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# Evolutionary allometry reveals a shift in selection pressure on male horn size

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**RUNNING HEAD:** Horn size evolutionary allometry in Bovids

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## Abstract

How selection pressures acting within species interact with developmental constraints to shape macro-evolutionary patterns of species divergence is still poorly understood. In particular, whether or not sexual selection affects evolutionary allometry, the increase in trait size with body size across species, of secondary sexual characters, remains largely unknown. In this context, bovid horn size is an especially relevant trait to study because horns are present in both sexes, but the intensity of sexual selection acting on them is expected to vary both among species and between sexes. Using a unique dataset of sex-specific horn size and body mass including 91 species of bovids, we compared the evolutionary allometry between horn size and body mass between sexes while accounting for both the intensity of sexual selection and phylogenetic relationship among species. We found a non-linear evolutionary allometry where the allometric slope decreased with increasing species body mass. This pattern, much more pronounced in males than in females, suggests either that horn size is limited by some constraints in the largest bovids or is no longer the direct target of sexual selection in very large species.

*Keywords:* non-linear allometry, weapons, ungulates, constraint, ornaments.

## Introduction

Morphological traits vary markedly in size both within and among species, and a large part of this variation results from the allometric relationship linking trait size and body size. In general, allometric relationships allow assessing the proportional increase in the size of a focal trait with a proportional increase in the size of the whole organism. These relationships are particularly important because they correspond to fundamental developmental properties that determine the size distribution of traits both within and among species (Gould, 1966; Pélabon *et al.*, 2014). The link between allometry and development was first established by Huxley (1932) who showed that when the growth of a trait Y and of body size X is under the control of a common regulating factor, X and Y are linked by the power function:

$$Y = \alpha X^{\beta} \quad (1)$$

referred to as allometry (see also Savageau, 1979). On a log-log scale, this relationship is linear:

$$\mathrm{Ln}(Y) = \mathrm{Ln}(\alpha) + \beta \mathrm{Ln}(X) \quad (2)$$

with $\mathrm{Ln}(\alpha)$ and $\beta$ representing the allometric intercept and allometric slope, respectively. In ontogenetic allometry (i.e. the allometry between traits measured on the same individual across developmental stages), the slope, β, describes how fast the trait Y grows proportionally to the increase in body size during ontogeny, and the intercept, α, corresponds to the ratio between X and Y at the origin (i.e. when X=0 on a log-scale). In static allometry (i.e. the allometry between traits measured at a given developmental stage across individuals), the slope represents the change in trait size relative to body size among individuals at similar developmental stage. The static allometric intercept, or elevation (for mean standardized body size, Egset *et al.*, 2011), represents the average trait size for an individual of average body size. Finally, in evolutionary allometry (i.e. the allometry between traits measured across species), the slope represents the change in the average trait size relative to the average body size across populations or species. Authors generally characterized allometry as positive and negative when the allometric slope β is larger or smaller than 1, respectively, and isometry when β equals 1. With positive and negative allometry, the shape of the organism (or species in the case of evolutionary allometry) changes with an increasing size, while it remains unaffected with isometry.

Secondary sexual characters often display positive static allometry (Petrie, 1988; Green, 1992; Kodric-Brown *et al.*, 2006; Bonduriansky, 2007; Voje, 2016). Several models have been proposed to explain this pattern (Bonduriansky & Day, 2003; Kodric-Brown *et al.*, 2006). In these models, resource allocation strategies interact with the intensity of sexual selection to determine the costs (in terms of survival) and benefits (in terms of reproductive success) associated with the trait size relative to body size, and shape the fitness landscape that determines static allometry. While a constant ratio between costs and benefits with a change in body size should generate an isometric relationship (β=1; i.e. size-independent ratio between trait size and body size), changes in the cost/benefit ratio with increasing body size should select for a static allometry different from isometry. In support, Bonduriansky and Day (2003) showed that positive allometry is expected to evolve when marginal fitness gains of a large trait increase with an increasing body size. Although still debated (Bonduriansky, 2007; Shingleton & Frankino, 2013; Fromhage & Kokko, 2014), these models provide a valid framework to explain patterns of static allometry in secondary sexual traits. However, these models involving selection at the within-population level cannot satisfactorily explain why secondary sexual traits should display positive evolutionary allometry (Gould, 1974; Rosenberg, 2002). Indeed, in evolutionary allometry, both genetic constraints (linking body size with a large range of phenotypic traits) and among species variation in selection pressure on the average trait size relative to the average body size should affect the allometric slope (Gould, 1966; Lande, 1979; Cheverud, 1982; Armbruster & Schwaegerle, 1996; Pélabon *et al.*, 2014).

