and static allometries are  
 178 different ( $Cov(x_t, b) \neq 0$  or  $Cov(x_t, a) \neq 0$ ), invariance of static allometry across populations  
 179 with different mean body size implies changes in the ontogenetic parameters. Comparing  
 180 ontogenetic and static allometries and estimating the variation of the ontogenetic parameters  
 181 should therefore provide valuable insight in the possibility for static allometry to evolve.

182 Different body parts do not always grow simultaneously; some traits grow most  
 183 rapidly early in development (e.g. mammalian brain, [48]) while others continue to grow after  
 184 body mass has stopped increasing (e.g. appendages in holometabolous insects, secondary  
 185 sexual traits in vertebrates [49], and see [50] for the special case of deer antlers). Ontogenetic  
 186 allometry resulting from this type of growth pattern is necessarily non-linear [e.g. 45, 46], and  
 187 sometimes the link between ontogenetic and static allometry can be difficult to establish.  
 188 Nevertheless, even in such cases the overall growth of the trait may be coordinated with the  
 189 expected body size, despite the difference in the timing of growth. Static allometry could then  
 190 be interpreted as the reaction norm of a trait to changes in body size which represents the

Pélabon et al.

The evolvability of allometry

1  
2  
3 191 growth environment (see [16] for such a model). Variation in the allometric slope could then  
4  
5 192 have a component due to variation in the trait sensitivity to the growth state of the whole  
6  
7 193 organism. Lack of genetic variance in trait growth sensitivity to the size of the body or the  
8  
9 194 sharing of a large proportion of the developmental pathway therefore seem the most likely  
10  
11 195 sources of constraint on changes in static allometry. Importantly, such constraints would  
12  
13  
14 196 affect the allometric slope, but not necessarily the intercept.  
15  
16  
17  
18

197

198 *Sources of selection*

199 *Selection on trait and body size* – Change in the allometric slope may occur as a side effect of  
200 directional selection on trait or body size. This type of selection probably represents the most  
201 common selection in the wild, as demonstrated by variation in size among populations and  
202 closely related species. Following the model described above (Eq. 1 and 2), in absence of  
203 covariance between body size and the ontogenetic parameters, ontogenetic and static  
204 allometry should be similar, and changes in body size should not affect the static allometric  
205 slope (Fig. 1; scenario A), except if the ontogenetic allometry is non-linear. If one of the  
206 covariance terms between body size and the slope or the intercept of the ontogenetic  
207 allometry is different from zero and constant, changes in body size should generate changes in  
208 static allometric slope (Fig. 1; scenario D). Finally, changes in the mean trait ( $\bar{z}_t$ ) are  
209 expected to affect either the mean ontogenetic intercept ( $\bar{a}$ , Fig. 1 scenario C), the mean body  
210 size ( $\bar{x}_t$ , Fig. 1 scenario A), the mean ontogenetic slope ( $\bar{b}$ ), the covariance between these  
211 last two terms  $\sigma(b, x_t)$ , or any combination of these parameters. Changes in static allometric  
212 slope with increasing body size may also occur if the sensitivity of trait growth to the growth  
213 environment is non-linear. In presence of threshold or saturation effects, one can predict that  
214 changes in body size may result in changes in the static allometric slope.  
215

Pélabon et al.

The evolvability of allometry

1  
2  
3 216 *Selection on the slope* – Alternatively the static allometric slope can evolve as a result of  
4  
5 217 selection on the slope itself, with no change in  $\bar{x}_i$  or  $\bar{z}_i$  (Fig. 1, scenario B), which is  
6  
7  
8 218 equivalent to assuming correlated selection on size and the trait. With correlated selection,  
9  
10 219 there will be an adaptive ridge that links the bivariate distribution of the traits to fitness (Fig.  
11  
12 220 2A). We can completely separate selection on the allometric slope from selection on trait  
13  
14 221 means by imagining an adaptive landscape that selects on trait (co)variances but not on trait  
15  
16 222 mean (i.e. no directional selection). We generally expect that trait means will evolve more  
17  
18 223 rapidly than trait variation, so when a change in selection regime affects both means and  
19  
20 224 (co)variances, we will rapidly approach the situation where only the (co)variances continue to  
21  
22 225 be selected. A simple example of such changes would be selection for a decrease in trait  
23  
24 226 variance combined with either an increase or constant variance in body size, which would  
25  
26 227 decrease the allometric slope. Selection for increasing variance in trait size combined with a  
27  
28 228 decreasing variance in body size should generate an increase in the allometric slope. Figure  
29  
30 229 2B shows a case of disruptive selection favoring extreme combinations of trait and body size  
31  
32 230 over those near the means. This type of selection maximizes selection on variances and  
33  
34 231 covariances, and therefore should lead to the maximum rate of response in the allometric  
35  
36 232 slope. Strong disruptive selection balanced precisely to lead to no directional selection is  
37  
38 233 probably an extremely rare event in nature, however. In theory, the presence of a selective  
39  
40 234 ridge should be sufficient to favor a particular slope in the absence of disruptive selection, but  
41  
42 235 the strength of selection on the slope will be quite weak, because many individuals the center  
43  
44 236 of the distribution (i.e. with non-informative genotype) will be selected (Compare Fig. 2A and  
45  
46 237 B).

47  
48 238 Verbal models of selection on allometric slope have been proposed to explain the  
49  
50 239 positive allometry often observed in sexually selected traits [12,13, 17, 18, 51]. In these  
51  
52 240 models, positive allometry evolves either because large males, presumably in better condition,  
53  
54  
55  
56  
57  
58  
59  
60

Pélabon et al.

The evolvability of allometry

1  
2  
3 241 are able to invest more in costly traits, or because the benefits of large traits increased with  
4  
5 242 body size. By applying various selection regimes on an allocation model of growth,  
6  
7 243 Bonduriansky and Day (2003) [16] showed that the conditions under which positive allometry  
8  
9 244 evolved were more restrictive than previously thought, but that an increase in the relative  
10  
11 245 fitness gain for larger traits with an increase in body size should select for positive allometry.  
12  
13 246 Canalizing selection on trait size, on the other hand, has also been suggested to affect static  
14  
15 247 allometry by generating negative allometries as for example for male copulatory organs in  
16  
17 248 insects [14, 19].

20  
21 249 The variational properties that generate variance and covariance among traits are  
22  
23 250 pivotal to the evolution of static allometry. Although selection experiments have suggested  
24  
25 251 that variation may respond to selection [52] it remains unclear how efficiently selection can  
26  
27 252 mold genetic and environmental variation [53, 54, 55, 56]. The evolution of covariance  
28  
29 253 between trait size and body size directly links the evolution of the static allometric slope with  
30  
31 254 the evolution of the phenotypic and genetic covariance matrices (**P** and **G** on log scale). Much  
32  
33 255 theoretical and empirical work shows that genetic covariances do evolve [54, 57, 58, 59, 60],  
34  
35 256 but it remains unclear what forces drive these changes, and how rapidly they can take place.  
36  
37 257 The various hypotheses listed here suggest that, in many cases, selection on the allometric  
38  
39 258 slope is rather weak and indirect. If combined with a low evolvability, this may result in slow  
40  
41 259 evolutionary change in allometry.  
42  
43  
44

260

### 261 *Evolvability and evolution in static allometry*

48  
49 262 Because changes in ontogenetic allometry are expected to provoke changes in static allometry  
50  
51 263 (Eq. 1), we first consider here evidence for the evolution of ontogenetic allometry. Such  
52  
53 264 evidence is provided by several studies comparing ontogenetic allometries among species  
54  
55 265 [e.g. 61, 62, 63, 64]. However, few studies have tested the relationship between ontogenetic  
56  
57  
58  
59  
60

Pélabon et al.

The evolvability of allometry

1  
2  
3 266 and static allometry [34, 65, 66, 67, 68], and fewer have analyzed how variation in the  
4  
5 267 parameters of ontogenetic allometry affected static allometry. The only study, to our  
6  
7 268 knowledge, that compared the relationship between ontogenetic and static allometry among  
8  
9 269 populations [47], showed that static allometry between caudal fin length and body length in  
10  
11 270 female Guppies (*Poecilia reticulata*) was steeper than the ontogenetic allometry, but was  
12  
13 271 similar among three populations with different adult female length. This was achieved, among  
14  
15 272 other things, by differences in the average ontogenetic allometric slope among populations.  
16  
17 273 The relevance of these results regarding the rate at which ontogenetic allometry evolve is  
18  
19 274 unclear, however, because guppy populations from different drainages may have been  
20  
21 275 separated for hundred thousands of generations [69]. Furthermore, although individual  
22  
23 276 variation in ontogenetic allometry has been observed [47], the genetic basis of this variation  
24  
25 277 remains unknown, and overall we found only one study that reported heritability of  
26  
27 278 ontogenetic slopes of chest circumference ( $h^2 = 0.25 \pm 0.07$ ) and tail length ( $h^2 = 0.39 \pm 0.08$ )  
28  
29 279 on body weight within six laboratory strains of rats selected for larger or smaller weight [70].  
30  
31  
32  
33

34 280 Microevolutionary changes in phenotypic covariances among traits are suggested by  
35  
36 281 studies reporting rapid changes in the **G**- or **P**- matrices within populations [71, 72, 73]. These  
37  
38 282 observations are difficult to interpret in terms of evolution of allometry, however, because  
39  
40 283 traits are not always strongly correlated in the first place and **G**-matrices are rarely analyzed  
41  
42 284 on log scale. Furthermore, studies analyzing changes in the **P**-matrix cannot distinguish  
43  
44 285 between environmental and genetic changes in the patterns of covariation among traits.  
45  
46

47 286 Estimates of genetic variance in static allometric slopes are scarce, and we found only  
48  
49 287 one study reporting heritabilities of allometric slopes measured on log scale [74]. In this  
50  
51 288 study, heritabilities of the static allometric slope between the length of several bones and the  
52  
53 289 cubic root of body weight, and between the weight of internal organs and body weight were  
54  
55 290 all statistically significant but relatively small (all  $h^2 < 0.13$ ) despite being measured in the lab.  
56  
57  
58  
59  
60

Pélabon et al.

