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The evolution of fighting structures in hartebeest

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ABSTRACT

Question: Is sexual selection for the evolution of larger horns and related fighting structures opposed by food constraints in bovids?

Data studied: Horn circumference and length, pedicel height, skull weight, and body size (skull length) were measured on 382 skulls belonging to all eight hartebeest subspecies (*Alcelaphus* spp.). We used mean group size and length of the breeding season for each subspecies as surrogates for the intensity of sexual selection through the potential for polygyny; mean annual rainfall and index of seasonality of each subspecies range quantified habitat primary production. The phylogeny of the hartebeest tree and the branch lengths were based on Flagstad *et al.* (2001).

Search methods: *Within- and across-taxa variation in fighting structures:* One-way analysis of variance and independent sample *t*-tests. *Phylogenetically uncorrected:* Dimorphism, as Log (M/F), regressed against independent variables (surrogates of sexual selection and habitat productivity, plus Log female size to check for allometry) with stepwise regressions weighted by the sample size of specimens measured for each ssp. *Phylogenetically corrected:* Independent contrasts using the program CAIC (Purvis and Rambaut, 1995).

Conclusions: The length of the breeding season was the only predictor for dimorphism in pedicel height and skull weight and the best, albeit non-significant, predictor for horn circumference. Only mean annual rainfall predicted horn length dimorphism. Thus, taller pedicels and heavier skulls appear to be under sexual selection, while natural selection seems to affect the evolution of fighting structures by limiting investment in longer horns. We argue that the pedicel, by increasing the defence to the head during clashes, might reduce the selective pressures on horns as protective structures.

Keywords: *Alcelaphus*, horns, natural selection, sexual dimorphism, sexual selection.

INTRODUCTION

The horns of bovids are remarkably diverse in shape and size (MacDonald, 2001), and their function has been long debated. It has been suggested that they evolved for anti-predator

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defence, as display structures that advertise individual quality, or as weapons in contests with conspecifics for access to mates (reviewed in Geist, 1966). Although horns are occasionally employed against predators, there is good evidence that their main use is in male intra-sexual competition (reviewed in Geist, 1966; Estes, 1991). Mechanical analyses of the forces incurred during fighting showed that horns with greater basal diameter are more able to resist strong clashes: species in which males adopt more forceful fighting styles, such as sheep and goats, have larger horns at the base, relative to their body weight, than species in which agonistic encounters are less intense, such as the neotragines (Schaffer and Reed, 1972; Kitchener, 1985, 1988). Furthermore, in Soay sheep (*Ovis aries*), heavier rams with relatively longer horns for their size achieve higher reproductive success (Preston *et al.*, 2003). All this evidence, together with a comparative analysis that showed that horn length in African antelopes increases with the potential for polygyny, as quantified using group size (Popp, 1985), supports Darwin's hypothesis (Darwin, 1871) that horns evolved under sexual selection.

Recent studies on the effect of environmental variation on individual development in wild populations have shown that a reduced food supply affects the phenotypic expression of both body size and horn dimensions (Toigo *et al.*, 1999; Le Blanc *et al.*, 2001; Festa-Bianchet *et al.*, 2004). In contrast to females that can compensate for a poor early growth by delaying their first reproduction, males are constrained from growing to a large adult size in years with scarce trophic resources; in addition, they appear to limit investment in horns (Toigo *et al.*, 1999; Le Blanc *et al.*, 2001; Festa-Bianchet *et al.*, 2004). As a result, dimorphism in both body and horn size is lower in cohorts of individuals born in unfavourable years, although horn size in the largest males is similar across cohorts, regardless of trophic resource availability (Festa-Bianchet *et al.*, 2004). These studies highlight the costs of maintaining fighting structures and suggest how natural selection may act on the evolution of weaponry, opposing or facilitating the investment in horns in relation to habitat productivity. In particular, they suggest that such selection pressures could result in the evolution of smaller horns in species living in poorer environments.