Considering genetic constraints, variation in selection pressures or both, several scenarios can be suggested to explain why evolutionary allometry may differ from isometry (i.e. slope $\beta$=1). Assuming that the genetic correlation between trait size and body size constrains the direction of phenotypic evolution, Lande (1979, 1985) showed that selection on body size only should also generate an indirect response of the correlated trait resulting in an evolutionary allometry in the same direction as the static (genetic) allometry in the ancestral population. Therefore, if static allometry in the ancestral population is positive ($\beta$>1), due for example to the effect of sexual selection, the evolutionary allometry resulting from population or species divergence due to selection on body size should also be positive (Fig. 1 scenario A; see also Voje *et al.*, 2014). According to this model, the type of selection shaping static allometry in the ancestral population should affect the evolutionary allometric slope and we can expect sexually selected traits to display positive evolutionary allometry. In an extension of Lande's model, Zeng (1988) showed that selection on trait size, in addition to the selection on body size, could increase (positive selection on trait size; Fig. 1 scenario B) or decrease (negative selection; Fig. 1 scenario C) the slope of the evolutionary allometry compared to the static allometric slope (e.g. Thorén *et al.*, 2006). In these two cases, we do not expect any specific relationship between static and evolutionary allometry, and the slope of the evolutionary allometry should not reflect the type of selection acting on the trait at the within-population level, but instead the difference among species in the relative strength of selection on both traits. Accordingly, in a recent review, Voje *et al.* (2014) showed that, although static allometric slopes tend to change very slowly, evolutionary allometries are rarely similar to static allometries mostly because intercepts of static allometries evolve (see also Egset *et al.*, 2011, 2012; Bolstad *et al.*, 2015). In previous models, changes in the selection on body size and trait size have been assumed constant over the observed range of body size. This is not necessarily the case, however, and a non-linear increase or a decrease of the selection on trait size with increasing body size could generate a non-linear evolutionary allometry (e.g. Fig. 1 scenario D). Note that the static allometry may also change in a systematic way among populations or species in response to a change in body size (e.g. Rosenberg, 2002). This may occur, for example, when the allocation of resources to trait growth (measured either in terms of amount or duration) changes among species (Higginson *et al.*, 2015). These considerations underline the fact that positive (resp. negative) evolutionary allometries are not necessarily expected for traits displaying positive (resp. negative) static allometries. Still, for sexually selected traits, a positive evolutionary allometry could result from an increase in the strength of sexual selection acting on the trait of interest (ornament or armament) with an increasing body size.

Horn size in male Bovids is assumed to be under strong sexual selection (Darwin, 1871; Geist, 1966; Coltman *et al.*, 2002; Bro-Jørgensen, 2007; Emlen, 2008). However, the allometry of horn size in Bovids has been largely neglected compared to Cervids or other taxa (Clutton-Brock *et al.*, 1980; Emlen & Nijhout, 2000; Kodric-Brown *et al.*, 2006; Plard *et al.*, 2011; Voje *et al.*, 2014), and positive static allometry has been only reported for very few species (mountain goat, *Oreamnos americanus*, Côté *et al.*, 1998; African antelopes, Gould 1974). However, to the best of our knowledge, no study has yet investigated the shape and slope of evolutionary allometry between horn size and body mass across the whole range of Bovids. We filled this knowledge gap by analyzing sex-specific allometry in horn size and body mass across 91 species of bovids in order to understand better evolutionary allometry of an emblematic trait linked to sexual selection literature. The large range of variation in sexual size dimorphism across bovid species, the diversity of size and morphology of horns in bovids, and the fact that in about 70 % of the extant species (Lundrigan 1996) both sexes carry horns make this conspicuous trait particularly relevant to study sex-specific evolutionary allometry. Furthermore, previous studies have reported that relative male horn length is a reliable predictor of sexual size dimorphism (Jarman, 1983) and that the increase in sexual size dimorphism with body mass results from an increase in the intensity of sexual selection (Loison *et al.*, 1999). As suggested above, if sexual selection directly affects horn size relative to body size, and increases with body size, we may expect horn size to display a positive evolutionary allometry in male bovids (Fig. 1, scenario B), while a weaker allometric slope could characterize female bovids because horn size in females is not expected to be under sexual selection.

Moreover, recent theoretical and empirical studies have suggested that some curvatures in evolutionary allometry patterns might be more common than previously thought (MacLeod, 2010), notably for secondary sexual traits (Lemaître *et al.*, 2014). We thus test for such possible non-linearity in evolutionary allometry of bovid horn size. To further understand whether sexual selection affects evolutionary allometry in secondary sexual characters, we analyze, in both sexes, how differences in the intensity of sexual selection influence the shape and the steepness of the allometric relationship.

## Materials and methods

### Dataset

We obtained sex-specific body mass (in kg) and horn size (in cm) in free-ranging populations of bovids from Bro-Jørgensen (2007) (Table S1). The maximum length following the horn curvature was available in males for 91 species and in females for 54 species. The sampling difference between sexes is caused by the absence of horns in females of some species. We used the species' typical mating system obtained from literature (Table S1) to measure the intensity of sexual selection exerted on males of a given species. Three main types of mating system: monogamy (males and females mate with the same partner during a given reproductive bout), promiscuity (males and females mate with several partners with no continuing bond between individuals), and polygyny (males mate with several females while females mate with a single male during a given reproductive bout) (Clutton-Brock, 1989). Inter-male competition for mating is expected to be higher in polygynous and promiscuous species than in monogamous species. For 8 species we did not identify the mating system (Table S1) so these species have been removed for the analyses of allometric shape according to the intensity of sexual selection.

