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Revisiting the allometry of antlers among deer species: male–male sexual competition as a driver

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The positive allometry between antlers and shoulder height reported for cervids has previously been interpreted as resulting from a high male-male competition in large species that form large breeding groups. We aim at revisiting relative antler size variation among deer species by including more species ($n = 31$) and by testing both direct and indirect influences of different sexual selection proxies on the relative antler length using path analysis. The absence of direct effect of mating tactic on relative antler allometry indicates that the strength of fights does not differ among mating tactics. On the other hand, the main effect of breeding group size is revealed by the level of polygyny. Highly polygynous species have relatively longer antlers than less polygynous ones but the difference in the relative effect of breeding group size on relative antler length is weak. Strong direct effect of breeding group size and indirect effect of mating tactic shaped the observed variation in the relative antler size among deer, suggesting that the amount of male–male competition is the main evolutionary force of antler allometry in cervids.

After Gould (1973) demonstrated the positive evolutionary allometry (sensu Bonduriansky 2007) of antlers in cervids, Clutton-Brock et al. (1980) investigated the influence of sexual selection on the evolution of antler size relative to body size. Clutton-Brock et al. (1980) found that the strong male–male competition occurring in large deer species was the main driver of the allometric relationship between antler length and shoulder height. Species forming the largest breeding group size ($BGS \geq 6$, BGS being defined as the number of males and females within a group during the breeding period) have relatively larger antlers than those forming smaller breeding group size ($BGS < 6$). While the key role of sexual selection on the evolution of antlers in cervids is now well established (Gould 1974, Kodrick-Brown et al. 2006), the analysis proposed by Clutton-Brock et al. (1980) has not been updated. This analysis was indeed based on a limited availability of data (59% of living deer species). Moreover, the phylogenetic dependence of data was not accounted for, and the potential effects of confounding variables (intra-sexual competition) on the allometry of antlers were not quantified. Lastly, whether breeding group size influences the relative antler size through direct or indirect effects of mating tactic and of intersexual competition has not yet been investigated.

We propose here to revisit the allometry of antlers in cervids by using an extended dataset (76% of living deer species), by applying recent methods of comparative analysis taking into account phylogenetic dependency in the data, and by using new proxies of sexual selection (sexual size dimorphism, BGS, and mating tactic) to quantify the contribution of different components of sexual selection on shaping antler allometry. We used sexual size dimorphism as an overall proxy of sexual selection (Ralls 1977) including both intra- and inter-sexual selection. Breeding group size measure the amount of male–male competition (Wade and Shuster 2004). Finally, we used male mating tactics, i.e. the way by which males attempt to gain mates to measure the strength of intra-sexual competition within each tactic.

Using path analyses, we investigated direct and indirect influences of mating tactics in addition to breeding group size on antler sized relative to body mass to differentiate the amount of male–male competition due to the party size and the strength of the competition involved in a given mating tactic (e.g. number and strength of combats). We tested the following predictions: (1) large BGS should increase the relative antler length because in polygynous species, large-antlered males enjoy higher mating success (Clutton-Brock et al. 1980); (2) By conditioning female distribution in space, the distribution of food resources drives male mating tactics (Emlen and Oring 1977). In species of large herbivores, the largest and most dimorphic species live in open habitats where food resources are abundant and evenly distributed in space, whereas the smallest and less dimorphic species live in closed habitats with a clumped distribution of food resources (Jarman 1974). Female defense polygyny should thus be the most rewarding tactic in terms of mating success for males of large species, whereas males of smaller species should better be territorial and defend resources (Emlen and Oring 1977). We therefore expect the largest relative antler length to occur in the most dimorphic species showing a female defense mating tactic such as harem defense; (3) since the mating tactic co-varies with BGS (i.e. BGS is larger in harems than in territories (Emlen and Oring 1977)), we investigated the indirect effects of mating tactic through BGS and the direct effects of mating tactic on relative antler length. We predicted an indirect effect of mating tactic on antler length through BGS due to a higher mating success in mating tactics gathering more females by males.