To our knowledge, no study has yet attempted to explain how variation in horn dimensions evolved within a single clade or to define the role of both natural and sexual selection. Because selection acts at a low taxonomic level, studying variation within species, or closely related species, is important to help understand the mechanisms that drive evolutionary changes and adaptation (Schluter, 2000). The hartebeest (*Alcelaphus* sp.), a monophyletic and young lineage of antelopes whose evolutionary pattern and phylogeny has been recently clarified using molecular techniques (Flagstad *et al.*, 2001), is particularly well suited for this investigation. Hartebeest diverged into eight allopatric subspecies (Flagstad *et al.*, 2001), belonging to two species (*A. buselaphus* and *A. lichtensteini*), and exhibit great variation in body size, horn shape and size (both sexes are horned), and colouration (Kingdon, 1997). They have colonized all the African savannahs from Morocco to the Cape (Sidney, 1965; Kingdon, 1997) (see Fig. 1), being able to live in diverse environments in terms of habitat structure and openness, seasonality, and primary production. A peculiarity of hartebeest is the presence of the pedicel, a bony and hollow structure that bears the horns (Kingdon, 1982; Vrba, 1997). The pedicel varies in size across subspecies, for example being very tall in Lelwel hartebeest (*A. b. lelwel*) but short and broad in Lichtenstein's hartebeest (*A. lichtensteini*) (Kingdon, 1997). According to Gosling (1975), this structure may increase the protection to the head during fighting by taking the impact point of clashes during fights farther away from the braincase. Moreover, Grubb (2000) suggested that not only more complex and thicker horns, but also taller pedicels and more robust skulls, could be an adaptive response to intense sexual selection. Heavier

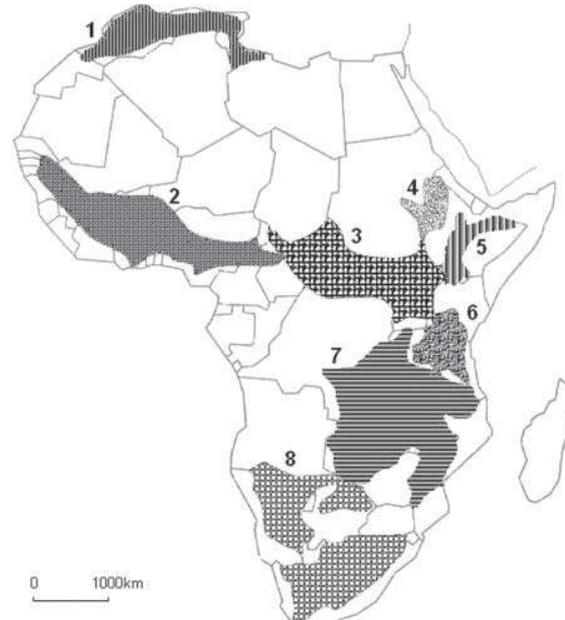


Fig. 1. Historical distribution (early twentieth century) of hartebeest subspecies across Africa. Subspecies are indicated as: (1) the extinct Bupal hartebeest (*A. b. buselaphus*) of North Africa; (2) Western hartebeest (*A. b. major*); (3) Lelwel hartebeest (*A. b. lelwel*); (4) Tora hartebeest (*A. b. tora*); (5) Swayne's hartebeest (*A. b. swaynei*); (6) Coke's hartebeest (*A. b. cokei*); (7) Lichtenstein's hartebeest (*A. lichtensteini*); (8) Red hartebeest (*A. b. caama*).

skulls might allow more forceful blows and provide better defence against the opponent's clashes (Geist, 1966).

We tested the hypothesis that horns, pedicel, and skull robustness are under sexual selection within the hartebeest group using dimorphism in these structures, since sexual selection tends to increase divergence between the sexes (Andersson, 1994). If sexual selection was the principal force responsible for variation in fighting structures, we predicted that dimorphism in fighting structures would be positively correlated with the potential for polygyny in space (i.e. group size, commonly used as a surrogate of the intensity of sexual selection) and negatively with the potential for polygyny in time (i.e. the length of the breeding season) across hartebeest subspecies. If natural selection played a role in the evolution of fighting structures, either opposing or favouring the investment in weaponry through the availability of trophic resources, we predicted that dimorphism in fighting structures would correlate positively with habitat primary production and negatively with seasonality, since more seasonal savannahs provide a less consistent food supply over the year (Bourliere, 1983).