### Phylogeny

We controlled all analyses for phylogenetic inertia using phylogenetic generalized least-squares (PGLS) models (Freckleton *et al.*, 2002). This method provides an estimate of the phylogenetic signal "λ", which varies between 0 (phylogenetic independence) and 1 (species' traits co-vary in direct proportion to their shared evolutionary history). In this study, we built a phylogeny for the 91 species of bovids using a phylogenetic tree of ruminants published by Fernández and Vrba (2005) (Fig. S1-S4). This phylogeny resulted from a combination of morphological, ethological and molecular information of 197 species of extant and recently extinct ruminants. We also controlled the robustness of our results according to the phylogeny using Bininda-Emonds *et al.* (2007, 2008)'s mammal super-tree. This latter included only 85 of the 91 species from our dataset and we added in polytomy with closely related species each of the 6 missing species. Results were qualitatively the same as those obtained when using Fernández and Vrba (2005)'s phylogeny (Table S2) so we kept Fernández and Vrba (2005)'s phylogeny for the analyses. Analyses were performed using the R-package *caper* (Orme, 2012).

### Assessing the allometric relationship between horn size and body mass

We used log-transformed horn size and body mass to study their allometric relationship. Log-transformation of variables in allometric studies has been questioned (Packard, 2014, 2015), but estimates obtained from models fitted on arithmetic scale are difficult to interpret (Kerkhoff & Enquist, 2009; Glazier, 2013; Lemaître *et al.*, 2015). We thus fitted, for both sexes separately, two different models with log-transformed variables: a linear model and a quadratic model. We selected quadratic models over threshold models (e.g. Lemaître *et al.*, 2014) because the formers provide a better biological interpretation of the quadratic term as the progressive change in the allometric slope with increasing body mass instead of an abrupt change at a given body mass suggested by the threshold models. We estimated sex-specific allometries because PGLS models cannot be run with repeated measures for a same species. When looking at the allometric relationship between horn size and body mass in bovids without correcting for phylogeny (i.e. using a linear model), we indeed found evidence of between-sex differences in the allometric parameters (Table S3, Fig. S5). To test the effect of the intensity of sexual selection, both linear and quadratic models were fitted for each sex separately, in each group of mating system (monogamous, promiscuous and polygynous species). We expected body mass to increase three times faster than horn size because body mass is proportional to the volume of the animal while horn size is a linear measurement. Therefore isometry between horn length and body mass should correspond to an allometric slope of 1/3.

We selected models using the Akaike Information Criterion (AIC) and retained the model with the lowest AIC (Burnham & Anderson, 2002) and performed all the analyses with the R version 2.14.0 (R Development Core Team, 2011) and provided parameter estimates ± SE or 95% confidence intervals.

## Results

### Intersexual difference in evolutionary allometry

Overall we found a strong phylogenetic signal in the evolutionary allometry between horn size and body mass in both sexes across bovid species (Table 1). Males generally displayed longer horns than females both in absolute value and relative to body mass (Fig. 2). The evolutionary allometry between horn size and body mass in males was best described by a quadratic model (Table S4) with a decrease in the allometric slope with increasing body mass (Table 1). This indicates that the relative horn size increases more rapidly with body mass among small than among large species (Fig. 2). Among small species, the allometric slope was steeper than isometry ($\beta=0.76\pm0.04$ for a 10 kg bovid). Among the largest species, the evolutionary allometric slope tended to be lower than isometry ($\beta=0.24\pm0.06$ for a 850 kg bovid), isometry being reached for bovid species between 350 and 400 kg. We observed that in one species, the Nilgai (*Boselaphus tragocamelus*), males display unexpectedly small horns (19.5 cm) for their average body mass (253 kg) despite being subjected to intensive sexual selection (polygynous mating system). In comparison, male horns of the similar-sized Sable antelope (*Hippotragus niger*; 235 kg) are almost six times larger (122 cm). However, replicating the analyses without the Nilgai produced similar results (Table S5).

In females, the evolutionary allometry between horn size and body mass was linear and positive ($\beta=0.66\pm0.09$; Tables 1 and S4), indicating that females from large species display relatively larger horns than females from small species (Fig. 2). We noticed, however, that a non-linear model with a negative quadratic term still had some statistical support (Table S4). When the effect of sex on allometric shape was tested (using a simple linear model, see methods), we observed that the best model selected included an interaction between the sex and body mass (Table S3). For both sexes, the allometric shape was quadratic but the slope of the quadratic model decreased faster for males than for females (Fig. S5). It is noteworthy that between-sex differences in allometry led sexual dimorphism in horn size to peak for species of intermediate body mass (ca. 100 kg) and to decrease subsequently towards very large species (Fig. 2).

### Effect of sexual selection intensity on evolutionary allometric patterns

When estimated within groups of different mating system with contrasting intensity of sexual selection (i.e. monogamous, promiscuous and polygynous species), the evolutionary allometry in males tended to be linear within each group (Fig. 3A, Table S6). The allometric slope was positive ($\beta = 0.61$, 95% CI = 0.40; 0.82) for males of the monogamous species, but shallower and not different from isometry for polygynous species ($\beta = 0.38$, 95% CI = 0.23; 0.54, Fig. 3A, Table 2). When excluding the Nilgai from polygynous species, the best model selected remained the linear model (AIC of 8.09 for the linear model vs. 8.69 for the quadratic model; $\beta = 0.41$, 95% CI = 0.27; 0.55). Finally, for males of promiscuous species, the allometric slope was not different from 0 ($\beta = 0.11$, 95% CI = -0.18; 0.40), which indicates an absence of detectable allometric relationship between horn size and body mass for those species (Fig. 3A, Table S7). These results demonstrate that an increase in the level of sexual selection does not necessarily translate into steeper evolutionary allometry and therefore in larger horns relative to body size.