Material and methods

Database

We collected data on antler length (main beam, in mm and noted AL) and body mass (in kg and noted BM) from the literature on 31 species of *Cervidae* (Supplementary material Appendix 1, Table 1). We retained measures taken in a given population and on adults to avoid any confounding effect of the age structure. When data from several populations were available for a given species, we used the median of each trait. We used species-specific male body mass instead of shoulder height as in Clutton-Brock et al. (1980) because body mass is most frequently reported in empirical studies. Our allometric relationship then reads $Y = Y_o \times BM^b$, where Y is the independent variable (antler length), BM is the species-specific male body mass, Y_o is the normalization constant and b is the allometric exponent. As this allometric relationship links a length (AL, equation-dimension of 1) with a volume (BM, equation-dimension of 3), a positive allometry between antler length and body mass is therefore observed for a slope (b) greater than 1/3. This is equivalent to a slope greater than 1 when plotting antler length (equation-dimension of 1) against shoulder height (equation-dimension of 1).

To test the influence of sexual selection on relative antler length, we used sexual size dimorphism, BGS, and mating tactic as proxies of its different components. Sexual size dimorphism, given as the residuals of the regression of male against female body mass on a log-scale (Ranta et al. 1994), is a synthetic variable that encompasses the intensity of both intra- and inter-sexual selection. We used breeding group size following Clutton-Brock et al. (1980) categorization (2, 3–5 and ≥ 6 animals) to assess the amount of intra-sexual competition due to party size. BGS counts the mean number of males and females by group during the mating period (it was unclear in Clutton-Brock et al. (1980) whether males belong or not to the so-called BGS). Finally, we only retained polygynous species because the number of monogamous species was too small ($n = 2$) to perform a reliable analysis. We considered three mating tactics: harem, territoriality and tending. The possible direct effect of mating tactic on relative antler length would represent the strength of intra-sexual competition independently of the BGS. In harem, males attempt to gather and defend a group of females. Territoriality includes a continuum from large territories with abundant food resources (either permanently or seasonally defended) to very small territories without any resources but females (lek). Finally, in tending, males mate with a succession of females without forming a harem. They guard a female, mate with her and once the female is no longer receptive, will look for another female. As male mating tactics may vary between populations within a species (Lott 1991), we retained for each species the mating tactic corresponding to the populations used for antler and mass measurement when this information was available. Otherwise, we used the most commonly reported mating tactic for each species.

Comparative analysis

To account for the phylogenetic inertia of phenotypic traits (Harvey and Pagel 1991), we used the strict consensus supertree established by Fernández and Vrba (2005) to extract branch length and to model relationships among species (Supplementary material Appendix 1). We followed Purvis and Garland's (1993) recommendation to deal with polytomies (i.e. unresolved nodes, $n = 3$) by correcting the number of degrees of freedom of the residual variance.

To test whether a pattern of similarity occurred among relative species (i.e. the occurrence of a phylogenetic signal) in antler length, male body mass and sexual size dimorphism, we used a randomization procedure (Blomberg et al. 2003) with 1000 permutations. We then ran both standard and phylogenetic analyses to test for the effects of sexual size dimorphism, BGS, and mating tactic on the allometric relationship between antler length and male body mass as

Table 1. Analyses of the effects of species-specific male body mass (BM), breeding group size (BGS), sexual size dimorphism (SSD), and mating tactic (MT) on antler length (AL) in 31 cervid species. k stands for the number of estimated parameters, LL is the maximum log-likelihood, ΔAICc indicates the differences of corrected Akaike's information criterion between two competitive models, and w_i provides Akaike weights. The selected model is in bold. We compared the fit of ordinary least square (OLS) and phylogenetic generalized least square models (PGLS) with AICc to assess the influence of phylogenetic inertia on the allometric relationship between antler size and body mass.

	OLS				GLS			
Model	k	LL	ΔAICc	w_i	k	LL	ΔAICc	w_i
Ln(AL)~Ln(BM)+BGS	**5**	**–15.6**	**0.00**	**0.38**	5	–22.7	14.2	0.00
Ln(AL)~Ln(BM)+BGS+MT	7	–12.16	0.34	0.32	7	–19.07	14.14	0.00
Ln(AL)~Ln(BM)+BGS+DIM	6	–14.82	1.55	0.18	6	–20.42	12.75	0.00
Ln(AL)~Ln(BM)+BGS+DIM+MT	8	–11.85	3.68	0.06	8	–16.89	13.77	0.00
Ln(AL)~Ln(BM)+DIM	4	–21.23	8.4	0.01	4	–22.65	11.25	0.00
Ln(AL)~Ln(BM)	3	–23.1	9.5	0.00	3	–24.85	12.99	0.00
Ln(AL)~Ln(BM)+MT	5	–21.04	11.21	0.00	5	–22.63	14.39	0.00