METHODS

Basal horn circumference, horn length (along the frontal midline), pedicel height (from the middle point on the line connecting the superior edges of the orbits to the top of the

pedicel), skull weight, and basal skull length (from the anterior edge of the foramen magnum to the tip of the premaxillae) were measured on specimens for which subspecies, sex, and locality of collection were known, in nine museums and thirteen private collections (Table 1). Skull length and pedicel height were measured with a folding ruler, while a non-elastic plastic rope, commonly used for trophy records, was preferred for horn length and circumference because of its greater flexibility and ease of measurement over curves. Skull weight was measured with a spring balance on complete specimens. Only adults [specimens with the third molar erupted through the gum (Gosling, 1975)], were used, since some traits (e.g. horn dimensions) are not fully grown in sub-adults. As horn tips are worn with time due to horning the ground, old individuals, particularly males, have shorter horns than younger animals (Gosling, 1975; Kok, 1975). Therefore, only prime age specimens were considered for the analysis on horn length [those with light to moderately worn teeth (see details in Gosling, 1975)]. In contrast, horn circumference is not affected greatly by horning the ground and, in this respect, horns probably retain similar dimensions throughout life.

Altogether, 382 skulls (126 females, 256 males) representing all the hartebeest subspecies were measured (Table 1). Very small sample size in both sexes of Bubal (*A. b. buselaphus*: one female, two males) and in female Tora hartebeest (*A. b. tora*: one female) prevented their inclusion in all of the statistical analyses on variation within subspecies and sex (see below). Among all the specimens, 40 were prime age females and 85 were prime age males. However, no prime age Tora hartebeest males and only two female Swayne's hartebeest (*A. b. swaynei*) were present in the museum collections that we used. Hence these taxa were excluded from the analysis of variation in horn length. Finally, there were no complete female Bubal skulls, and only one male Bubal and female Tora hartebeest; thus these subspecies could not be included in the analysis of skull weight.

Table 1. Numbers of museum specimens measured for each hartebeest subspecies and sex

Subspecies	Females	Males
Bubal	2	3
Red hartebeest	48	93
Coke's hartebeest	15	38
Lelwel hartebeest	16	48
Lichtenstein's hartebeest	21	40
Western hartebeest	18	20
Swayne's hartebeest	5	8
Tora hartebeest	1	6
Subtotal	126	256
Total		382

Note: Specimens belonged to the Natural History Museum of London, Royal Belgian Institute and Museum of Natural Sciences of Brussels, Museum of Central Africa of Tervuren (Belgium), Museum für Naturkunde of Berlin, Senckenberg Museum of Natural History of Frankfurt, Museum National d'Histoire Naturelle of Paris, Museo di Storia Naturale La Specola of Florence, Museo di Storia Naturale of Milan, Museo di Storia Naturale G. Doria of Genoa. Thirteen private collections were also measured and included eleven collections at the Seeis Conservancy (Namibia), the private collections of L.M. Gosling and A.V. Oriani.

The dimensions of each trait were divided by skull length to correct for body size and, since ratios tend to deviate from normality, they were log-transformed before statistical analysis (Smith, 1999). Skull weight was divided by skull length cubed to ensure similar dimensionality. Skull length correlated with shoulder height (which was extracted from the literature) and could thus be used as a surrogate of body size (females: $F_{1,7} = 21.36$, $R^2 = 0.78$, $P = 0.004$; males: $F_{1,7} = 21.61$, $R^2 = 0.78$, $P = 0.004$). All of the resulting variables fulfilled the requirements for parametric statistics, and hence variation across subspecies within each sex was explored using one-way analysis of variance (ANOVA) and *post-hoc* Tukey's tests, and dimorphism within each subspecies using independent sample *t*-tests. Specimens with broken premaxillae could not be used in these analyses because a correction for body size could not be applied; however, they were included in the cross-taxa analyses, where estimates of mean trait values for subspecies and sex (see below) were used.