In females, the evolutionary allometry was linear whatever the mating system (Fig. 3B, Table S6). The allometric slope was steeper than isometry for both monogamous and polygynous species, but the slope in polygynous species tended to be shallower (monogamous $\beta = 0.67$, 95% CI = -0.03; 1.37; polygynous $\beta = 0.53$, 95% CI = 0.40; 0.67), although the relative horn size was larger in this group (Fig. 3B, Table 2). Notice that the large confidence interval that prevents the slope in the monogamous species to be statistically significant is due to the low sample size in this group. For females of promiscuous species, the allometric slope was not different from isometry ($\beta = 0.44$, 95% CI = 0.31; 0.56, Fig. 3B, Table 2).

## Discussion

Using an emblematic secondary sexual character in mammals, our findings highlight that evolutionary allometries of sexually selected traits are not necessarily positive, and can be explained by the strength of sexual selection. Indeed, the evolutionary allometry between horn size and body mass across bovid species is not linear and becomes shallower with increasing body mass. Consequently, a positive evolutionary allometry between horn size and body mass is only observed among species of small and intermediate size, the allometric slope being shallower than isometry for species above ca. 375 kg. In females, although a linear evolutionary allometry had the strongest statistical support, we also observed a tendency for a non-linear allometry less pronounced than the one observed in males. Including the intensity of sexual selection as a predictor variable, we observed that the change in slope with the degree of sexual selection associated with the increasing size follows the quadratic pattern observed when all the data are included. Horn size relative to body mass generally increases with the intensity of sexual selection, both in male and female horns, but the allometric slope decreases with increased strength of sexual selection. Remarkably, in species with promiscuous mating systems, male horn size does not consistently increase with body mass across species. In females, the slope of the evolutionary allometry is weak among the largest species in which males are exposed to high sexual selection.

MacLeod (2014) showed that the existence of upper and lower limits to the proportional allocation in testes mass in amniotes generated a sigmoidal allometry. He further argued that true allometric relationships were often misidentified because individuals or species occurring at the ends of the size range were little or not at all considered (MacLeod & MacLeod, 2009; MacLeod, 2010, 2014). In our study, non-linearity in the evolutionary allometry was partly generated by a change in allometric slope and intercept among heterogeneous groups of increasing body mass within bovids. A decrease in the allometric slope with increasing size has been previously reported in other taxa. For instance, Knell *et al.* (2004) found a quadratic allometry between mandible length and body size within the beetle genus *Lucanus*, and Lemaître *et al.* (2014) showed that antler length does not increase any further for cervid species heavier than ca. 100 kg. In both cases, the cost of growing very large ornaments was suggested to generate a constraint limiting ornament size in the largest species. A similar argumentation can be made here for bovid horns. Indeed, if the evolutionary allometry between horn length and body mass had remained linear with a slope equal to that observed for males of species weighing 50 kg ($\beta$=0.57), males of species weighing 600 kg should have carried horns of about 120 cm, compared to the 80 cm horn length observed in the Yak (*Bos grunniens*) who's body mass is about 600 kg (horn size one third smaller than expected under linear allometry). Therefore, a possible interpretation of our results is the existence of some constraints that prevent the largest species to display very long horns. As large herbivores are long-lived species for which survival is a key component of individual fitness (Gaillard *et al.*, 2000), it can be further suggested that such a constraint in the energy allocation to horn growth evolved to avoid the production of costly secondary sexual traits that could jeopardize survival. However, it is unlikely that horn growth in itself is energetically constrained because the actual cost of incremental annual horn growth over the years is likely to be very small, particularly during the prime-age stage (Toïgo *et al.*, 2013). Rather, large horns may be costly in terms of carrying and maneuvering and costly only indirectly for survival, and independently of the energy allocated to horn growth. Natural selection could thus constrain horn size to limit survival costs associated with bearing handicapping ornaments (Zahavi, 1975). Horn size may be also limited by biomechanical constraints. Long horns mean a high bending strength at the base, which may greatly increase the risk of breakage, as recently proposed by Ceacero (2016) to explain the decrease of allometric slope in Cervids (Lemaître *et al.*, 2014). However, in Bovids, horns are often twisted (e.g. addax) or rolled (e.g. mouflon) in large species. This should decrease the risk of breakage by increasing the bending force.