The evolvability of allometry

1  
2  
3 291           Alternatively, artificial selection can be used to uncover genetic variation and  
4  
5 292 covariation in quantitative traits [75]. During the last two decades, several authors have  
6  
7 293 claimed to have altered patterns of static allometry by artificial selection. In addition, a few  
8  
9 294 artificial selection studies on size have shown changes in the covariance patterns between the  
10  
11 295 size of some traits and body size. Unfortunately, most of these studies have adopted the  
12  
13 296 broad-sense definition of allometry, seriously hampering our ability to interpret their results in  
14  
15 297 terms of the evolution of allometry [23]. For example, in a study on a stalk-eyed fly  
16  
17 298 (*Cyrtodiopsis dalmanni*), selection exerted on the ratio between eye span and body length  
18  
19 299 significantly affected the covariance between the two traits when measured on arithmetic  
20  
21 300 scale [76]. Reanalysis of the regression line on the log scale shows that changes in the  
22  
23 301 allometric slope are still present but much weaker than those reported in the original study  
24  
25 302 (Table 1). A similar selection procedure was used in two experiments on the butterfly  
26  
27 303 *Bicyclus anynana* [77, 78]. In both experiments, the intercepts of the relationships on  
28  
29 304 arithmetic scale were strongly affected by selection, but the slopes were apparently not,  
30  
31 305 although no formal tests of change in slope were reported. What were the consequences of the  
32  
33 306 selection on the allometric slope remains unknown.

34  
35  
36  
37  
38 307           The only artificial selection experiment on narrow-sense allometry conducted so far  
39  
40 308 combined stabilizing and disruptive selection on body area and caudal fin area to select for a  
41  
42 309 change in static allometric slope (procedure similar as the one described in Fig. 2B; [79].  
43  
44 310 Selection to increase and decrease the intercept was also applied on two separate lines.  
45  
46 311 Results suggested that the allometric slopes had very little capacity to vary compared to the  
47  
48 312 allometric intercepts. This conclusion, however, was weakened by the small number of  
49  
50 313 generations of selection.

51  
52  
53  
54 314           Two studies investigating the effects of artificial selection on body size on correlated  
55  
56 315 traits provide some evidence for rapid change in static allometric slope. In a selection  
57  
58  
59  
60

Pélabon et al.

The evolvability of allometry

1  
2  
3 316 experiment to increase or decrease body mass in the moth *Manduca sexta*, static allometry  
4  
5 317 between wing mass and body mass became steeper in the line selected for smaller body mass  
6  
7 318 and shallower in the line selected for larger body mass after 10 generations of selection ([80];  
8  
9 319 and see [23] for reanalysis using standard regression). Similarly, estimation of the static  
10  
11 320 allometric slopes in the different lines of a selection experiment to increase body size in  
12  
13 321 *Drosophila melanogaster* [81] reveals that allometries between wing length and thorax length  
14  
15 322 or between wing length and tibia length increased in the line selected for smaller thorax  
16  
17 323 length, and decreased in the line selected for larger thorax length (Table 1). Additionally,  
18  
19 324 Cayetano et al. (2011) [82] while relaxing sexual selection for ca. 21 generations in the seed  
20  
21 325 beetle *Callosobruchus maculatus* observed a change in the allometry between two traits of the  
22  
23 326 genital apparatus in males and elytron length. The reanalysis of the data from this last  
24  
25 327 experiment showed, however, a very poor fit of the traits with the allometric model and casted  
26  
27 328 doubt on the validity of the interpretation of the results [23].  
28  
29  
30

31  
32 329 One factor that has not been considered in these experiments, however, is the  
33  
34 330 possibility of plasticity in the allometric slope. Plasticity in allometric relationships has been  
35  
36 331 little studied, but one study clearly shows that static allometry varies in response to different  
37  
38 332 environmental treatments [83]. Similarly, a selection experiment on *Drosophila* wings in  
39  
40 333 which selection was performed on the relative position of some veins [55, 84, 85] shows  
41  
42 334 erratic but sometimes statistically significant variation in static allometry (Fig. 3). The  
43  
44 335 differences in slope apparent in Figure 3, could, if observed in isolation, be misinterpreted as  
45  
46 336 change in allometry due to selection. To avoid such problem we strongly recommend  
47  
48 337 following the changes in allometry from generation to generation, and experiments that fail to  
49  
50 338 do so should be interpreted with caution.  
51  
52

53  
54 339 The dissection of the insulin/IGF signaling pathway that controls trait size in animals  
55  
56 340 provides a nice illustration of how the growth of specific traits responds to changes in the  
57  
58  
59  
60



Pélabon et al.

The evolvability of allometry

1  
2  
3 341 growth environment, that is, changes in body size [86, 87]. Interestingly, recent experiments  
4  
5 342 have uncovered mutations at specific loci that could affect the organ sensitivity to variation in  
6  
7 343 the growth environment and therefore affect the slope of the static allometry [74, 88].  
8  
9 344 Although these studies provide clear evidence for genetic variation in allometric slope, they  
10  
11 345 also suggest that this variation results from complex genetic architecture [74] that may not  
12  
13 346 easily respond to selection.

14  
15  
16 347 Neither inter-population variation nor quantitative genetics experiments provide  
17  
18 348 conclusive evidence for genetic variation in the allometric slope. For the intercept,  
19  
20 349 quantitative genetic studies provide clear evidence for high evolvability.  
21  
22

350

351 Does static allometry constrain phenotypic evolution?

352

353 *Theoretical considerations*

354 Micro-evolutionary studies reviewed in the last section suggest that the evolvability of the  
355 allometric slope is low relative to the evolvability of the intercept. At the macro-evolutionary  
356 level, reviews on allometry of secondary sexual characters clearly show that allometry of  
357 homologous traits can vary among sexes from the same species or among species [89, 90].  
358 Such information is by itself, not very informative about the constraint hypothesis because we  
359 do not know anything about the strength of selection on the allometric relationships, and the  
360 time scale for divergence can be very long. Therefore, it remains unclear whether there are  
361 meaningful evolutionary constraints due to allometry.

362 In the absence of empirical knowledge regarding selection on allometry, we are left  
363 with the option of generating predictions based on scenarios where static allometry constrains  
364 phenotypic evolution under various hypothetical selection regimes. In this context, a general  
365 prediction is that, if static allometric parameters represent evolutionary constraints they

Pélabon et al.

The evolvability of allometry

1  
2  
3 366 should strongly shape patterns of populations and species divergence. This was initially  
4  
5 367 suggested by Gould [6, 7] and placed in a quantitative genetic framework by Lande [32, 33]  
6  
7 368 who showed that, under constant patterns of covariance between traits (constant **G**-matrix),  
8  
9 369 selection acting only on the body size ( $x$ ), will generate a correlated response on the trait size  
10  
11 370 ( $z$ ). In this case, the evolutionary allometric slope ( $b_e$ ) along which populations and species  
12  
13 371 evolve, will correspond to the ratio of the correlated response in  $z$  divided by the direct  
14  
15 372 response in  $x$ , that is, the slope of the genetic regression between the two traits:  $b_s = \sigma_{A(x,z)}$   
16  
17 373  $/\sigma_A^2(x)$ , where  $\sigma_A^2(x)$  and  $\sigma_{A(x,z)}$  are the additive genetic variance in  $x$  and the covariance  
18  
19 374 between  $x$  and  $z$ , respectively (Fig. 4 scenario A).  
20  
21  
22

23 375 Because static allometry is defined at the phenotypic level, the static allometric slope  
24  
25 376 ( $b_s$ ) combines both additive genetic and residual variances and covariances:  $b_s =$   
26  
27 377  $[\sigma_{A(x,z)} + \sigma_R(x,z)] / [\sigma_A^2(x) + \sigma_R^2(x)]$ , where  $R$  denotes all other residual components of the  
28  
29 378 variance, including environmental and non-additive genetic variance. Static and evolutionary  
30  
31 379 regression coefficients,  $b_s$  and  $b_e$ , will be similar when the relative contributions of the  
32  
33 380 residual variance and covariance are similar to the relative contributions of their additive  
34  
35 381 genetic counterparts. In this case, the genetic and phenotypic variance-covariance matrices, **G**  
36  
37 382 and **P**, will be proportional for these elements. If this condition is not fulfilled, evolutionary  
38  
39 383 allometry will not follow the trajectory defined by the static allometry, contrary to previous  
40  
41 384 claims by Gould [91] and others (Fig. 4 scenarios B and C; [33]). Furthermore, if the additive  
42  
43 385 genetic and residual contributions to static allometry are different but remain constant, the  
44  
45 386 static allometric slope should remain constant across populations and species while the  
46  
47 387 intercept will change with changing mean size (Fig. 4 scenario B and C).  
48  
49  
50  
51

52 388 It is important to realize that when Lande's model [33] is generalized to allow  
53  
54 389 selection on the trait and both size, and there is at least some additive genetic variation in  
55  
56 390 both, the means obtained in the long term depend only on the selective optima for size and the  
57  
58  
59  
60

Pélabon et al.

The evolvability of allometry

1  
2  
3 391 trait, and not at all on the patterns of covariance among them [35]. If this is the case, and if  
4  
5 392 selective optima are spread more or less randomly in the bivariate morphospace, we would  
6  
7 393 expect no relationship between evolutionary and static allometry (Fig. 4 Scenario C and D).  
8  
9 394 Scenario C represents a situation where the slope is an absolute constraint but the trait and  
10  
11 395 body size means can evolve more or less freely in the morphospace (Fig. 4 Scenario C). This  
12  
13 396 provides the other major explanation for evolutionary allometry: it is not the pattern of genetic  
14  
15 397 variation, but the pattern of natural and sexual selection that dictates allometry.

16  
17  
18 398 These considerations underline the problem we have of testing the allometry as a  
19  
20 399 constraint hypothesis without knowing the selection patterns acting on allometric  
21  
22 400 relationships, and in most cases, only speculative interpretation of the macro-evolutionary  
23  
24 401 patterns can be achieved. Although specific predictions have been suggested regarding the  
25  
26 402 effect of selection on allometric slope for genitals and secondary sexual characters, these  
27  
28 403 predictions only concerned the type of allometry expected (positive or negative allometry),  
29  
30 404 but not the strength of selection. Furthermore, in the case of secondary sexual characters, it has  
31  
32 405 been shown that positive allometry was only expected under specific selection pressures [16],  
33  
34 406 and a later review [89] confirmed that static allometric slopes in this type of character was  
35  
36 407 not necessarily larger than one.

408

#### 409 *Empirical patterns*

410 Although many studies have compared relationships between trait size and body size among  
411 populations and species, Voje et al. [23] identified only 10 studies that allowed estimation of  
412 the variation in static allometric slope and intercept (studies on log scale with sufficient  
413 information about the allometric parameters). Excluding genital traits, their analysis revealed  
414 inter-specific variation in static allometric slope within genera (median standard deviation  
415 corrected for sampling error:  $SD = 0.27$ ). Within species, the static allometric slope varies

Pélabon et al.

The evolvability of allometry

1  
2  
3 416 among populations but this variation is more limited (median SD = 0.07). For the allometric  
4  
5 417 intercept, patterns of variation were similar with higher variation among species (median SD  
6  
7 418 = 0.15) than among populations (median SD = 0.02).

