biology letters

Research

CrossMark
click for updates

Author for correspondence:
J. F. Lemaître
e-mail: jeff.lemaitre@gmail.com;
jean-francois.lemaitre@univ-lyon1.fr

Royal Society Publishing

Evolutionary biology

The allometry between secondary sexual traits and body size is nonlinear among cervids

J. F. Lemaître, C. Vanpé, F. Plard and J. M. Gaillard

Université de Lyon, F-69000, Lyon; Université Lyon 1; CNRS, UMR5558, Laboratoire de Biométrie et Biologie Evolutive, F-69622 Villeurbanne, France

Allometric relationships between sexually selected traits and body size have been extensively studied in recent decades. While sexually selected traits generally display positive allometry, a few recent reports have suggested that allometric relationships are not always linear. In male cervids, having both long antlers and large size provides benefits in terms of increased mating success. However, such attributes are costly to grow and maintain, and these costs might constrain antler length from increasing at the same rate as body mass in larger species if the quantity of energy that males can extract from their environment is limiting. We tested for possible nonlinearity in the relationship between antler size and body mass (on a log–log scale) among 31 cervids and found clear deviation from linearity in the allometry of antler length. Antler length increased linearly until a male body mass threshold at approximately 110 kg. Beyond this threshold, antler length did not change with increasing mass. We discuss this evidence of nonlinear allometry in the light of life-history theory and stress the importance of testing for nonlinearity when studying allometric relationships.

1. Introduction

In ungulates, both weapon size and sexual size dimorphism increase positively with the intensity of sexual selection [1,2]. The underlying reason for this relationship is that body size and weapon size are positively correlated with male mating success, and thereby with reproductive success, in polygynous species [3,4]. Across ungulate species such as cervids, the length of antlers has been repeatedly found to display positive allometry in analyses correcting [5] or not [6,7] for the confounding effects of phylogeny.

Previous studies focused on the coevolution between sexual traits and body size have assumed the existence of linear allometric relationships [5–7]. However, it has been recently emphasized that allometric relationships often deviate from linearity and thus display a great variety of shapes (see [8] for a review). For instance, the allometric relationship of testes mass in cetaceans [9] is curvilinear. Moreover, a key tenet in evolutionary biology holds that individuals have to allocate their limited resources among tissues or organs that are costly to grow and maintain [10], especially when these tissues are involved in the same biological function (e.g. sexual competition: [11]). In cervids, males replace antlers every year and have to allocate resources to both body mass and antlers at the same time before the rut period. Males from species allocating substantially to body mass might thus have to reduce their allocation to antler mass and length, which thus might lead to a nonlinear allometric relationship between antler size and body mass.

We investigated the shape of the allometric relationship between antler length and body mass across 31 cervid species using log-transformed variables (as advocated by Houle *et al.* [12]). We expected that the largest species should trade antler size for heavy mass and we thus predicted a lower allometric exponent for these species compared with smaller ones.

2. Material and methods

(a) Dataset

We gathered data on male body mass and antler length of 31 cervid species from a recently published comparative study [5]. These data were taken from adult individuals only, and when possible from the same population [5]. All data are provided as the electronic supplementary material, table S1.

(b) Statistical analyses

To assess the shape of the allometric relationship between antler length and body mass, we first fitted a linear model on log-transformed variables. Then, we fitted a quadratic and two threshold models. One threshold model included one slope and a constant antler length beyond the threshold value, and the other included two slopes, one before and one after the body mass threshold. To estimate the threshold value, the deviance profile of the models including slopes was used and the body mass leading to the lowest deviance was selected as the threshold value [13]. The best model was selected based on the Akaike's information criterion corrected for small sample size (AICc). We calculated AICc weights (AICcw) to assess the relative likelihood that each model was the best among all fitted models [14]. The model with the highest AICcw was the best model, but when the difference in AICc (ΔAICc) between competing models was less than 2, we retained the model with the lowest number of parameters to satisfy parsimony rules. All analyses were repeated using antler weight instead of antler length but based on a smaller dataset (20 species) due to the scarcity in antler weight data in the literature. These analyses provided qualitatively similar results and are presented in the electronic supplementary material, table S2 and figure S1. An important point when analysing data at the interspecific level is to control for phylogenetic dependence among species [15]. We thus re-analysed our data using the method of phylogenetic independent contrasts [16]. Unfortunately, the phylogeny of artiodactyla is not fully resolved [17] and the number of contrasts was thus relatively low ($n = 23$ contrasts) compared with the number of species in our dataset ($n = 31$). However, despite this difference in sample size, similar trends were found in analyses with or without corrections for phylogeny. Results of phylogenetic independent contrasts analyses are provided in the electronic supplementary material, table S3 and figure S2.