Alternatively, the change in evolutionary allometry in horn size may result from some shift in the traits targeted by sexual selection with increasing body mass. In medium-sized species like sheep sp. (i.e. Caprinae), horn size is the most important determinant of male reproductive success (Geist, 1966; Coltman *et al.*, 2002; Preston *et al.*, 2003) and thus corresponds to the main target of sexual selection. The reduced allometric slope in species with the largest body mass could also reflect a dominant role of body mass over that of horn size in these species. For instance, body mass is closely associated with mating success in male bison (*Bison bison*), whereas age is not (Wyman *et al.*, 2012). Body mass and mating system can be confounding factors in bovids because, as a general rule, large species are mostly polygynous while small species are mostly monogamous. When restricting our analysis to species weighing less than 375 kg (that corresponds to the threshold after which the allometric slope is less than isometry), we did not observe any statistically significant difference in allometric slope among species with different mating systems (Table S7 and Fig. S5). This additional finding indicates that the change in evolutionary allometry with an increasing body size we reported is most likely due to an effect of body mass per se and, hence, that there is no constraint on horn size for small- and medium-sized species whatever the mating system. As horn size grows over most of the lifetime while mass reaches an asymptote in the early prime-age stage, horn size is more tightly linked with age than body mass, which supports a dominant role of mass over horn size as determinant of male reproductive success in largest bovids. Indeed, male's horn size increases isometrically with female's horn size until female horn size reaches 32.5 cm (see Fig. 4). Beyond this threshold, male's horn size no longer increase with an increase in female's horn size. On the other hand, male's body mass increases isometrically with female's body mass throughout the entire range of female's body mass, without reaching any maximum body mass (Fig. 4). This pattern suggests that horn size is in some way limited at ca.120 cm (i.e. maximum size reached by horns of both sexes), maybe due to physical constraints, whereas no limit exists for body mass. Moreover, the linear and isometric relationship between female's and male's horn size could support the theory of a between-sex genetic correlation of horn size determination. Finally, sexually selected traits like horn size are often used as a proxy of the intensity of sexual selection assuming a positive and linear evolutionary allometry. Our findings highlight, however, that the evolutionary allometry of a sexual selected trait is not necessarily linear, and the shape of this allometry can be influenced by the strength of sexual selection exerted on the species. For horn size, we observed that this sexually selected trait cannot be directly used as a proxy of the strength of sexual selection in species under strong sexual selection. There is then a need for a careful study of the slope and shape of allometry before using any sexually selected trait as a relative measure of the strength of sexual selection across species.

Female horn size follows a linear and positive evolutionary allometry. As a consequence, females from very large species carry horns as long as males, and the sexual dimorphism of horn length peaks for species of intermediate size (see Fig. 2). Still, we also report a tendency for the evolutionary allometry in female horn size to be shallower among the largest species. Then, females from species with intense sexual selection carry larger horns relative to their body mass compared to females from species with weak sexual selection. This result partly supports the genetic correlation hypothesis (Darwin, 1871; Lande, 1980), which predicts that costly traits selected in males also evolve in females because both sexes share most of their genomes (e.g. Fairbairn & Preziosi, 1994; Fairbairn & Roff, 2006). This hypothesis suggesting that the genetic determination of horn size should be carried by autosomes is also supported by a study in Soay sheep (*Ovis aries*) (Johnston *et al.*, 2011). Therefore, when horns are present in females, sexual selection exerted on males also leads to increase the horn size of females through intersexual genetic correlation. This hypothesis is partly supported by the similar pattern of allometric relationship in both sexes we reported (Fig. S6).

## Conclusion

Our findings demonstrate that the evolutionary allometry between horn size and body mass is non-linear in male bovids because of a decrease of the allometric slope with increasing body mass. Such non-linear evolutionary allometry possibly reveals a shift of the target of sexual selection from horn size to body mass across species of increasing size. These results, in accordance with the

Scenario D in Fig. 1, suggest that the strength of sexual selection exerted on body size is partly decoupled from that exerted on secondary sexual traits. Finally, our findings challenge the widespread idea that the evolutionary allometry of sexual ornaments is linear and caution against using a sexually selected trait like horn size as a measure of the intensity of sexual selection without a careful assessment of the shape and strength of allometric relationships.

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**Table 1** Parameter estimates from the models selected to assess the allometric relationship between horn size and body mass (on a log-log scale) in males and in females of Bovid species. For both sexes **λ** was statistically different from 0, allowing parameters to be reliably estimated using PGLS models.

| | **Allometry** | | **Estimate** | **95% CI** | **λ** | **95% CI** |
|---|---|---|---|---|---|---|
| Males | Quadratic | Intercept | 0.296 | -0.526;1.116 | 0.982 | 0.852;1.000 |
| N = 91 species | | Body mass | 1.023 | 0.672;1.374 | | |
| | | Body mass$^2$ | -0.058 | -0.098;-0.018 | | |
| Females | Linear | Intercept | 0.316 | -0.561;1.194 | 0.689 | 0.420;0.889 |
| N = 54 species | | Body mass | 0.661 | 0.478;0.844 | | |

**Table 2. Parameter estimates from the model selected to assess the allometric relationship between horn size and body mass in males and females of Bovid species for each mating system.** For males, **λ** was statistically different from 0 (95% confidence interval (CI)) whatever the mating system, allowing parameters to be reliably estimated using PGLS models. For females, the lambda was not statistically different from 0 and parameters were reliably estimated from simple linear models. Allometric slopes statistically different from 1/3 (i.e. different from isometry) occur in bold.