9  
10 419 Because the slope and intercept are on different scales, their level of variation is not  
11  
12 420 directly comparable. Using the concept of conditional variance [39, 41], Voje et al. [23]  
13  
14 421 estimated the influence of changes in size or in allometric slope and intercept in the evolution  
15  
16 422 of trait size. This method allowed them to compare variation in slope and intercept on a  
17  
18 423 common scale (variance in trait size). At the interspecific level, 74% of the variation in trait  
19  
20 424 size was associated with changes in species mean size. The contribution of the changes in  
21  
22 425 static allometric slope or intercept were more limited (13% and 29% of the log trait variance  
23  
24 426 explained, respectively, e.g. Fig. 5A). The contributions of these three parameters to trait  
25  
26 427 diversification at the among-population level were similar, with size variation explaining  
27  
28 428 71%, slope explaining 36%, and intercept variation explaining 40%. However, as previously  
29  
30 429 mentioned, much less variation in static allometry was observed among populations, and the  
31  
32 430 evolutionary allometry was often very similar to the pattern of static allometry (Fig. 5B).

33  
34  
35  
36 431 Finally, Voje et al. [23] showed that within species, the average static allometry across  
37  
38 432 populations was a good predictor of the evolutionary allometry, while across species within  
39  
40 433 genera the average static allometry was poorly correlated with the evolutionary allometry.

41  
42 434 These results are compatible with the “allometry as a constraint” hypothesis if  
43  
44 435 selective optima were spread more or less randomly in the bivariate morphospace. Indeed,  
45  
46 436 morphological evolution more constrained along static allometric trajectories at the within-  
47  
48 437 species level than at the among-species level could be interpreted as signature of evolutionary  
49  
50 438 constraint.

51  
52  
53  
54 439 In an attempt to estimate the rate of morphological evolution towards a predicted  
55  
56 440 optimum, Voje and Hansen [92] reanalyzed data on the evolution of the static allometry

Pélabon et al.

The evolvability of allometry

1  
2  
3 441 between eye-span and body length in various species of stalk-eyed fly (Diopsidae). Using  
4  
5 442 sexual size dimorphism as a measure of the strength of sexual selection in order to estimate  
6  
7 443 optima, they showed that the static allometric slope in male trait was tracking these optima,  
8  
9 444 but this took millions of years to accomplish.  
10

445

11  
12  
13 446 *The “one size fits all” hypothesis*

14  
15  
16 447 The various studies analyzing static allometry of genital traits in arthropods and vertebrates  
17  
18 448 showed consistently shallow static allometric slopes ( $\beta < 1$ ) for these traits, as expected from  
19  
20 449 the “one size fits all” hypothesis [14, 19]. Eberhardt [19] reported few exceptions to this  
21  
22 450 pattern. However, all these exceptions came from studies where static allometry was  
23  
24 451 estimated using major axis regression, a method that will over-estimate the slope for  
25  
26 452 relationships with low  $r^2$ . Accordingly, for all exceptions reported, the relationship between  
27  
28 453 the genitalia and the measure of body size was poor (range  $r^2$ : 0.0 – 0.58). In all cases where  
29  
30 454 data were reanalyzed using standard regression methods, genital traits showed negative ( $b < 1$ )  
31  
32 455 static allometry [23, 93].  
33  
34  
35

36 456 The “one size fits all” hypothesis has also been extended for reproductive organs in  
37  
38 457 flowering plants with insect pollination, where the fit between pollen donor and pollen  
39  
40 458 receiver organs and pollinators of relatively constant size and behavior is expected to produce  
41  
42 459 stabilizing selection [94]. Several studies have provided clear evidence for the relative  
43  
44 460 invariance of floral traits compared to vegetative traits [95, 96] and the two studies that have  
45  
46 461 tested the effect of pollination accuracy on the allometry of the pollen transport organs both  
47  
48 462 reported shallow allometry for these traits [97, 98].  
49  
50

51  
52 463 If results from studies on the “one size fits all” hypothesis provide clear evidence of a  
53  
54 464 possible effect of selection on static allometry, they do not provide evidence for high  
55  
56 465 evolvability of the allometric slope. Indeed, intraspecific comparison of static allometry in  
57  
58  
59  
60

Pélabon et al.

The evolvability of allometry

1  
2  
3 466 insect genitalia show that variation in the allometric slope explains only a small proportion of  
4  
5 467 the variation in genitalia size, 92% of the variance of log-size genitalia being independent of  
6  
7 468 the variation in allometric slope [23]. This is particularly clear when observing the allometric  
8  
9 469 slope between genitalia size and body size in various populations of the beetle species *Dorcus*  
10  
11 470 *titanus* (Fig 5C).  
12

13  
14 471

## 15 16 472 Conclusions

17  
18 473

19  
20 474 Despite the huge interest morphological allometry has focused among evolutionary biologists  
21  
22 475 for nearly a century, we are left with a limited understanding of its evolution. Key  
23  
24 476 observations such as genetic variation in ontogenetic allometry or in the static allometric  
25  
26 477 slope are surprisingly scarce. Although micro- and macroevolutionary patterns seem to point  
27  
28 478 at a constraining effect of morphological allometry on phenotypic evolution, the complete  
29  
30 479 lack of data on the nature of direct or indirect selection on allometry, and the near absence of  
31  
32 480 data on genetic variation in allometric parameters precludes the interpretation of these  
33  
34 481 patterns as evidence for or against the constraint and adaptation hypotheses. Until such data  
35  
36 482 are obtained the evolution of allometry will remain a mystery.  
37  
38  
39  
40

41 483

## 42 43 484 Acknowledgments

44  
45 485 The authors want to thank Jarle Tufto for great discussions on allometry. This work was  
46  
47 486 supported by grant 196434/V40 from the Norwegian Research Council to CP at NTNU.  
48  
49

50 487  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

Pélabon et al.

The evolvability of allometry

488 **References**

- 489 1 - Calder, W.A. 1984. *Size, function and life history*. Harvard Univeristy Press.
- 490 2 - Schmidt-Nielsen, K. 1984. *Scaling: Why is animal size so important?* Cambridge  
491 University Press, Cambridge.
- 492 3 - Brown, J.H. & G.B. West 2000. *Scaling in biology*. Oxford University Press, Oxford.
- 493 4 - Hudson, L.N., Isaac, N.J.B. & D.C. Reuman. 2013. The relationship between body mass  
494 and field metabolic rate among individual birds and mammals. *J. Anim. Ecol.* 82: 1009  
495 – 1020.
- 496 5 - Huxley, J. S. 1932. *Problems of relative growth*. L. MacVeagh, New York.
- 497 6 - Gould, S.J. 1966. Allometry and size in ontogeny and phylogeny. *Biol. Rev. Camb. Philos.*  
498 *Soc.* 41:587-640.
- 499 7 - Gould, S.J. 1977. *Ontogeny and phylogeny*. Harvard Univ. Press. Cambridge MA, USA.
- 500 8 - Darveau CA, Suarez RK, Andrews RD, Hochachka PW (2002) Allometric cascade as a  
501 unifying principle of body mass effects on metabolism. *Nature* 417:166–170.
- 502 9 - Gould, S.J., & R.C. Lewontin. 1979. The spandrels of San Marco and the panglossian  
503 paradigm: A critique of the adaptationist programme. *Phil. Trans. R. Soc. London B.*  
504 205:581-598.
- 505 10 - Charnov, E.L. 1993. *Life History Invariants: Some Explorations of Symmetry in*  
506 *Evolutionary Ecology*. Oxford Univeristy Press, Oxford.
- 507 11 - West, G.B. & J.H. Brown. 2005. The origin of allometric scaling laws in biology from  
508 genomes to ecosystems: towards a quantitative unifying theory of biological structure  
509 and organization. *J. Exp. Biol.* 208: 1575-1592.
- 510 12 - Petrie, M. 1988. Intraspecific variation in structures that display competitive ability: large  
511 animals invest relatively more. *Anim. Behav.* 36: 1174-1179.
- 512 13 - Petrie, M. 1992. Are all secondary sexual display structures positively allometric and, if

Pélabon et al.

The evolvability of allometry

- 1  
2  
3 513 so, why? *Anim. Behav.* 43: 173-175.  
4  
5 514 14 - Eberhard, W.G., Huber, B.A., Rodriguez, R.L., Briceno, R.D., Salas, I., & V. Rodriguez.  
6  
7 515 1998. One size fits all? Relationships between the size and degree of variation in  
8  
9 516 genitalia and other body parts in twenty species of insects and spiders. *Evolution.*  
10  
11 517 52:415-431.  
12  
13 518 15 - Frankino, W.A., Emlen, D.J. & A.W. Shingleton. 2009. Experimental approaches to  
14  
15 519 studying the evolution of animal form. In Garland Jr., T, and Rose, M. R. (Eds.)  
16  
17 520 *Experimental evolution: Concepts, methods, and applications of selection*  
18  
19 521 *experiments*. University of California Press, Ltd, Berkeley. Pp: 419-478.  
20  
21 522 16 - Bonduriansky, R., & T. Day. 2003. The evolution of static allometry in sexually selected  
22  
23 523 traits. *Evolution.* 57: 2450-2458.  
24  
25 524 17 - Green, A. 1992 Positive allometry is likely with mate choice, competitive display and  
26  
27 525 other functions. *Anim. Behav.* 43: 170-172.  
28  
29 526 18 - Kodric-Brown, A., Sibly, R.M. & J.H. Brown. 2006. The allometry of ornaments and  
30  
31 527 weapons. *Proc. Natl. Acad. Sci. USA.* 103:8733-8738.  
32  
33 528 19 - Eberhard, W.G. 2009. Static allometry and animal genitalia. *Evolution.* 63:48-66.  
34  
35 529 20 - Eberhard, W., Rodriguez, R. L. & M. Polihronakis, M. 2009. Pitfalls in understanding the  
36  
37 530 functional significance of genital allometry. *J. Evol. Biol.* 22: 435-445.  
38  
39 531 21 - Mezey J.G. & D. Houle. 2005. The dimensionality of genetic variation for wing shape in  
40  
41 532 *Drosophila melanogaster*. *Evolution.* 59: 1027-1038.  
42  
43 533 22 - Houle, D., Pélabon, C., Wagner, G. P. & T.F. Hansen. 2011. Measurement and meaning  
44  
45 534 in biology. *Q. Rev. Biol.* 86: 3–34.  
46  
47 535 23 - Voje K.J., Hansen, T.F., Egset, C.K., Bolstad, G.H., & C. Pélabon. 2014. Allometric  
48  
49 536 constraints and the evolution of allometry. *Evolution.* (in press).  
50  
51 537 24 - Haldane, J.B.S. 1932. *The causes of evolution*. Princeton University Press, Princeton.  
52  
53  
54  
55  
56  
57  
58  
59  
60



Pélabon et al.