Dimorphism for each subspecies was computed as a male/female (M/F) ratio of trait dimension and the ratio was logged before being regressed against the independent variables (following Smith, 1999). Stepwise multiple regressions were first used to identify the best model, and then simple linear regressions allowed further assessment of the relative importance of each predictor. All regressions were weighted by sample size to give appropriate importance to those means estimated from larger samples. The analyses were replicated with phylogenetic independent contrasts to factor out similarity between taxa due to common ancestry (Harvey and Pagel, 1991; Garland *et al.*, 1992; Nunn and Barton, 2001) using the program CAIC (Purvis and Rambaut, 1995) and the tree and branch lengths provided in Flagstad *et al.* (2001). Regressions of contrasts were forced through the origin, after checking assumptions for contrast analyses (Harvey and Pagel, 1991; Garland *et al.*, 1992; Nunn and Barton, 2001). Because of the low sample size ($n = 8$ taxa) and the uncertain systematic position of the Bubal (Flagstad *et al.*, 2001), the results of both the conventional and phylogenetic analyses will be presented and discussed.

Variation in environmental conditions across ranges was assessed using data from climatic stations given in the tables of the Meteorological Office of Great Britain (1972) and Griffiths (1972). Mean annual rainfall was used as a surrogate of habitat primary production (Rosenzweig, 1968; Bourliere and Hadley, 1970; Bourliere, 1983), and an index was computed to represent seasonality (equation 1):

$$SI = \frac{\sum_{i=1}^{i=12} \left| \bar{X}_i - \left(\bar{R} / 12 \right) \right|}{\bar{R}} \quad (1)$$

where \bar{X}_i = mean rainfall in month i and \bar{R} = mean annual rainfall.

This index of relative seasonality [SI (from Walsh, 1981)] potentially ranges between 0.00 and 1.83, with higher values indicating greater seasonality. Climatic values were assigned to each specimen from the weather station closest to the locality of collection, after which means were calculated for each subspecies. Finally, mean female skull length (log-transformed) was used to determine whether there was an allometric effect of body size on dimorphism in fighting structures.

Mean group size, extracted from the literature, was used as the best available surrogate of the potential for polygyny in space, and thus as an index of the intensity of sexual selection. Data from different populations were averaged and each value weighted by its sample size or, where this was not recorded in the original publication, by the minimum value of 2 (as

this is the lowest number that could be used to obtain a mean). Males fight more fiercely and for longer in the presence of receptive females and at the beginning of the breeding season (Gosling, 1975; Clutton-Brock *et al.*, 1979), when the reproductive benefits are higher. Similarly, since the reproductive benefits for males of polygynous species, such as the hartebeest, are potentially greater when the breeding season is shorter (Gosling, 1986), mean length of the peak of the breeding season was used to represent the potential for polygyny in time. There are no data in the literature on breeding of the extinct Bubal of North Africa and Tora hartebeest of Ethiopia, and therefore the analyses involving this variable could employ only six taxa.

Because females tend to calve when the availability of trophic resources is high during lactation and weaning, the timing and length of the breeding season is dependent on environmental seasonality. Other factors, however, also have an influence on the length of the breeding season. For example, Estes (1966) suggested that the short (2–3 weeks) calving season in wildebeest (*Connochaetes taurinus*) is an anti-predator strategy that increases calf survival. We thus checked if our measure of seasonality (see above) correlated with the length of the breeding season across taxa. There was a non-significant negative correlation between these two factors (Pearson's correlation coefficient: $r = -0.33$, $n = 6$, $P = 0.519$). It thus follows that the length of the breeding season could be a more direct proxy for male intra-sexual selection in relation to the potential for polygyny in time, while the index of seasonality would better estimate the temporal distribution of trophic resources.