| | **Allometry** | | **Estimate** | **95% CI** | **λ** | **95% CI** |
|---|---|---|---|---|---|---|
| **Males** | | | | | | |
| *monogamous* | Linear | Intercept | 0.718 | 0.171;1.265 | 0.668 | 0.06;1.00 |
| *(22 species)* | | Body mass | **0.612** | 0.403;0.822 | | |
| *promiscuous* | Linear | Intercept | 3.508 | 1.967;5.048 | 0.909 | 0.21;1.00 |
| *(25 species)* | | Body mass | 0.111 | -0.179;0.401 | | |
| *polygynous* | Linear | Intercept | 2.053 | 1.280;2.825 | > 0.999 | 0.91;1.00 |
| *(35 species)* | | Body mass | 0.381 | 0.226;0.536 | | |
| **Females** | | | | | | |
| *monogamous* | Linear | Intercept | -0.432 | -2.300;1.436 | < 0.001 | 0.00;1.00 |
| *(9 species)* | | Body mass | 0.670 | -0.034;1.374 | | |
| *promiscuous* | Linear | Intercept | 1.483 | 0.897;2.069 | < 0.001 | 0.00;0.87 |
| *(19 species)* | | Body mass | 0.437 | 0.310;0.563 | | |
| *polygynous* | Linear | Intercept | 1.293 | 0.716;1.870 | < 0.001 | 0.00;0.76 |
| *(19 species)* | | Body mass | **0.534** | 0.400;0.668 | | |