The evolvability of allometry

- 1  
2  
3 538 25 - Hansen, T. F. 2014. *Evolutionary constraints*. In Oxford Bibliographies in Evolutionary  
4  
5 539 Biology. Ed. Losos, J. New York. Oxford University Press. In review.  
6  
7 540 26 - Arnold, S.J. 1992. Constraints on phenotypic evolution. *Am. Nat.* 140: 85-107.  
8  
9 541 27 - Maynard Smith, J., Burian, R., Kauffman, S., Alberch, P., Campbell, J., Goodwin, B.,  
10  
11 542 Lande, R., Raup, D. & L. Wolpert. 1985. Developmental Constraints and Evolution: A  
12  
13 543 Perspective from the Mountain Lake Conference on Development and Evolution.  
14  
15 544 *Quart. Rev. Biol.* 60:265-287.  
16  
17 545 28 - Wagner G.P. & K. Schwenk. 2000. Evolutionarily stable configurations: Functional  
18  
19 546 integration and the evolution of phenotypic stability *Evol. Biol.* 31:155 -217.  
20  
21 547 29 - Schwenk K. & G.P. Wagner. 2004. The relativism of constraints on phenotypic  
22  
23 548 evolution. In M. Pigliucci and K. Preston, (Eds.): *Phenotypic integration*. Oxford  
24  
25 549 University Press, Oxford. Pp 390-408.  
26  
27 550 30 - Gould, S.J. 1974. The origin and function of "bizarre" structures: antler size and skull  
28  
29 551 size in the "Irish Elk" *Megaloceros giganteus*. *Evolution* 28:191-220.  
30  
31 552 31 - Alberch, P., Gould, S.J., Oster, G.F. & D. B. Wake. 1979. Size and Shape in Ontogeny  
32  
33 553 and Phylogeny. *Paleobiol.* 5: 296-317.  
34  
35 554 32 - Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain –  
36  
37 555 body size allometry. *Evolution.* 33:402–416.  
38  
39 556 33 - Lande, R. 1985. Genetic and evolutionary aspects of allometry. In W. L. Jungers (Ed.).  
40  
41 557 *Size and scaling in primate biology*. Plenum Press, New York.  
42  
43 558 34 - Cheverud, J. M. 1982. Relationships among ontogenetic, static, and evolutionary  
44  
45 559 allometry. *Am. J. Phys. Anthropol.* 59:139-149.  
46  
47 560 35 - Zeng, Z.B. 1988. Long-term correlated response, interpopulation covariation, and  
48  
49 561 interspecific allometry. *Evolution.* 42:363-374.  
50  
51 562 36 - Hansen, T.F., Pélabon, C. & D. Houle. 2011. Heritability is not evolvability. *Evol. Biol.*  
52  
53  
54  
55  
56  
57  
58  
59  
60

Pélabon et al.

The evolvability of allometry

- 1  
2  
3 563 38:258–277.  
4  
5 564 37 - Björklund, M. 1996. The importance of evolutionary constraints in ecological time  
6  
7 565 scales. *Evol. Ecol.* 10:423-431.  
8  
9 566 38 - Schluter, D. 1996. Adaptive radiation along genetic lines of least resistance.  
10  
11 567 *Evolution* 50: 1766–1774.  
12  
13 568 39 - Hansen, T.F., Armbruster, W.S., Carlson, M.L., & C. Pélabon. 2003. Evolvability and  
14  
15 569 genetic constraint in *Dalechampia* blossoms: Genetic correlations and conditional  
16  
17 570 evolvability. *J. Exp. Zool.* 296B:23-39.  
18  
19 571 40 - Hansen, T.F. & D. Houle. 2004. Evolvability, stabilizing selection, and the problem of  
20  
21 572 stasis. In M. Pigliucci and K. Preston, (Eds.): *Phenotypic integration*. Oxford  
22  
23 573 University Press, Oxford. Pp. 130-150.  
24  
25 574 41 - Hansen, T.F. & D. Houle. 2008. Measuring and comparing evolvability and constraint in  
26  
27 575 multivariate characters. *J. Evol. Biol.* 21:1201-1219.  
28  
29 576 42 - Blows, M.W. & A.A. Hoffman. 2005. A reassessment of genetic limits to evolutionary  
30  
31 577 change. *Ecology*. 86: 1371-1384.  
32  
33 578 43 - Walsh, B. & M.W. Blows. 2009. Abundant genetic variation + strong selection =  
34  
35 579 multivariate genetic constraints: A geometric view of adaptation. *Annu. Rev. Ecol.*  
36  
37 580 *Evol. Syst.* 40:41–59.  
38  
39 581 44 - Wagner, G.P. & L. Altenberg. 1996 Complex adaptations and evolution of evolvability.  
40  
41 582 *Evolution*. 50, 967–976.  
42  
43 583 45 - Nijhout, H.F. & D.E. Wheeler 1996. Growth Models of Complex Allometries in  
44  
45 584 Holometabolous Insects. *Am. Nat.* 148:40-56.  
46  
47 585 46 - Nijhout H. F. 2011 Dependence of morphometric allometries on the growth kinetics of  
48  
49 586 body parts. *J. Theor. Biol.* 288: 35 – 43.  
50  
51 587 47 - Pélabon, C., Bolstad, G.H., Egset, C.K., Cheverud, J.M., Pavlicev, M. & G. Rosenqvist.  
52  
53  
54  
55  
56  
57  
58  
59  
60

Pélabon et al.

The evolvability of allometry

- 1  
2  
3 588 2013. On the relationship between ontogenetic and static allometry. *Am. Nat.* 181:213-  
4  
5 589 222.  
6  
7 590 48 - Deacon, T.W. 1990. Problems of ontogeny and phylogeny in brain size evolution. *Int. J.*  
8  
9 591 *Primatol.* 11:237–281.  
10  
11 592 49 - Anderson, M. 1994. *Sexual selection*. Princeton University Press, Princeton.  
12  
13 593 50 - Lincoln, G.A. 1994. Teeth, horns and antlers: the weapons of sex. In *The differences*  
14  
15 594 *between sexes*. Sort R.V. and Balaban E. Eds. Pp 131-158, Cambridge University  
16  
17 595 Press, Cambridge.Pp 131-158.  
18  
19  
20 596 51 - Simmon L.W. & J.L. Tomkins. 1996 Sexual selection and the allometry of earwig  
21  
22 597 forceps. *Evol. Ecol.* 10: 97-104.  
23  
24 598 52 - Scharloo, W., Hoogmoed, M. S. & A. Ter Kuile. 1967. Stabilizing and disruptive  
25  
26 599 selection on a mutant character in *Drosophila*. I. The phenotypic variance and its  
27  
28 600 components. *Genetics* 56:709–726.  
29  
30 601 53 - Hermisson J., Hansen, T.F. & G.P. Wagner. 2003 Epistasis in polygenic traits and the  
31  
32 602 evolution of genetic architecture under stabilizing selection. *Am. Nat.* 161: 708-734.  
33  
34 603 54 - Hansen, T.F. 2006. The evolution of genetic architecture. *Ann. Rev. Ecol. Evol. Syst.* 37:  
35  
36 604 123-157.  
37  
38 605 55 - Pélabon, C., Hansen, T.F., Carter, A.J.R. & D. Houle. 2010. Evolution of variation and  
39  
40 606 variability under fluctuating, stabilizing and disruptive selection. *Evolution.* 64: 1912-  
41  
42 607 1925.  
43  
44 608 56 - Le Rouzic, A., Alvarez-Castro, J.M.& T.F. Hansen. 2013 The Evolution of Canalization  
45  
46 609 and Evolvability in Stable and Fluctuating Environments. *Evol. Biol.* 40: 317-340.  
47  
48 610 57 - Stepan, S.J., Phillips, P.C. & D. Houle. 2002. Comparative quantitative genetics:  
49  
50 611 evolution of the G matrix. *Trends Ecol. Evol.* 17: 320-327.  
51  
52 612 58 - Jones, A.G., Arnold, S.J. & R.J. Bürger. 2003. Stability of the G-matrix in a population  
53  
54  
55  
56  
57  
58  
59  
60

Pélabon et al.

The evolvability of allometry

- 1  
2  
3 613 experiencing pleiotropic mutation, stabilizing selection, and genetic drift. *Evolution*.  
4  
5 614 57: 1747-1760.  
6  
7 615 59 - Arnold, S.J., Pfrender, M. E. & A.G. Jones. 2001. The adaptive landscape as a conceptual  
8  
9 616 bridge between micro- and macroevolution. *Genetica*. 112/113:9–32.  
10  
11 617 60 - Arnold, S.J., Bürger, R., Hohenlohe, P.A., Ajie, B.C. & A.G. Jones. 2008.  
12  
13 618 Understanding the evolution and stability of the G-matrix. *Evolution*. 62: 2451-  
14  
15 619 2461.  
16  
17 620 61 - Strauss R.E. & R. Altig 1992. Ontogenetic body form changes in three ecological  
18  
19 621 morphotypes of anuran tadpoles. *Growth Development and aging*. 56: 3-16.  
20  
21 622 62 - Weston, E.M. 2003. Evolution of the ontogeny in the hippopotamus skull: using  
22  
23 623 allometry to dissect developmental change. *Biol. J. Linn. Soc.* 80: 625-638.  
24  
25 624 63 - Frédérich, B. & H.D. Sheets. 2010. Evolution of ontogenetic allometry shaping giant  
26  
27 625 species: a case study from the damselfish genus *Dascyllus* (Pomacentridae). *Biol. J.*  
28  
29 626 *Linn. Soc.* 99: 99-117  
30  
31 627 64 - Urosevic, A., Ljubicavljovic, K. & A. Ivanovic. 2013. Patterns of cranial ontogeny in  
32  
33 628 lacerid lizards: morphological and allometric disparity. *J. Evol. Biol.* 26: 399-415.  
34  
35 629 65 - Leamy, L., and D. Bradley. 1982. Static and growth allometry of morphometric traits in  
36  
37 630 randombred house mice. *Evolution* 36: 1200 – 1212.  
38  
39 631 66 - Klingenberg, C. P. & M. Zimmermann. 1992. Static, ontogenetic, and evolutionary  
40  
41 632 allometry: a multivariate comparison in nine species of waterstriders. *Am. Nat.*  
42  
43 633 140:601–620.  
44  
45 634 67 - Klingenberg, C.P.1996. *Multivariate allometry*. In: L. F. Marcus, M. Corti, A. Loy, G. J.  
46  
47 635 P. Naylor, D. E. Slice, Eds.), *Advances in Morphometrics*. Plenum Press, New York,  
48  
49 636 Pp. 23–49.  
50  
51 637 68 - Klingenberg, C.P.1998. Heterochrony and allometry: the analysis of evolutionary change  
52  
53  
54  
55  
56  
57  
58  
59  
60

Pélabon et al.