RESULTS

One-way ANOVA revealed significant differences in horn circumference across males ($F_{6,145} = 35.83$, $P < 0.001$) – *post-hoc* tests identified four subgroups – but none across females ($F_{5,70} = 1.62$, $P = 0.165$). Among males, Lichtenstein's hartebeest were distinct from all others, having the largest horn circumference; Lelwel hartebeest were similar to both Red (*A. b. caama*) and Western hartebeest (*A. b. major*), although these latter two subspecies were separated from each other; lastly, the eastern African clade formed a common cluster (Fig. 2a, b). The subspecies also differed in horn length (females: $F_{4,31} = 27.40$, $P < 0.001$; males: $F_{5,63} = 31.85$, $P < 0.001$) and exhibited similar trends in both sexes: Red hartebeest had the longest horns, followed by Western and Lelwel hartebeest together, and by the eastern African taxa (Fig. 2c, d). Pedicel height and skull weight varied significantly across subspecies also (pedicel height: females, $F_{5,63} = 15.98$, $P < 0.001$; males, $F_{6,137} = 6.26$, $P < 0.001$; skull weight: females, $F_{5,57} = 9.42$, $P < 0.001$; males, $F_{6,132} = 11.00$, $P < 0.001$). Two groups were identified with respect to pedicel height: of the males, Lelwel hartebeest were the largest and distinct from all others; of the females, Swayne's and Lichtenstein's hartebeest had the shortest pedicels (Fig. 2e, f). Regarding skull weight, female Red, Lelwel, and Western hartebeest formed a cluster separate from the eastern African group, and Lichtenstein's hartebeest lay in between (Fig. 2g). Among males, Red hartebeest had the heaviest skulls and the remaining taxa grouped together; Lelwel hartebeest were associated with both of these groups (Fig. 2h).

All subspecies exhibited significant sexual dimorphism in all traits (Table 2). Coke's hartebeest had the lowest dimorphism in horn circumference (M/F ratio = 1.22 before log-transformation) and Lichtenstein's hartebeest the greatest (1.48; Table 2). Dimorphism in horn length ranged between 1.05 in the Bubal and 1.43 in Lichtenstein's hartebeest; dimorphism in pedicel height ranged between 1.08 in Tora and 1.18 in Lichtenstein's

hartebeest. Lastly, skull weight dimorphism was the largest, varying from 1.63 in Coke's to 1.97 in Swayne's hartebeest (Table 2).

In the conventional cross-taxa analysis with stepwise multiple regression, the length of the breeding season was the only significant predictor for dimorphism in horn circumference ($F_{1,5} = 11.50$, $R^2 = 0.74$, $P = 0.03$; Fig. 3a), pedicel height ($F_{1,5} = 12.87$, $R^2 = 0.76$, $P = 0.02$; Fig. 3c), and skull weight ($F_{1,5} = 7.27$, $R^2 = 0.65$, $P = 0.05$; Fig. 3d). No predictor explained variation in horn length dimorphism across taxa; however, dimorphism in this trait exhibited a tendency to increase with mean annual rainfall ($F_{1,7} = 5.40$, $R^2 = 0.47$, $P = 0.06$; Fig. 3b). Simple linear regressions confirmed these results (Table 3).