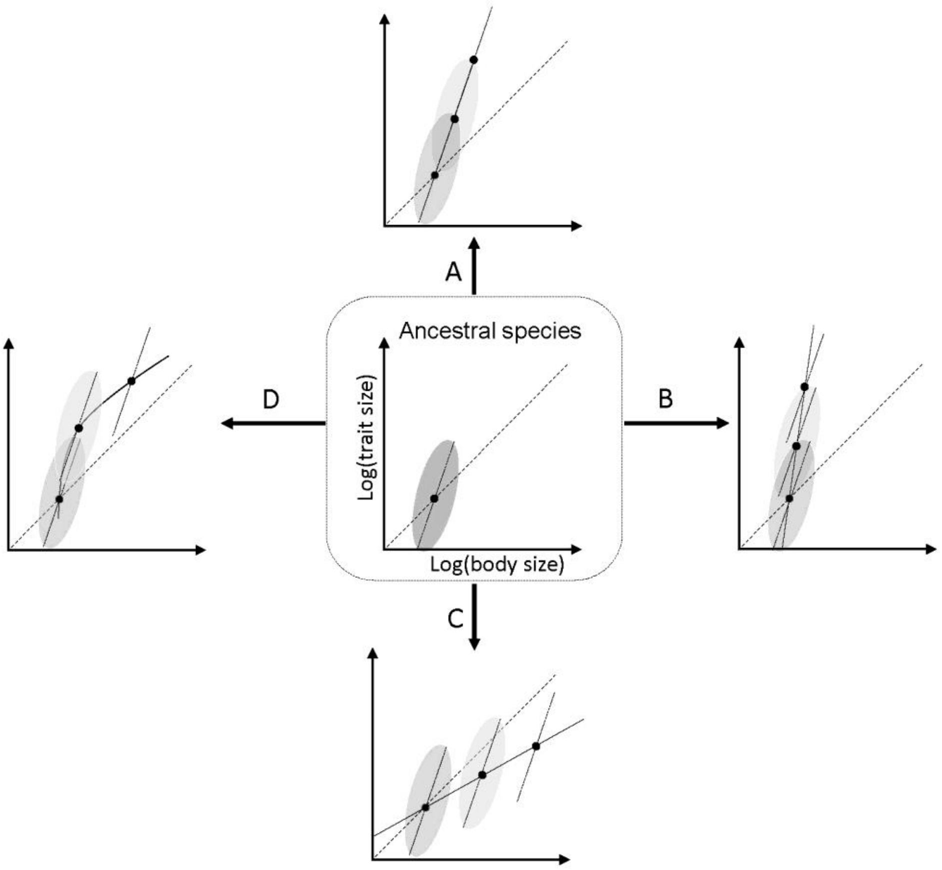
## Figures' legend

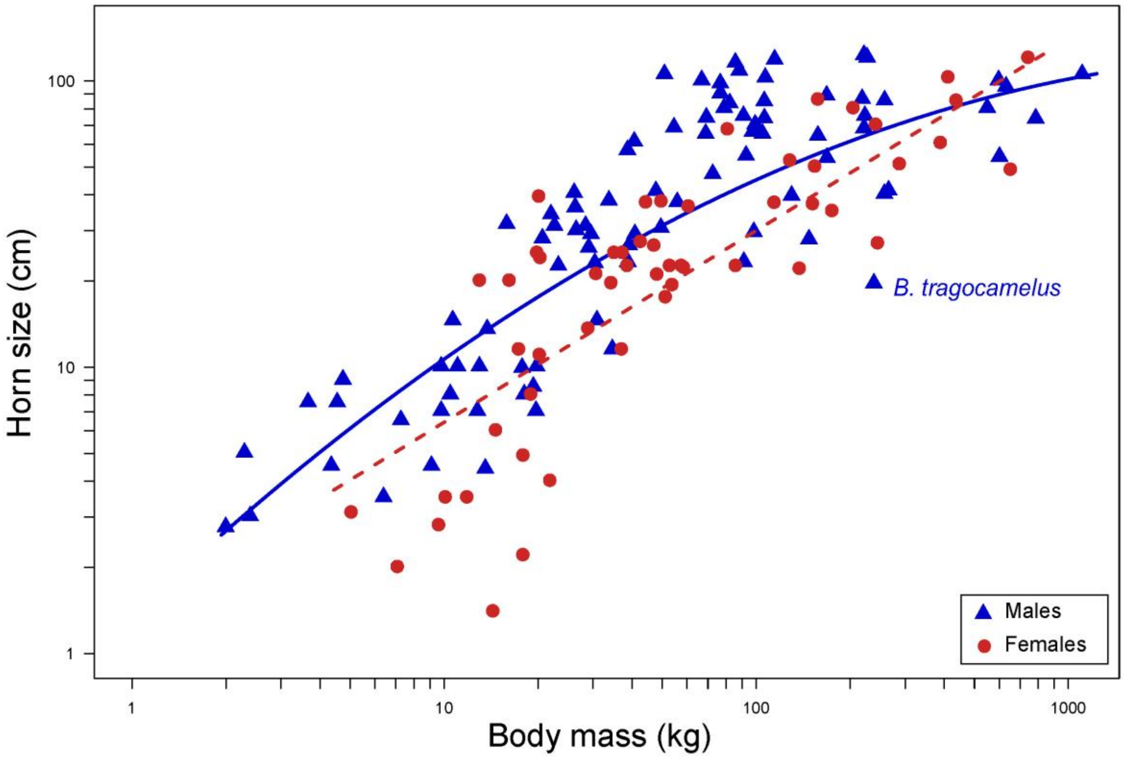
**Figure 1** Different types of evolutionary allometry originating via species diversification from a single ancestral species. The ancestral species in the central panel displays a positive static (genetic) allometry (dark grey ellipse, dashed line) with a slope steeper than isometry (large dashed line). The species mean log(trait size) and log(body mass) is represented by a black dot. In scenario A, directional selection on body size generates an evolutionary allometry (solid line) among divergent species with scaling coefficient (intercept) and factor (slope) similar to the static allometry. Additional selection on trait size generates an increase (positive selection, scenario B) or a decrease (negative selection, scenario C) of the evolutionary allometric slope. In scenario D, the selection on the relative trait size changes with an increasing body size, which generates a non-linear evolutionary allometry.

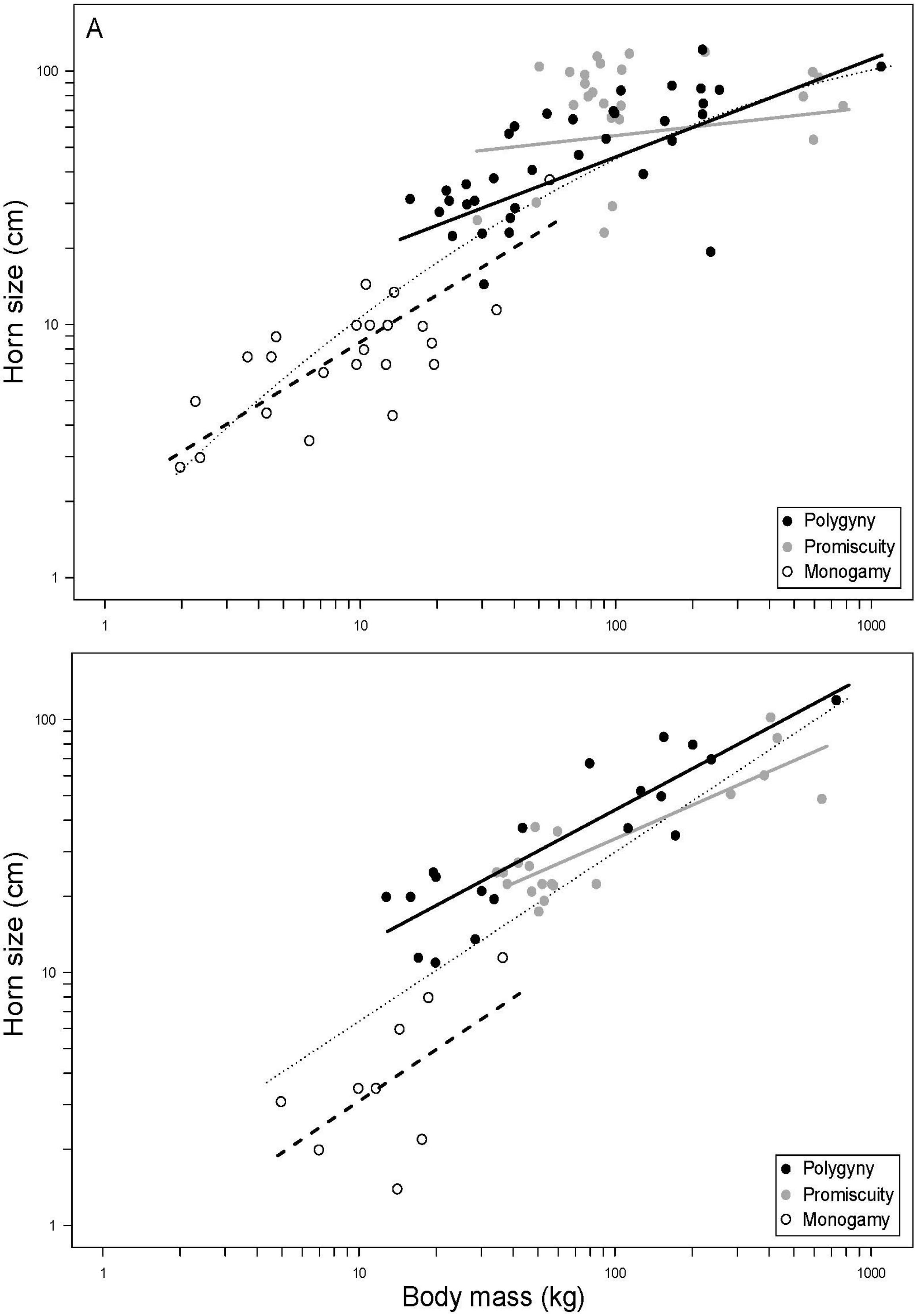
**Figure 2** Allometric relationship between horn size and body mass (on a log-log scale) in male (triangles, 91 species, solid line) and female (circles, 54 species, dashed line) bovids. For males, the evolutionary allometry is non-linear, positive for small body mass, and the allometric slope decreases with increasing body mass. For females, the evolutionary allometry is linear and positive. Models are corrected for phylogenetic relatedness among species while dots correspond to raw data without any correction for phylogenetic relatedness.