The evolvability of allometry

- 1  
2  
3 638 in ontogeny. *Biol. Rev.* 73:79–123.
- 4  
5 639 69 - Magurran A.E. 1998. Population differentiation without speciation. *Phil. Trans. R. Soc.*  
6  
7 640 *Lond. B.* 353: 275 – 286.
- 8  
9 641 70 - Atchley, W.R. & J.J. Rutledge. 1980. Genetic components of size and shape. I. Dynamics  
10  
11 642 of components of phenotypic variability and covariability during ontogeny in the  
12  
13 643 laboratory rat. *Evolution.* 34:1161-1173.
- 14  
15 644 71 - Doroszuk, A., Wojewodzic, M.V., Gort, G. & J.E. Kammenga. 2008. Rapid divergence  
16  
17 645 of genetic variance-covariance matrix within a natural population. *Am. Nat.* 171: 291-  
18  
19 646 304.
- 20  
21 647 72 - Eroukhanoff F. & E.I. Svensson. 2011. Evolution and stability of the G-matrix during  
22  
23 648 the colonization of a novel environment. *J. Evol. Biol.* 24: 1363 – 1373.
- 24  
25 649 73 - Björklund, M., Husby, A., & L. Gustafsson. 2013. Rapid and unpredictable changes of  
26  
27 650 the G-matrix in a natural bird population over 25 years. *J. Evol. Biol.* 26: 1-13.
- 28  
29 651 74 - Pavlicev, M., Norgard, E.A., Fawcett, G.L. & J.M. Cheverud. 2011. Evolution of  
30  
31 652 pleiotropy : Epistatic pattern supports a mechanistic model underlying variation in  
32  
33 653 genotype-phenotype map. *J. Exp. Zool. (Mol. Dev. Evol.)*. 316 : 371-385.
- 34  
35 654 75 - Conner, J.K. 2003. Artificial selection: A powerful tool for ecologists. *Ecology.* 84:  
36  
37 655 1650-1660.
- 38  
39 656 76 - Wilkinson, G. S. 1993. Artificial sexual selection alters allometry in the stalk-eyed fly  
40  
41 657 *Cyrtodiopsis dalmanni* (Diptera: Diopsidae). *Genet. Res.* 62:213-222.
- 42  
43 658 77 - Frankino, W.A., Zwaan, B.J., Stern, D.L. & P.M. Brakefield. 2005. Natural selection and  
44  
45 659 developmental constraints in the evolution of allometries. *Science* 307:718-720.
- 46  
47 660 78 - Frankino, W.A., Zwaan, B.J., Stern, D.L., & P.M. Brakefield. 2007. Internal and external  
48  
49 661 constraints in the evolution of morphological allometries in a butterfly. *Evolution.*  
50  
51 662 61:2958-2970.
- 52  
53  
54  
55  
56  
57  
58  
59  
60

Pélabon et al.

The evolvability of allometry

- 1  
2  
3 663 79 - Egset, C.K., Hansen, T.F., Le Rouzic, A., Bolstad G.H., Rosenqvist, G., & C. Pélabon.  
4  
5 664 2012. Artificial selection on allometry: change in elevation but not slope. *J. Evol. Biol.*  
6  
7 665 25:938–948.  
8  
9  
10 666 80 - Tobler, A. & H.F. Nijhout. 2010. Developmental constraints on the evolution of wing-  
11  
12 667 body allometry in *Manduca sexta*. *Evol. Dev.* 12:592-600.  
13  
14 668 81 - Wilkinson, G.S., Fowler, K. & L. Partridge.1990. Resistance of genetic correlation  
15  
16 669 structure to directional selection in *Drosophila melanogaster*. *Evolution*. 44: 1990-  
17  
18 670 2003.  
19  
20  
21 671 82 - Cayetano, L., Maklakov, A.A., Brooks, R.C., & R. Bonduriansky. 2011. Evolution of  
22  
23 672 male and female genitalia following release from sexual selection. *Evolution*. 65:  
24  
25 673 2171-2183.  
26  
27 674 83 - Shingleton, A.W., Estep, C.M., Driscoll, M.V. & I. Dworkin. 2009. Many ways to be  
28  
29 675 small: different environmental regulators of size generate distinct scaling relationships  
30  
31 676 in *Drosophila melanogaster*. *Proc. R. Soc. London B.* 276, 2625-2633.  
32  
33  
34 677 84 - Pélabon, C., Hansen, T.F., Carter, A.J.R. & D. Houle. 2006. Response of fluctuating and  
35  
36 678 directional asymmetry to selection on wing shape in *Drosophila melanogaster*. *J.*  
37  
38 679 *Evol. Biol.* 19: 764-776.  
39  
40  
41 680 85 - Le Rouzic, A., Houle, D.& T.F. Hansen. 2011. A modelling framework for the analysis  
42  
43 681 of artificial-selection time series. *Genetics Research*. 93: 155-173.  
44  
45 682 86 - Emlen, D.J., Warren, I.A., Johns, A., Dworkin, I. & L. Corley Lavine. 2012. A  
46  
47 683 mechanism of extreme growth and reliable signaling in sexually selected ornaments  
48  
49 684 and weapons. *Science*. 337: 860-864.  
50  
51  
52 685 87 - Shingleton, A.W. & W.A. Frankino. 2012. New perspectives on the evolution of  
53  
54 686 exaggerated traits. *Bioessays*. 35: 100-107.  
55  
56 687 88 - Shingleton, A.W. & H.Y. Tang. 2012. Plastic flies: the regulation and evolution of trait  
57  
58  
59  
60

Pélabon et al.

The evolvability of allometry

- 1  
2  
3 688 variability in *Drosophila*. *Fly* 6: 147-152.
- 4  
5 689 89 - Bonduriansky, R. 2007. Sexual selection and allometry: a critical reappraisal of the  
6  
7 690 evidence and ideas. *Evolution*. 61: 838-849.
- 8  
9 691 90 - Cuervo, J.J. & A.P. Møller. 2009. The allometric pattern of sexually size dimorphic  
10  
11 692 feather ornaments and factors affecting allometry. *J. Evol. Biol.* 22: 1503–1515.
- 12  
13 693 91 - Gould, S.J. 1975. Allometry in primates, with emphasis on scaling and the evolution of  
14  
15 694 the brain. Pp. 244–292 in F. Szalay, ed. *Approaches to primate paleobiology*. Karger,  
16  
17 695 Basel.
- 18  
19 696 92 - Voje, K. L. & T.F. Hansen. 2013. Evolution of static allometries: adaptive change in  
20  
21 697 allometric slopes of eye span in stalk-eyed flies. *Evolution*. 67:453–467.
- 22  
23 698 93 - Sharma, M.D., Tregenza, T. & D.J. Hosken. 2011. Sex combs, allometry, and asymmetry  
24  
25 699 in *Drosophila*. *Biol. J. Linn. Soc.* 103: 923-934.
- 26  
27 700 94 - Armbruster, W.S., Pélabon, C., Hansen, T.F. & G.H. Bolstad. 2009 Macroevolutionary  
28  
29 701 patterns of pollination accuracy: a comparison of three genera. *New Phytol.* 183: 600 –  
30  
31 702 617.
- 32  
33 703 95 - Hansen, T.F., Pélabon, C. & W.S. Armbruster. 2007. Comparing variational properties of  
34  
35 704 homologous floral and vegetative characters in *Dalechampia scandens*: Testing the  
36  
37 705 Berg Hypothesis. *Evol. Biol.* 34: 86-98.
- 38  
39 706 96 - Pélabon, C. Hansen, T.F. & W.S. Armbruster. 2011. Experimental evidence for the Berg  
40  
41 707 hypothesis: vegetative traits are more sensitive than pollination traits to environmental  
42  
43 708 variation. *Funct. Ecol.* 25, 247–257.
- 44  
45 709 97 - Armbruster, W.S., Di Stilio, V.S., Tuxill, J.D. Flores, T.C. & J.L. Velasquez Runk. 1999.  
46  
47 710 Covariance and decoupling of floral and vegetative traits in nine Neotropical Plants: A  
48  
49 711 re-evaluation of Berg's correlation-pleiades concept. *Am. J. Bot.* 86: 39-55.
- 50  
51 712 98 - Ushimaru, A. & K. Nakata. 2001. Evolution of flower allometry and its significance for  
52  
53  
54  
55  
56  
57  
58  
59  
60

Pélabon et al.

The evolvability of allometry

- 1  
2  
3 713 pollination success in the deceptive orchid *Pogonia japonica*. *Int. J. Plant Sci.* 162:  
4  
5 714 1307 – 1311.  
6  
7 715 99 - Huxley, J. S. 1924. Constant differential growth-ratios and their significance. *Nature*  
8  
9 716 114:895-896.  
10  
11 717 100 - Savageau, M.A. 1979. Allometric morphogenesis of complex systems: Derivation of the  
12  
13 718 basic equations from first principles. *Proc. Natl. Acad. Sci. USA.* 76:6023–6025.  
14  
15 719 101 - White, J.F. & S.J. Gould. 1965. Interpretation of the coefficient in the allometric  
16  
17 720 equation. *Am. Nat.* 99:5–18.  
18  
19 721 102 - Gould, S.J. 1971. Geometric similarity in allometric growth: a contribution to the  
20  
21 722 problem of scaling in the evolution of size. *Am. Nat.* 105:113–136.  
22  
23 723 103 - Egset, C.K., Bolstad G.H., Rosenqvist, G. Endler, J.A. & C. Pélabon. 2011.  
24  
25 724 Geographical variation in allometry in the guppy (*Poecilia reticulata*). *J. Evol. Biol.*  
26  
27 725 24:2631–2638.  
28  
29 726 104 - Packard, G.C. 2009. On the use of logarithmic transformations in allometric analyses. *J.*  
30  
31 727 *Theor. Biol.* 257:515-518.  
32  
33 728 105 - Packard, G.C. 2013. Is logarithmic transformation necessary in allometry? *Biol. J. Linn.*  
34  
35 729 *Soc.* 109: 476-486.  
36  
37 730 106 - Kerkhoff, A.J. & B.J. Enquist. 2009. Multiplicative by nature: Why logarithmic  
38  
39 731 transformation is necessary in allometry. *J. Theor. Biol.* 257:519-521.  
40  
41 732 107 - Kelly, C. & T.D. Price. 2004. Comparative methods based on species mean values.  
42  
43 733 *Math. Biosci.* 187: 135–154.  
44  
45 734 108 - Hansen, T.F. & K. Bartoszek, K. 2012. Interpreting the evolutionary regression: the  
46  
47 735 interplay between observational and biological errors in phylogenetic comparative  
48  
49 736 studies. *Sys. Biol.* 61:413-425.  
50  
51 737 109 - Retief, T.A., Bennett, N.C., Kinahan, A.A. & P.W. Bateman. 2013. Sexual selection and  
52  
53  
54  
55  
56  
57  
58  
59  
60



Pélabon et al.