well as two-way interactions among these factors. Using ordinary least square method (OLS), we assumed no influence of phylogenetic inertia in the data (standard procedure), whereas using general least squared method (PGLS, Grafen 1989), we assumed a Brownian motion evolution of phenotypic traits. We used the Matlab program Regression ver. 2.M (Lavin et al. 2008) to perform all these analyses. To compare the different models, we computed the Akaike's information criterion corrected for small sample size (AIC_c) and the AIC_c weights (w_i) to assess the relative likelihood of each model to be the best among the fitted models describing our data (Burnham and Anderson 2002). Finally, to decipher the direct from the indirect (through BGS) effects of mating tactic on antler length relative to body mass, we performed a path analysis using a Bayesian framework (Gelman and Hill 2007, p. 503) with OpenBUGS 3.0.3 (Lunn et al. 2009). We fitted models entering BGS categories as a covariate and reported the median of posterior distribution and 95% credible intervals to assess effect sizes and their associated uncertainty (see Mysterud et al. 2008 for a similar approach). Model selection was based on credible intervals and on a deviance information criterion (DIC). DIC is an information theoretic argument (Spiegelhalter et al. 2002), which balances the fit of the model as estimated by a Bayesian measure of adequacy (i.e. the posterior mean deviance, Dbar) with the effective number of required parameters (P_D). Similarly to AIC, models with smaller DIC are preferred to models with larger DIC. When two competing models differed by less than 2, we retained the simplest model as recommended by Burnham and Anderson (2002).

Results

Phylogenetic effects

We detected a phylogenetic signal in male body mass ($p < 0.001$) and in antler length ($p < 0.001$) but not in sexual size dimorphism ($p = 0.650$). However, OLS models had an overall better statistical support than PGLS models (Table 1). We therefore based our subsequent analyses and inferences of antler length on the OLS method (see Cohas and Allainé 2009 for similar arguments). The effect sizes were, however, qualitatively the same whether an OLS or a PGLS modeling was carried out (Table 1).

Allometric models

The first and the second best models describing the interspecific variation in antler length (Table 1) had similar Akaike weights ($w_i = 0.38$ and $w_i = 0.32$). Following the principle of parsimony we retained the simplest model that included both the allometric effects of male body mass and BGS. The second best model included an additional effect of the mating tactic (Table 1). Sexual size dimorphism only had a negligible influence on the relative antler length compared to the effect of body mass and BGS as predicted from our second hypothesis.

We found a positive allometry between antler length and male body mass ($b > 1/3$), which held even after accounting for BGS, sexual size dimorphism and mating tactic (Table 2). The allometric coefficient was, however, smaller in the selected models ($b = 0.60 \pm 0.12$) than in the raw allometric relationship ($b = 0.99 \pm 0.09$). Thus, once body mass was accounted for, BGS (mainly), mating tactic and sexual size dimorphism (to a much lesser extent) all contributed to decrease the allometric exponent and so, to the positive allometry of antlers (Table 1, proportion of variance explained: BGS = 21%, MT = 7%, SSD = 4%). In accordance with our first prediction, species with small breeding groups (BGS = 2) had a smaller relative antler length for a given male body mass than species with large breeding groups (BGS > 5) (difference of 28.1 ± 7.5 mm; Table 2, Fig. 1).

In agreement with our third prediction, the path analysis provided evidence for an indirect effect of mating tactic on antler length through its co-variation with BGS (Table 3) but no support was found for a direct effect of mating tactic on relative antler length (difference in DIC between the models with and without a direct effect of mating tactic on antler length is 1.39 in favour of the simplest model, Table 3). In contradiction with the indirect effects of mating tactics, the estimated coefficients of the direct effects of mating tactics on antler length included 0 except for tending (Fig. 2). For a given body mass, species forming harems had larger BGS and higher relative antler length than tending species. Similarly, territorial species had smaller BGS than tending species (Fig. 2). Whatever the mating tactic considered, the relative antler length increased at the same rate with increasing BGS (i.e. no effect of the interaction term).