3. Results

The best models describing the allometric relationship between antler length and body mass were the quadratic and the one-slope threshold models. These two models had the same number of parameters ($k = 4$) and very similar performance (quadratic: AICcw = 0.43; threshold with one slope: AICcw = 0.33), which was much higher than that of the linear model (AICcw = 0.03; electronic supplementary material, table S4). In these models (figure 1 and table 1), the positive linear allometric relationship between antler length and body mass does not hold over the whole range of body mass among cervids. The very low curvature of the quadratic model (figure 1) revealed that antler length stopped increasing with body mass at a body mass threshold of 100–110 kg. Similarly, the threshold model with one slope revealed a linear allometric relationship between antler length and body mass up to 113 kg, beyond which (up to 482.5 kg) antler length remained unchanged. When we restricted the analysis to species with body mass below 113 kg ($n = 22$), the linear model was the best (see the electronic supplementary material,
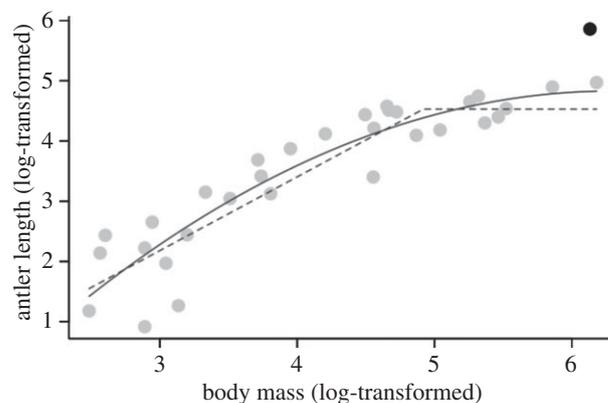

Figure 1. Relationship between antler length and body mass (on a log–log scale) across 31 extant cervids. The quadratic (solid line) and threshold (with one slope, dashed line) models best described the relationship. The black circle represents the extinct Irish elk (*Megaloceros giganteus*).

table S5) and revealed a linear and positive allometric relationship (slope of 1.33 ± 0.15) between antler length and male body mass.

4. Discussion

Our results reveal that the allometric relationship between antler length and body mass is not linear among cervid species. Typically, males from the largest species (more than 100–110 kg) have smaller antlers than expected from a positive linear allometric relationship. The decreasing allometric exponent in large species is apparently not caused by biomechanical constraints on the ability to carry large antlers, because the antlers of the extinct Irish elk (*Megaloceros giganteus*) exceed the largest size observed in our dataset ([18], figure 1). This is particularly interesting because the body mass of the Irish elk was close to that of the moose (*Alces alces*; about 460 kg, see [19]), a species at the upper limit of body mass range in extant cervids. Thus, large deer species have the biomechanical potential to carry particularly large antlers. Moreover, the substantive energetic costs associated with conspicuous reproductive traits might explain why the breakdown in resource quantity and quality at the end of the Pleistocene was fatal to this emblematic species [18].

Current life-history theory suggests an explanation for the failure of antler size (or antler weight, see the electronic supplementary material, figure S1) to keep pace with body size in large species. The principle of energy allocation states that individuals must share their energy budget among competing functions including growth, reproduction and survival [20]. With the constant exponent involved in the positive linear allometry, the allocation to antlers is particularly costly for males from large species. Therefore, a high amount of energy allocated to reproduction and sexual competition, notably through the growth of conspicuous antlers or large body mass in these species, could decrease the amount of energy available for maintenance and thereby jeopardize survival. A recent comparative study has failed to reveal any detrimental effect of large antlers on male survival or ageing rate [21]. In light of our results, this result is not surprising if large species have already decreased their putative survival costs by limiting allocation to antlers. Nevertheless, the exact ecological or physiological costs of growing such conspicuous weapons now require further investigation.

Table 1. Parameter estimates from the two best models (quadratic and threshold with one slope) of the allometric relationship linking antler length and body mass across 31 cervids (on a log–log scale).

		estimate	s.e.	t	p
quadratic	intercept	−4.47	1.43	−3.13	<0.001
	body mass	2.96	0.71	4.14	<0.001
	body mass^2	−0.23	0.08	−2.77	0.01
threshold (one slope)	intercept	−1.75	0.42	−4.14	<0.001
	body mass	1.33	0.10	12.65	<0.001

Overall, our findings add to the recent demonstrations [9,22] that allometric relationships are not always linear, even though linear allometries are assumed in most studies (see [8] for a review). Importantly, in species where male body mass is above 100–110 kg, males generally face intense sexual competition to control large breeding groups [5]. Therefore, our results suggest that natural selection might constrain the evolution of very long antlers when the strength of sexual selection is particularly high. Failure to assess the true shape of allometric relationships might thus have strong implications. For example, in evolutionary ecology, interspecific studies often assess the strength of sexual selection across species through the use of a unique sexually selected trait as a proxy. Our findings demonstrate that using antler length or body mass as independent and single predictor of the intensity of sexual competition could lead to different results. Namely, the use of antler length only will lead the intensity of sexual selection for species above 100–110 kg to be underestimated. Our results emphasize the need for careful investigations of covariation among sexual traits before focusing upon any trait as a unique measure of the intensity of sexual selection.