The evolvability of allometry

- 1  
2  
3 738 genital allometry in the Hottentot golden mole (*Amblysomus hottentotus*). *Mammal.*  
4  
5 739 *Biol.* 78:356-360.  
6  
7 740 110 - Jolicoeur, P. 1963. The multivariate generalization of the allometry equation. *Biometrics*  
8  
9 741 19:497-499.  
10  
11 742 111 - Gerber, S., Eble, G.J. & P. Neige. 2008. Allometric space and allometric disparity: a  
12  
13 743 developmental perspective in the macroevolutionary analysis of morphological  
14  
15 744 disparity. *Evolution.* 62: 1450-1457.  
16  
17  
18 745 112 - Wilson, L.A.B. & M.R. Sánchez-Villagra. 2010. Diversity trends and their ontogenetic  
19  
20 746 basis: an exploration of allometric disparity in rodents. *Proc. R. Soc. London B.* 277:  
21  
22 747 1227-1234.  
23  
24  
25 748 113 - Bookstein, F. L. 1989. "Size and Shape" - a comment on semantics. *Syst. Zool.* 38, 173-  
26  
27 749 180.  
28  
29  
30 750 114 - Mosimann, J., 1970. Size allometry: Size and shape variables with characterizations of  
31  
32 751 the lognormal and generalized gamma distributions. *J. Am. Stat. assoc.* 65: 930-948.  
33  
34 752 115 - Drake, A.G. & C.P. Klingenberg. 2008. The pace of morphological change: historical  
35  
36 753 transformation of skull shape in St Bernard dogs. *Proc. R. Soc. London B.* 275: 71-76.  
37  
38  
39 754 116 - Adams, D., Nistri, A., 2010. Ontogenetic convergence and evolution of foot  
40  
41 755 morphology in European cave salamanders (Family: Plethodontidae). *Bmc Evol. Biol.*  
42  
43 756 10, 216.  
44  
45 757 117 - Gonzalez, P.N., Kristensen, E., Morck, D.W., Boyd, S. & B. Hallgrímsson. 2013.  
46  
47 758 Effects of growth hormone on the ontogenetic allometry of craniofacial bones. *Evol.*  
48  
49 759 *Dev.* 15: 133-145.  
50  
51  
52 760  
53  
54 761  
55  
56  
57  
58  
59  
60

Pélabon et al.

## The evolvability of allometry

762 Table 1: Changes in arithmetic slope and allometric slope (log scale) in two artificial selection experiments. In the experiment on the stalk-eyed  
 763 fly (*Cyrtodiopsis dalmanni*) [76] selection was exerted for 13 generations to change the ratio between eye-span and body length. We estimated  
 764 the slope on the arithmetic scale from Fig. 3 in the original paper by estimating the values of the extreme points of the regression lines. These  
 765 data were subsequently log-transformed to obtain the allometric slopes. In the experiment on *Drosophila* [81], selection to increase or decrease  
 766 thorax length was conducted for 23 generations. Estimates of the allometric slopes were obtained from the variance and covariance parameters  
 767 scaled by the trait mean (male and female combined). Standard errors of the estimates are not available.

768

Species	Trait	Body size	Sex	Line	Arithmetic slope	Allometric slope
<i>Cyrtodiopsis dalmanni</i>	Eye-span	Body length	♀ rep1	Down	0.71	0.87
				Up	1.00	1.10
			♂ rep 1	Down	1.37	1.19
				Up	1.73	1.38
			♀ rep2	Down	0.56	0.68
				Up	0.66	0.74
			♂ rep 2	Down	1.10	0.98
				Up	1.43	1.10
<i>Drosophila melanogaster</i>	Wing length	Thorax length	♀+♂	large	0.49	0.30
			♀+♂	Small	0.68	0.38
			♀+♂	Control	0.42	0.24
	Tibia length	Thorax length	♀+♂	large	0.39	0.58
			♀+♂	Small	0.65	0.93
			♀+♂	Control	0.40	0.60

769

Pélabon et al.

The evolvability of allometry

1  
2  
3 770 Figure 1. Evolution of static allometry. The scenarios considered here correspond to the  
4  
5 771 expected evolution of static allometry from an ancestral state depending on the constraining  
6  
7 772 parameter (i.e. the parameter that is not evolvable). Vertical and horizontal dash lines  
8  
9 773 represent the mean trait value and body size. Body size is mean centered, so the allometric  
10  
11 774 intercept represent the trait value at the population mean (i.e. elevation of the allometric  
12  
13 775 regression). In the scenario A, both the slope and the intercept are constraining parameters.  
14  
15 776 Any change in body size will generate a change in trait size and vice versa. In the scenario B,  
16  
17 777 only the allometric slope changes while the intercept (elevation) does not change. In the  
18  
19 778 scenario C, the slope is the constraining parameter while the intercept can change. In the  
20  
21 779 scenario D, slope and intercept can evolve. This pattern may be also generated by the effect of  
22  
23 780 a negative covariance between body size and the ontogenetic slope when selection on body  
24  
25 781 size occurs (see Eq. 1).  
26  
27  
28  
29  
30

31  
32 783 Figure 2. Selection to change allometric slope via correlated selection on the trait and  
33  
34 784 body size. A) Selection is generated by the difference in the direction of the phenotypic  
35  
36 785 regression and the adaptive ridge. Black dots represent individuals and the blue dots represent  
37  
38 786 the selected individuals (with the highest fitness). B) Saddle fitness landscape that generates  
39  
40 787 disruptive selection on one of the two traits. This selection regime is more efficient to change  
41  
42 788 the slope because individuals in the middle of the distribution are not selected.  
43  
44  
45

46  
47 790 Figure 3. Phenotypic plasticity in static allometry. The figure presents the variation in the  
48  
49 791 slope of the static allometry between wing size (estimated by the centroid size) and the inter-  
50  
51 792 landmark distance 2 - 12 (see diagram for landmarks number) in two populations of *D.*  
52  
53 793 *melanogaster* selected to increase (grey arrows) or decrease (back arrows) a selection index.  
54  
55 794 Selection was performed for 26 generations. Idiosyncratic variation of the slope (estimated on  
56  
57  
58  
59  
60

Pélabon et al.

The evolvability of allometry

1  
2  
3 795 100 males at each generation) generates statistically significant differences between selection  
4  
5 796 lines at generation 4, 9 and 11. The data presented here correspond to the LHM 1 replicate,  
6  
7 797 but similar results were observed for the other three replicates, LHM 2 and IV 1 and 2 (see  
8  
9 798 [55] for more detail).

799

10  
11  
12  
13  
14 800 Figure 4. Static allometry as an evolutionary constraint. The various scenarios represent  
15  
16 801 the effect of constraining parameters of the static allometry on the evolutionary allometry,  
17  
18 802 assuming that selective optima are spread more or less randomly in the bivariate  
19  
20 803 morphospace. In scenario A, neither the slope nor the intercept vary. The divergence of  
21  
22 804 population means follow the genetic allometric regression (see text). If the slopes of the  
23  
24 805 genetic and phenotypic allometry are similar, evolutionary allometry will follow the patterns  
25  
26 806 of static allometry. In scenario B, the intercept is allowed to change but not the slope.  
27  
28 807 Although such a pattern may result from the evolution of the intercept itself, it may also result  
29  
30 808 from the difference between the phenotypic and genetic allometry (see text). Scenario C  
31  
32 809 presents a similar pattern but where selection does not favor any particular direction in the  
33  
34 810 morphospace. In scenario D, both intercept and slope can evolve (no constraint).

811

35  
36  
37  
38  
39  
40 812 Figure 5. Example of variation in static allometric and effect on evolutionary allometry  
41  
42 813 A) among population within species B) among species within genus C) among species  
43  
44 814 genitals (Figure from [23] Voje et al. 2014).

815

816

Pélabon et al.

The evolvability of allometry

**817 Box 1 – Narrow sense and broad sense allometry: conceptual and methodological issues**

818

819 In the recent years, the term allometry has been used for any type of monotonic relationships  
820 between two morphological variables, independently of the scale on which these variables  
821 were expressed. This broad definition of allometry is inconsistent with the biological  
822 interpretation of morphological allometry originally suggested by Huxley [5, 99]. Huxley [5]  
823 showed that if an arbitrary trait  $Z$  and body size  $X$ , grow at different rate but under the control  
824 of a common growth parameter  $G$ , such that  $dX/dt = \alpha XG$ , and  $dZ/dt = \beta ZG$ , where  $\alpha$  and  $\beta$   
825 are specific constants for  $X$  and  $Y$ , respectively, and  $t$  the time during growth, the relationship  
826 between  $Z$  and  $X$  follows a power law  $Z = AX^{\beta/\alpha}$ , where  $A$  is a constant that depends on the  
827 initial values of  $Z$  and  $X$ . On a log scale, this relationship is linear  $z = a + bx$ , where  $z =$   
828  $\log(Z)$ ,  $x = \log(X)$ ,  $a = \log(A)$ . Savageau [100] generalized this model and showed that  
829 whenever two or more variables are connected in a dynamic synergistic system controlled by  
830 one variable, their relationship follows an allometric relationship. Therefore, allometry, in its  
831 narrow sense is defined by two parameters of a power relation that can be expressed as the  
832 intercept  $a$  and the slope  $b$  of a linear regression on log scale. When the explanatory variable  
833 ( $x$ ) is mean centered, the intercept,  $a$ , becomes the elevation of the static allometry, that is, the  
834 trait size at the population mean body size [101, 102, 103].

835 Which statistical model should be used to estimate these parameters has been the  
836 subject of long debates. First, it has been suggested that the best estimation of these  
837 parameters should be done from a power relationship fitted on arithmetic scale [104, 105].  
838 This approach would be justified if the processes producing the error would act in an additive  
839 manner. Although this may be the case for measurement error, it is most likely that the  
840 biological error will be generated by multiplicative processes similar to those responsible for  
841 the growth of the trait [106]. Because most of the error on the response variable is likely to be

Pélabon et al.

The evolvability of allometry

1  
2  
3 842 of biological origin, estimates produced by linear regression on log scale should be better than  
4  
5 843 those produced by a power model fitted on arithmetic scale. Both approaches are valid,  
6  
7 844 however, and should ideally be conducted with proper modeling of both biological and  
8  
9 845 measurement error.

11 846 It has been repeatedly suggested that major-axis or reduced major-axis regression  
12  
13 847 should be used in place of ordinary least-squares regression to estimate allometric parameters  
14  
15 848 in order to account for the effect of observational error in the predictor variables. However,  
16  
17 849 neither of these models provides sensible estimates of allometric regression slopes when there  
18  
19 850 is biological ‘error’ (i.e. biological deviations from the allometric line) in the model [107,  
20  
21 851 108]. These models provide estimates of slopes, but these slopes are not proper estimates of  
22  
23 852 the exponent  $b$  in the narrow-sense allometric relation. A dramatic consequence of the  
24  
25 853 reduced major-axis regression is that, even in absence of covariance between the two traits, an  
26  
27 854 “allometric” slope can be estimated and its statistical significance tested [e.g. 82].