Discussion

Our results lent further support to the contention that sexual selection shapes the evolution of antlers of males in species of large herbivores (Kodric-Brown et al. 2006) but refine our understanding of which components of sexual selection are involved in this process. The positive allometry of antler size we obtained from the raw data (allometric coefficient of 0.99, n = 31) is consistent with previous works (0.86 in Gould 1973, n = 18; 0.78 in Clutton-Brock et al. 1980, n = 24). As male–male competition is expected to be stronger in polygynous species and because larger species are generally more

Table 2. Parameter estimates for the best model explaining the interspecific variation in antler length of 31 cervid species. AL stands for antler length, BM for species-specific male body mass, and BGS for breeding group size categories (small: two animals; medium: between three and five animals; large: more than five animals). We tested the estimated allometric coefficient against both the value of 0 (to assess the statistical significance of the relationship) and the theoretical value of 1/3 expected under the hypothesis of an isometric relationship between body mass and antler length.

Parameters for the best model: ln(AL) = a + b × ln(BM) + BGS	Estimate (sd)	p-value (test against 0)	p-value (test against 1/3)
a	3.77 (0.60)	< 0.001	–
b	0.60 (0.12)	< 0.001	0.035
Large vs medium	–0.25 (0.19)	0.209	–
Large vs small	–1.21 (0.30)	< 0.001	–

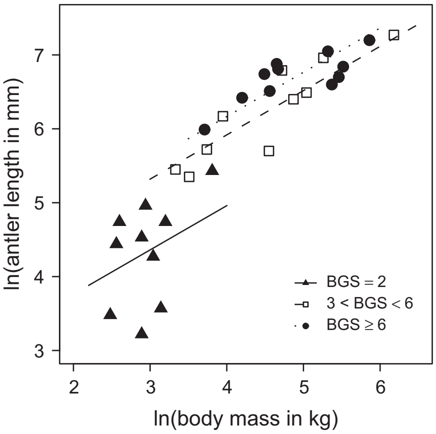

Figure 1. Observed and predicted allometric relationships of antler length in 31 cervid species. The best selected model included species body mass and the additive effect of breeding group size (BGS), see Table 2 for estimated parameters.

polygynous than smaller ones (Emlen and Oring 1977, Geist and Bayer 1988), large and polygynous species should bear relatively larger antlers than small and less polygynous ones if antlers evolved in response to sexual selection pressures.

The positive allometry of antler length remained even after accounting for BGS (Fig. 1). From our selected model including the additive effects of body mass and BGS, the allometric coefficient of 0.60 we found is close to 0.69; reported by Clutton-Brock et al. (1980) from the same model. Since the allometric coefficient we observed is still far greater than the value of 0.33 expected if only body size mattered, ecological or biological factors other than the BGS should also contribute to the positive allometry of antler size. Geist (1981) first suggested that larger species may have access to better resources by living in more open habitat or that they could have better digestion abilities than smaller species. These assets would allow males of larger species to assimilate more nutrients and could explain the remaining positive allometry. Moreover, females might use antler length as an honest signal of body condition (as shown in roe deer by Vanpé et al. 2007) to choose their mate. The possible role of inter-sexual competition (female choice) as a driver of the positive antler allometry remains to be clarified since this hypothesis, despite being less present in the literature could add an interesting contribution in the comprehension of antler allometry. If females would prefer large antlers, the best and largest males would spend more energy to have the largest antlers possible and this mechanism would explain a positive allometry. Finally, large animals might also be slower than small ones when fighting for mating (Blanckenhorn 2000) or when facing predators, and the development of large and forceful weapons could allow them compensating for a lesser agility (Geist 1981). This last hypothesis is, however, less satisfactory than the others since large animals tend to face lower predation risks than small ones (Sinclair et al. 2003).

Table 3. Analysis of the direct effects of mating tactic (MT) and breeding group size (BGS), and of the indirect effect of mating tactic through breeding group size on the relative antler length (${}_{r}$AL, antler length corrected for body mass) in 31 cervid species. As we used a Bayesian approach for the path analysis, model selection was based on the DIC (deviance information criterion). p_D provides an estimate of the number of parameters, Dbar is the posterior mean deviance (i.e. a measure of the adequacy of the model) and ΔDIC indicates the differences of DIC between two competing models. The best model (i.e. with the lowest DIC value) is in bold.