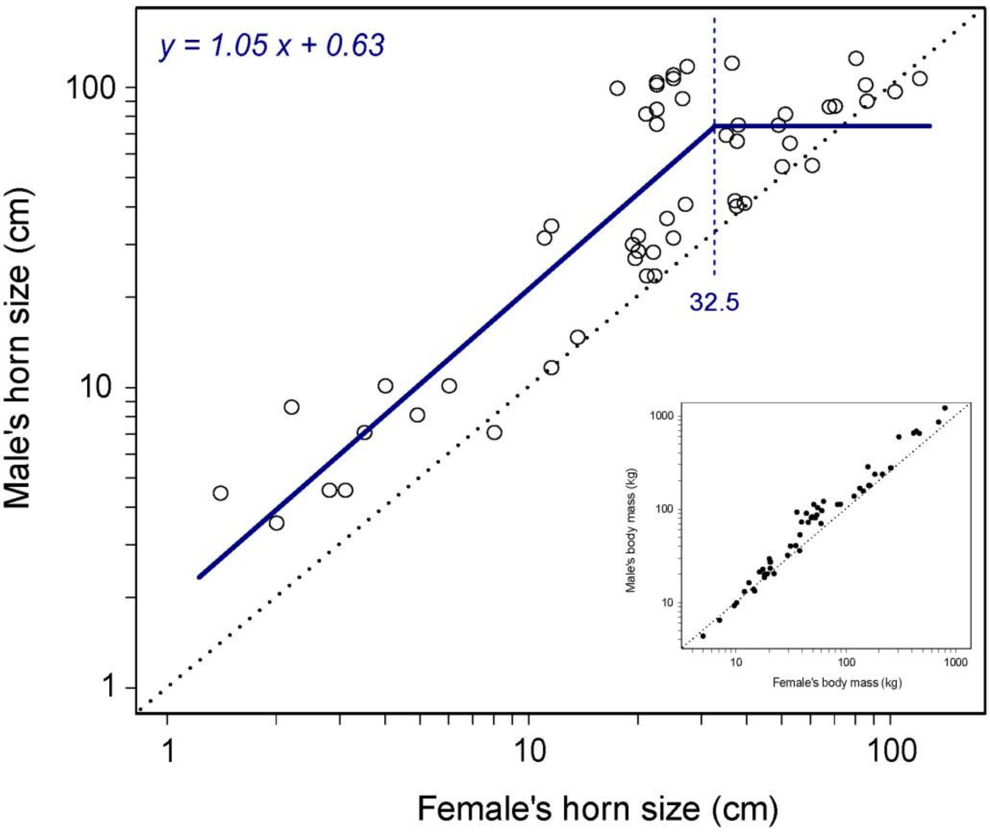
**Figure 3** Allometric relationship between horn size and body mass (on a log-log scale) in (A) male (83 species) and (B) female (47 species) bovids in relation to the mating system with monogamous (dashed black line), promiscuous (grey line), and polygynous (solid black line) species. For males, the allometric slope decreases from monogamous to promiscuous species with isometry for polygynous species. For females the allometric slope is higher than 0.33 but slightly decreases from monogamous to promiscuous species with an intermediate slope for polygynous species. Models are corrected for phylogenetic relatedness among species while circles correspond to raw data. General models obtained for each sex are indicated (dotted lines).

**Figure 4** Relationship between male's and female's horn size (on a log-log scale) for 54 bovid species (solid line). Isometry is indicated by the dotted line ($\beta$=1). An isometric relationship is observed between sexes when females of the species had horn size less than 32.5 cm and beyond this threshold male horn size is no longer related to females' horn size, whereas the relationship is isometric between male's and female's body mass.


Ancestral species
Log(trait size)
Log(body size)
A
B
C
D


Horn size (cm)
100
10
1
Body mass (kg)
1
10
100
1000
B. tragocamelus
▲ Males
● Females


A
Horn size (cm)
100
10
1
1
10
100
1000
● Polygyny
● Promiscuity
○ Monogamy
Horn size (cm)
100
10
1
1
10
100
1000
Body mass (kg)
● Polygyny
● Promiscuity
○ Monogamy


y = 1.05 x + 0.63
100
10
1
Male's horn size (cm)
32.5
1
10
100
Female's horn size (cm)
1000
100
10
Male's body mass (kg)
10
100
1000
Female's body mass (kg)