29 855 Finally, we notice that ignoring the consequences of trait dimension on the allometric  
30  
31 856 slope has led to some erroneous statements in the recent study of allometry. For example, a  
32  
33 857 positive allometry between testes size and body length has been reported in Hottentot golden  
34  
35 858 mole (*Amblysomus hottentotus*) as an exception to the “one size fits all” hypothesis [109].  
36  
37 859 However, this positive allometry is most likely generated by the difference in dimension  
38  
39 860 between the traits (body length – length vs. testes mass - volume).  
40  
41  
42  
43  
44

45 861

46 862

Pélabon et al.

The evolvability of allometry

**Box 2: From bivariate to multivariate allometry: drifting away from the Huxley's model**

864

865 Jolicoeur [110] suggested analyzing multivariate relative growth using the first principal  
866 component (or eigenvector) of the variance-covariance matrix of log-scaled trait values  
867 (herein PC1). He showed the relation between this approach and the Huxley model [5]  
868 arguing that the trait's loadings on PC1 are equivalent to their allometric exponents. This  
869 approach formalized multivariate isometric variation as a PC1 vector with all elements or  
870 loadings equal to  $1/\sqrt{k}$ , where  $k$  is the number of traits measured. Variation along such a  
871  $\{1/\sqrt{k}, \dots, 1/\sqrt{k}\}$  vector is associated to variation in organism size while its proportions  
872 remain constant. Group difference in multivariate allometry is commonly estimated as the  
873 angle between two within-group PC1 in the multivariate space [67]. This approach has been  
874 used to describe the plasticity of static multivariate allometry of *Drosophila* exposed to  
875 different environmental conditions [83], or to investigate the evolutionary diversity among  
876 species [111, 112].

877 However, the biological meaning of the PC1 loadings in this approach is not  
878 equivalent to the one of the standard regression estimates (i.e. Huxley's allometric exponent).  
879 Instead, these estimates are the slopes of the standard regressions of trait variables on size, as  
880 defined by PC1. Importantly, the ratios of the loadings do not correspond to the "variables'  
881 bivariate allometric coefficient" [67], at least not if they are properly estimated with a  
882 standard regression (Box 1), but these correspond to the ratio of their respective covariances  
883 with PC1. This can be interpreted as the relative change in the two traits for a given change  
884 along PC1. However, the orientation of the PC1 vector in the morphospace can vary with an  
885 increase in trait(s) variance even if covariances are kept constant.

886 This raises the problem of the use of an adequate definition of size in the study of its  
887 relation with shape (see [113] for review). The two most commonly used approaches for

Pélabon et al.

The evolvability of allometry

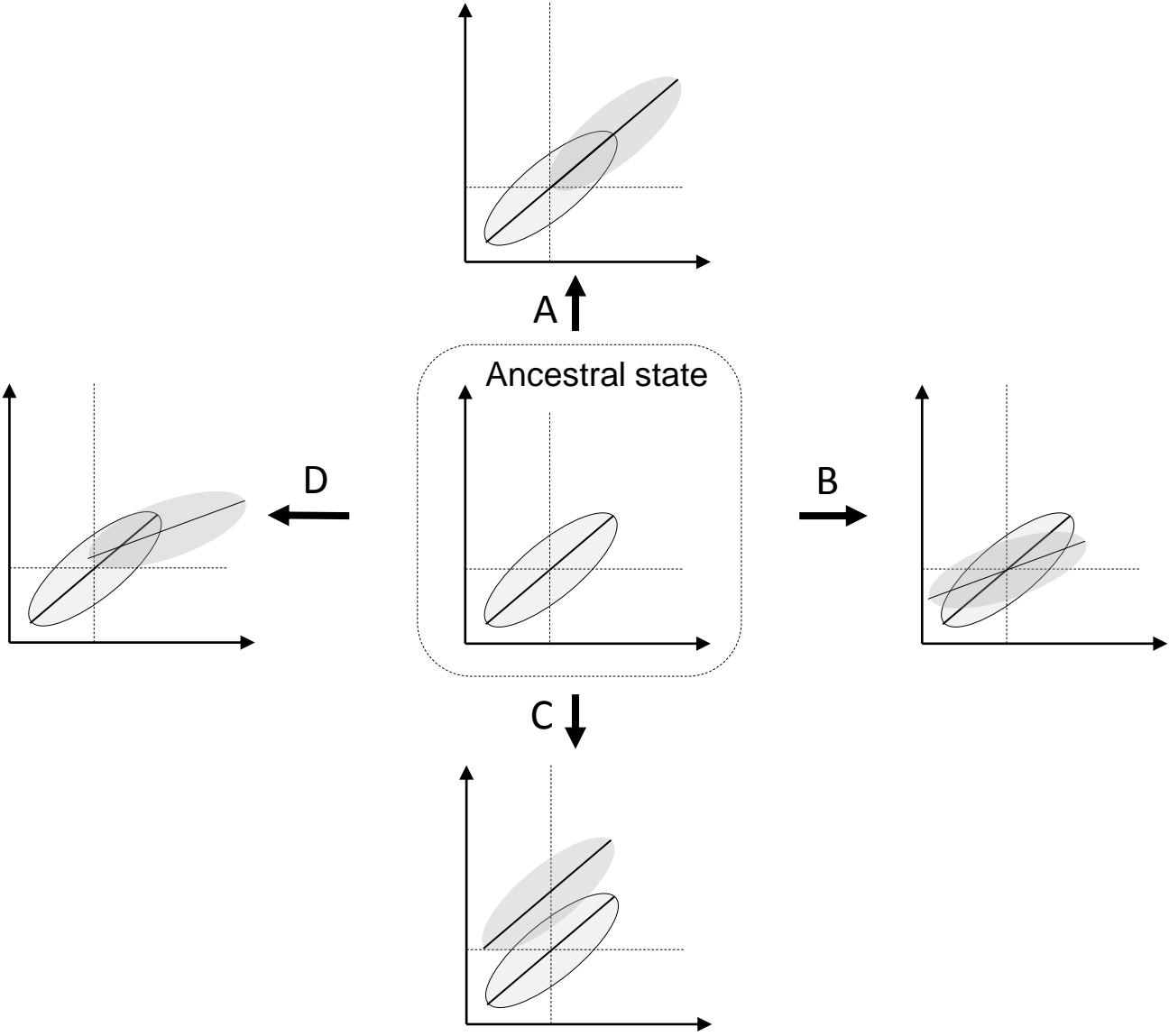
1  
2  
3 888 estimating size are the PC1-as-size approach described above and Mosimann's [114]  
4  
5 889 definition. Mosimann [114] defined size as any function  $G$  of the measurement vector  $\mathbf{x}$  that  
6  
7 890 satisfies the property:  $G(a\mathbf{x})=aG(\mathbf{x})$ ,  $G(\mathbf{x})$  having the same dimension than any element of  $\mathbf{x}$ .  
8  
9 891 Indeed, shape being on a ratio scale, multiplication of each element of the ratios by a constant  
10  
11 892  $a$  does not change shape and  $G$  is uncorrelated with any ratios under fully isometric  
12  
13 893 multivariate variation. It is worth noticing that Huxley [5] already defined traits' growth rate  
14  
15 894 as affected by a common growth factor (" $G$ ") that vanishes when the growth rates of the traits  
16  
17 895 are put in relation in the exponential relationship.  
18  
19

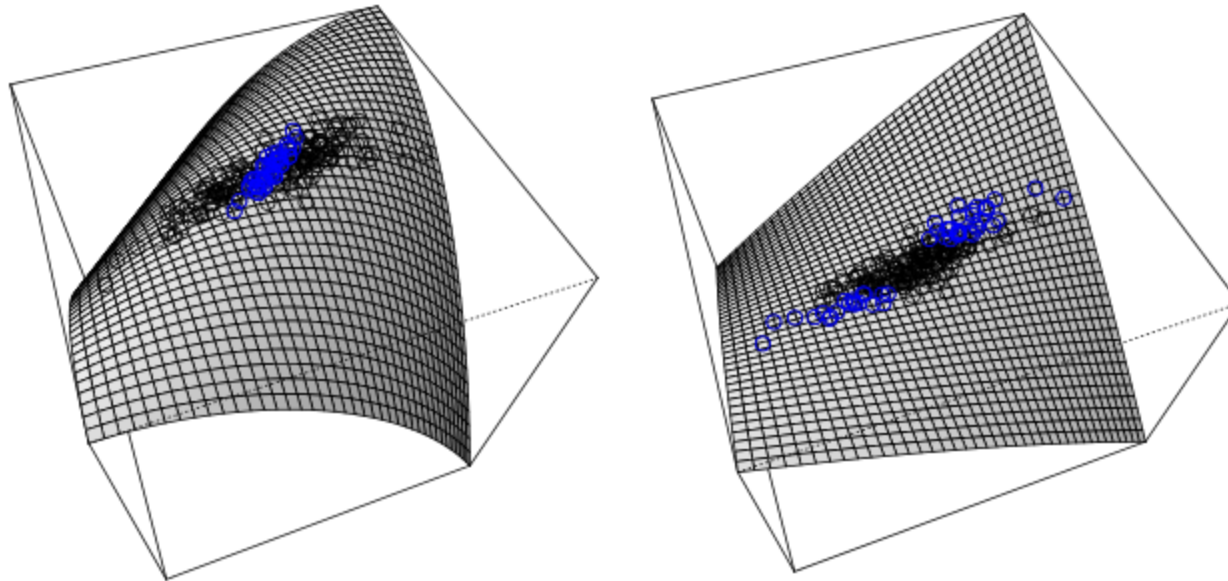
20  
21 896 Contrary to the PC1 approach, this geometric definition of size is not directly  
22  
23 897 dependent of the variance-covariance properties of the studied samples. As a measure of size,  
24  
25 898 geometric morphometrics conventionally use centroid size (CS), the square root of the sum of  
26  
27 899 squared distances of a set of landmarks from the centroid of the entire landmarks  
28  
29 900 configuration. Although this choice does not generally rely on biological arguments, centroid  
30  
31 901 size corresponds to a size vector according to Mosimann's definition. The Procrustes  
32  
33 902 superimposition algorithm scales landmark coordinates with CS, providing Mosimann's shape  
34  
35 903 vectors. The effect of CS on remaining shape variation therefore corresponds to multivariate  
36  
37 904 allometry. The effect of size variation on shape can be graphically depicted in computing the  
38  
39 905 product  $\mathbf{y}\beta'(\beta\beta')^{-0.5}$  [115] where  $\mathbf{y}$  is the shape variables and  $\beta$  the multivariate regression  
40  
41 906 coefficients, allowing to compare multivariate allometric patterns across different groups  
42  
43 907 [116, 117].  
44  
45  
46