References

1. Bro-Jørgensen J. 2007 The intensity of sexual selection predicts weapon size in male bovids. *Evolution* **61**, 1316–1326. (doi:10.1111/j.1558-5646.2007.00111.x)

2. Lindenfors P, Gittleman JL, Jones KE. 2007 Sexual size dimorphism in mammals. In *Sex, size, and gender roles: evolutionary studies of sexual size dimorphism* (eds DJ Fairbairn, WU Blanckenhorn, T Szekely), pp. 16–26. Oxford, UK: Oxford University Press.

3. Preston BT, Stevenson IR, Pemberton JM, Coltman DW, Wilson K. 2003 Overt and covert competition in a promiscuous mammal: the importance of weaponry and testes size to male reproductive success. *Proc. R. Soc. Lond. B* **270**, 633–640. (doi:10.1098/rspb.2002.2268)

4. Vanpé C, Gaillard J-M, Kjellander P, Liberg O, Delorme D, Hewison AJ. 2010 Assessing the intensity of sexual selection on male body mass and antler length in roe deer *Capreolus capreolus*: is bigger better in a weakly dimorphic species? *Oikos* **119**, 1484–1492. (doi:10.1111/j.1600-0706.2010.18312.x)

5. Plard F, Bonenfant C, Gaillard JM. 2011 Revisiting the allometry of antlers among deer species: male–male sexual competition as a driver. *Oikos* **120**, 601–606. (doi:10.1111/j.1600-0706.2010.18934.x)

6. Gould SJ. 1974 The origin and function of 'bizarre' structures: antler size and skull size in the 'Irish Elk,'

Megaloceros giganteus. *Evolution* **28**, 191–220. (doi:10.2307/2407322)

7. Clutton-Brock TH, Albon SD, Harvey PH. 1980 Antlers, body size and breeding group size in the Cervidae. *Nature* **285**, 565–567. (doi:10.1038/285565a0)

8. MacLeod CD. 2010 Assessing the shape and topology of allometric relationships with body mass: a case study using testes mass allometry. *Methods Ecol. Evol.* **1**, 359–370. (doi:10.1111/j.2041-210X.2010.00037.x)

9. MacLeod CD. 2010 The relationship between body mass and relative investment in testes mass in cetaceans: implications for inferring interspecific variations in the extent of sperm competition. *Mar. Mammal Sci.* **26**, 370–380. (doi:10.1111/j.1748-7692.2009.00348.x)

10. Pitnick S, Jones KE, Wilkinson GS. 2006 Mating system and brain size in bats. *Proc. R. Soc. B* **273**, 719–724. (doi:10.1098/rspb.2005.3367)

11. Fitzpatrick JL, Almbro M, Gonzalez-Voyer A, Kolm N, Simmons LW. 2012 Male contest competition and the coevolution of weaponry and testes in pinnipeds. *Evolution* **66**, 3595–3604. (doi:10.1111/j.1558-5646.2012.01713.x)

12. Houle D, Pélabon C, Wagner GP, Hansen TF. 2011 Measurement and meaning in biology. *Q. Rev. Biol.* **86**, 3–34. (doi:10.1086/658408)

13. Ulm K, Cox C. 1989 On the estimation of threshold values. *Biometrics* **45**, 1324–1328.

14. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*. New York, NY: Springer.

15. Harvey PH, Pagel MD. 1991 *The comparative method in evolutionary biology*. Cary, NC: Oxford University Press.

16. Felsenstein J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15. (doi:10.1086/284325)

17. Fernández MH, Vrba ES. 2005 A complete estimate of the phylogenetic relationships in Ruminantia: a dated species-level supertree of the extant ruminants. *Biol. Rev.* **80**, 269–302. (doi:10.1017/S1464793104006670)

18. Barnosky AD. 1986 'Big game' extinction caused by late Pleistocene climatic change: Irish elk (*Megaloceros giganteus*) in Ireland. *Q. Res.* **25**, 128–135. (doi:10.1016/0033-5894(86)90049-9)

19. Moen RA, Pastor J, Cohen Y. 1999 Antler growth and extinction of Irish elk. *Evol. Ecol. Res.* **1**, 235–249.

20. Stearns S. 1992 *The evolution of life histories*. Oxford, UK: Oxford University Press.

21. Lemaître JF, Gaillard JM. 2013 Male survival patterns do not depend on male allocation to sexual competition in large herbivores. *Behav. Ecol.* **24**, 421–428. (doi:10.1093/beheco/ars179)

22. Kolokotrones T, Van Savage EJ, Fontana W. 2010 Curvature in metabolic scaling. *Nature* **464**, 753–756. (doi:10.1038/nature08920)