Model	Variable	p_D	Dbar	ΔDIC
Direct effect on ${}_{r}$AL	BGS	**7.284**	**90.39**	**0**
Indirect effect on ${}_{r}$AL (through BGS)	MT			
Direct effect on ${}_{r}$AL	BGS + MT	9.330	89.73	1.39
Indirect effect on ${}_{r}$AL (through BGS)	MT			
Direct effect on ${}_{r}$AL	BGS	5.043	110.00	17.43
Indirect effect on ${}_{r}$AL (through BGS)	–			
Direct effect on ${}_{r}$AL	BGS + MT	7.335	109.60	19.33
Indirect effect on ${}_{r}$AL (through BGS)	–			

Clutton-Brock et al. (1980) found that species belonging to the largest BGS category bore relatively larger antlers than species having low or average BGS. Our results based on 31 species rather suggest that species belonging to the smallest BGS category had relatively smaller antlers than species having average or large BGS and thereby minimize the role of BGS per se on the relative antler length of cervids. Our result emphasises on the importance of polygyny in the evolution of antlers. Indeed, highly polygynous species have larger antlers than weakly polygynous species, but the difference in BGS among species with BGS >2 only has little effect on the relative antler size. Moreover, the indirect effect of mating tactic on relative antler size we report here demonstrates that BGS not only includes the strict party size but also involves other components of sexual selection such as the tactic for forming groups. This analysis did not reveal a marked direct effect of mating tactic on antler length, although previous studies have suggested that direct fighting between males may be less important in territorial species than in species with dominance-based mating tactics such as harems (Hoem et al. 2007, Vanpé et al. 2008).

At the intra-specific level, mating systems (i.e. polygyny, polyandry, monogamy and promiscuity) are much less variable than mating tactics (i.e. tending, territoriality, harem, lek…). Mating tactics are difficult to predict and have been reported to change within a given species among populations, years and even males (reviewed by Lott 1991). For instance, variable mating tactics have been documented for fallow deer *Dama dama* (Thirgood et al. 1999), pronghorn *Antilocapra americana* (Byers and Kitchen 1988) and red deer *Cervus elaphus* (Carranza et al. 1995), while the mating system remained polygynous in all these study cases. Consequently, average antler length should vary more consistently in relation to the mating system than to the mating tactic at the inter-specific level and could explain the relatively greater effect of mating system than of mating tactic we observed.

Our results suggest that the relative antler length should primarily arise as the outcome of male–male competition on the whole. Antlers are probably used as weapons in male to male combats to assess one's opponent physical condition as well to avoid costly fights (Clutton-Brock 1982). For instance, antlers could be used to decrease the costs of male–male competition by avoiding imbalanced fights when the outcome is largely predictable (Hoem et al. 2007). Besides its role in the

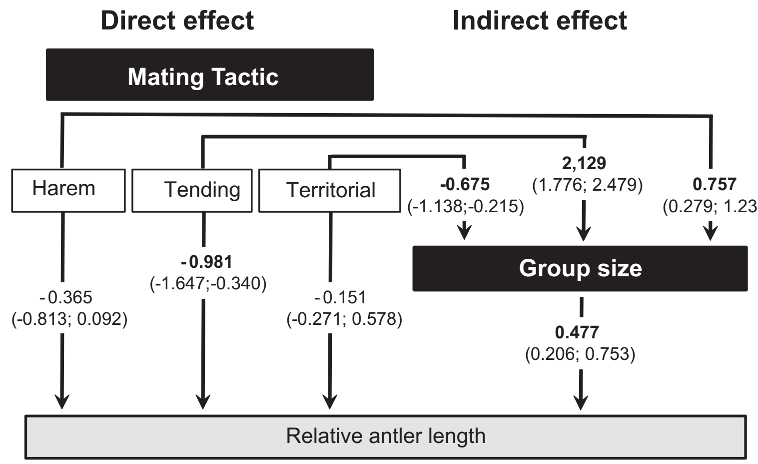

Figure 2. Path analysis of direct and indirect (through breeding group size) effects of mating tactic (tending, harem, territorial) on antler length controlled for body mass. Numbers on each arrow are the estimated parameters (in bold when statistically different from 0). Credible intervals at 95% are given within brackets. Tending is the reference mating tactic.

fighting behaviour of males, antlers could be used as an honest signal indicating male condition to its opponent (Vanpé et al. 2007) and maybe also to females (Malo et al. 2005). According to this hypothesis, antlers would have evolved in relation to BGS to diminish the cost of the access to females.

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Supplementary material (available online as Appendix O18934 at <www.oikosoffice.lu.se/appendix>). Appendix 1