47 908 Under specific conditions, a multivariate regression of shape on size certainly  
48  
49 909 represents the multivariate approach the most closely related to the original bivariate model  
50  
51 910 from Huxley. On the other hand, the broadly used geometric morphometric approach  
52  
53 911 abandons the notion of trait for a notion of shape analyzed as a whole, and hampers  
54  
55 912 interpretations of allometry in a context of relative growth.  
56  
57  
58  
59  
60



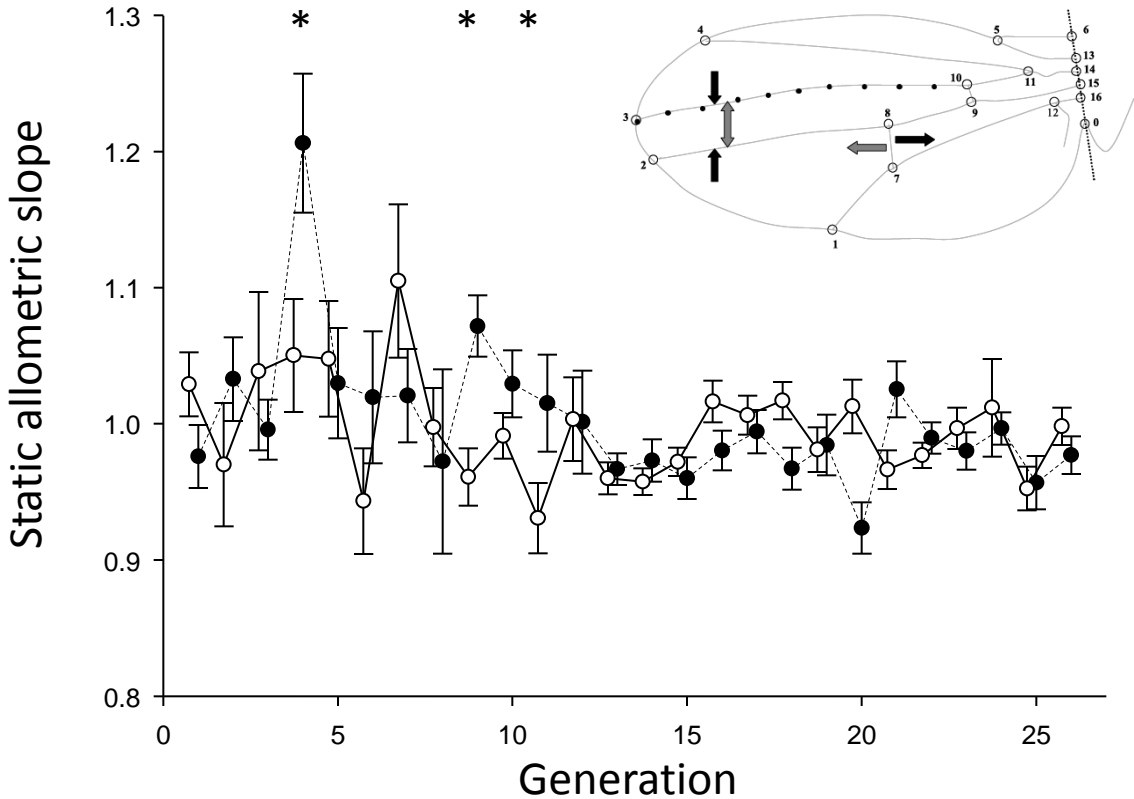
1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43

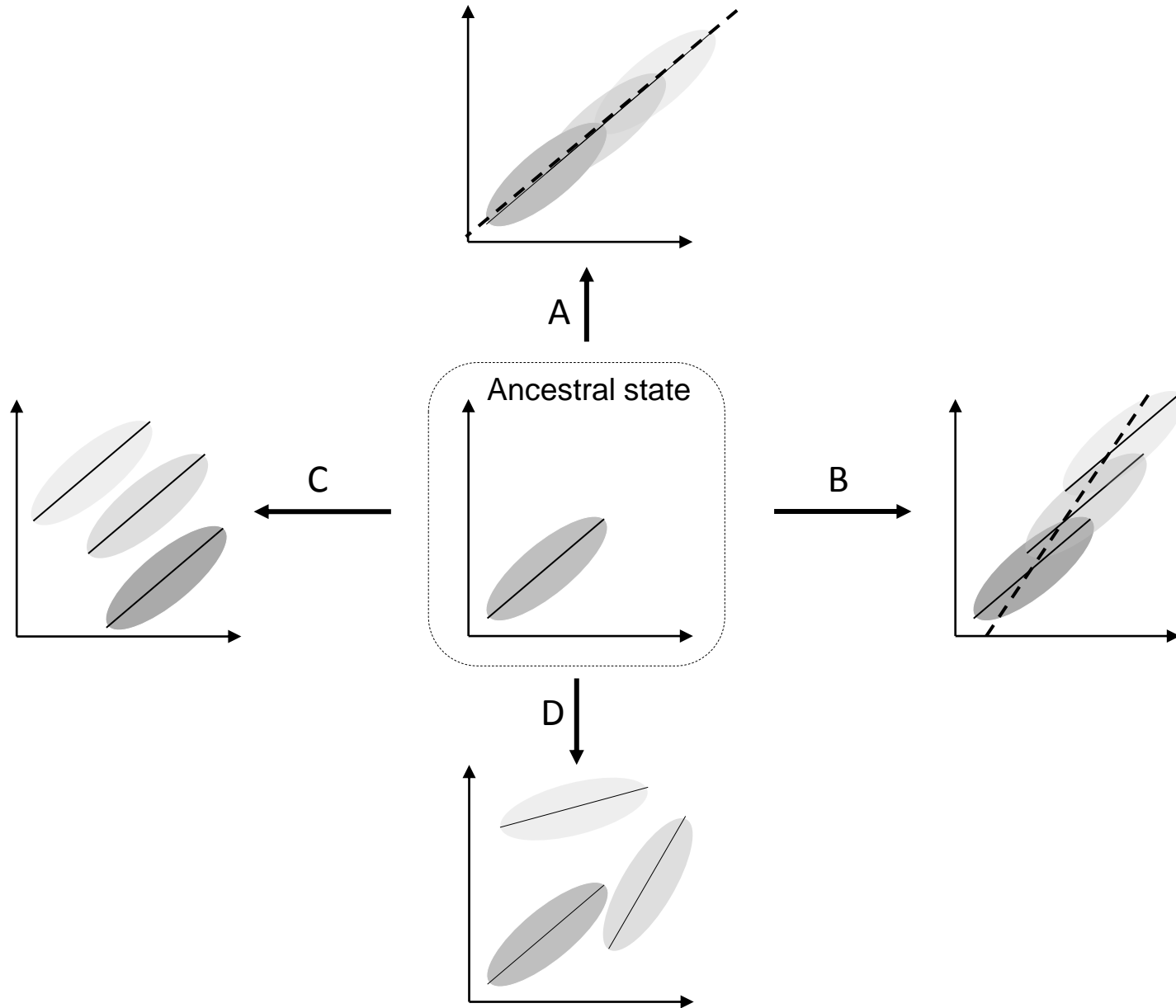




1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43

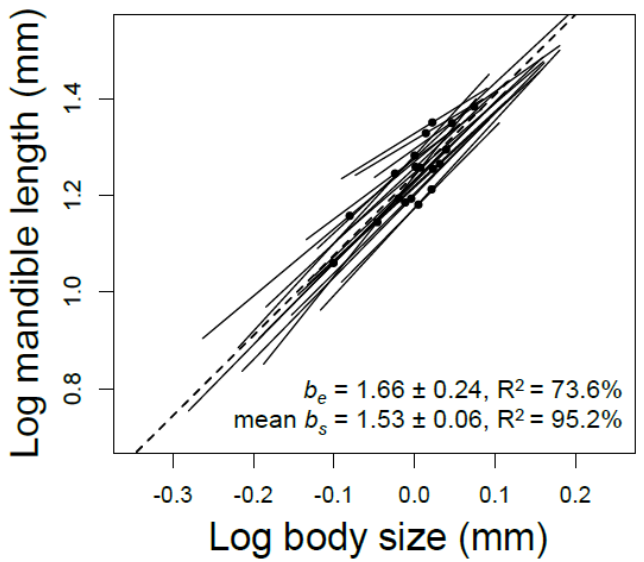
1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43



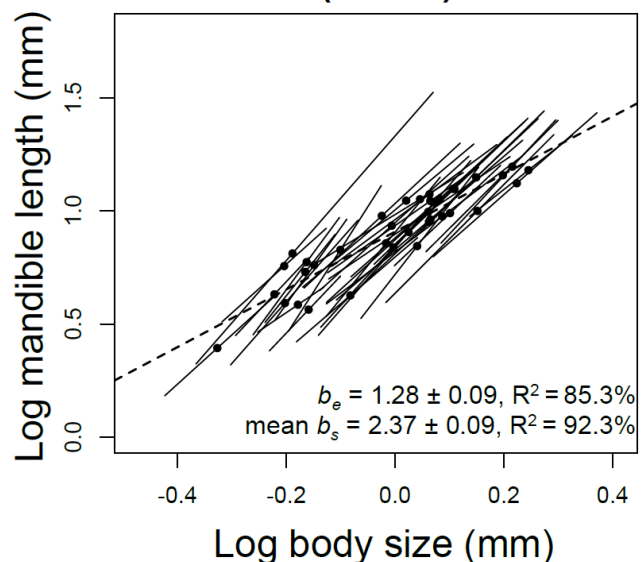


1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43

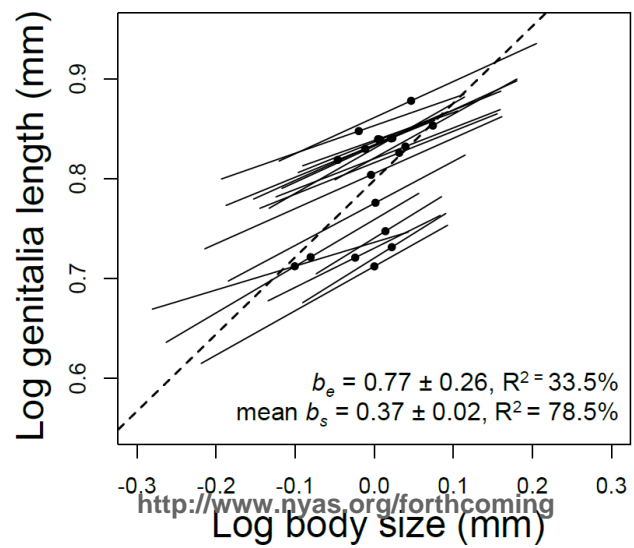
***Dorcus titanus***  
**(males) N = 19**



***Dorcus* (males) N = 37**



***Dorcus titanus***  
**(males) N = 19**



1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43