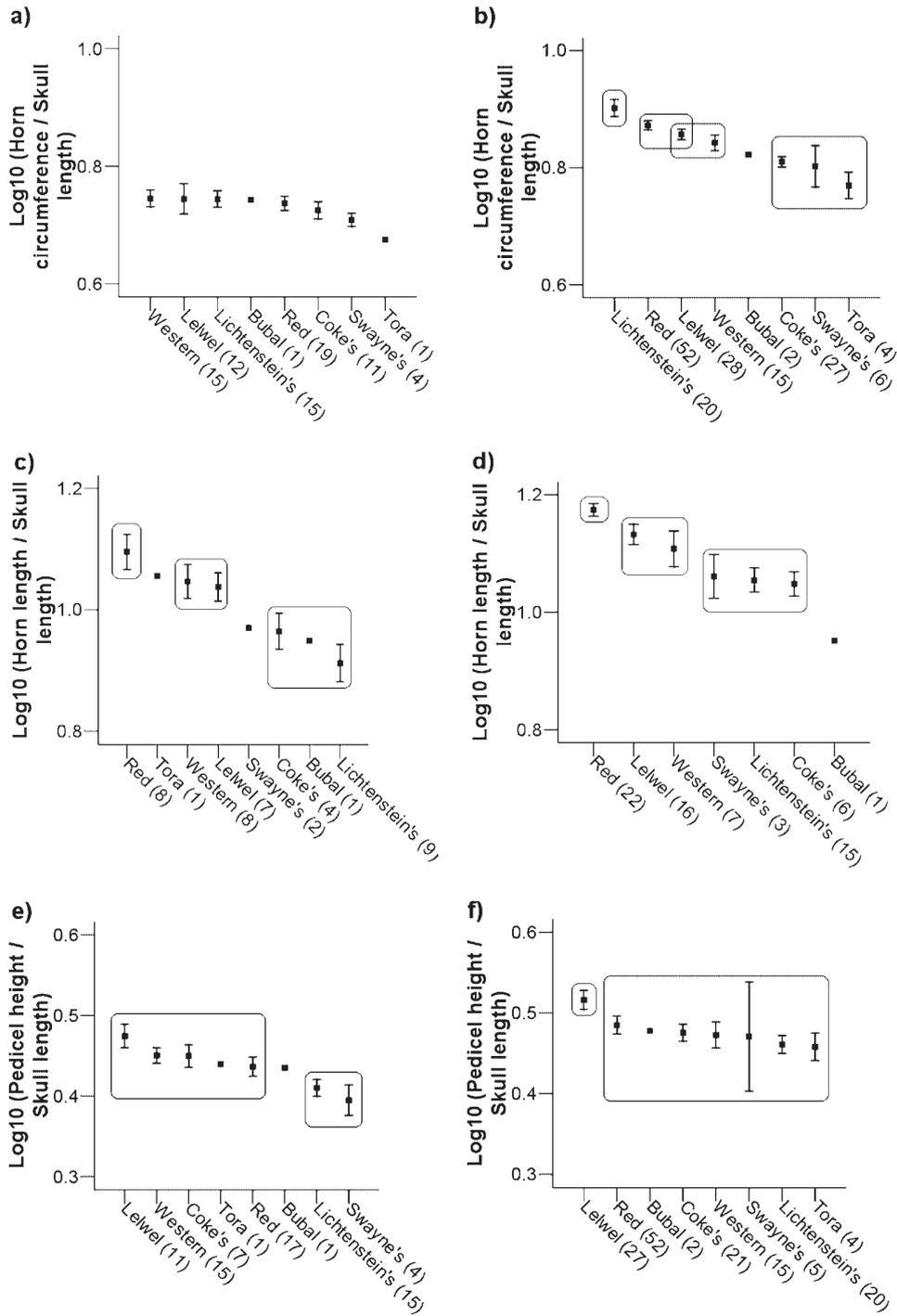
With phylogenetic independent contrasts, no variable could significantly explain dimorphism in horn circumference (Table 4). The length of the breeding season was still the best predictor for dimorphism in this trait, although it did not reach statistical significance ($F_{1,4} = 4.50$, $R^2 = 0.53$, $P = 0.10$). Conversely, the potential for polygyny in time explained dimorphism in pedicel height ($F_{1,4} = 47.89$, $R^2 = 0.92$, $P = 0.02$) and skull weight ($F_{1,4} = 18.87$, $R^2 = 0.83$, $P = 0.01$), while mean annual rainfall explained dimorphism in horn length ($F_{1,6} = 12.79$, $R^2 = 0.68$, $P = 0.01$; Table 4).

DISCUSSION

All the hartebeest subspecies exhibited sexual dimorphism in all traits. Males thus appear to invest relatively more than females in fighting structures, but to a variable extent, suggesting that selective pressures vary across taxa and sex. Broadly, two main subgroups could be identified within the genus, the first with the most heavily armed taxa (Lelwel, Red, Western, and Lichtenstein's hartebeest), and the second with the least armed (Swayne's, Coke's, and Tora hartebeest). However, some seemed to favour relatively greater investment in horns (Lichtenstein's and Red hartebeest), while others showed greater development of the pedicel (Lelwel hartebeest).

Our first hypothesis, that sexual selection promoted the evolution of fighting structures in hartebeest, was partially supported. In all traits, except horn length, the length of the breeding season was the best predictor of dimorphism, suggesting that sexual selection might promote the evolution of more armed structures in hartebeest males. In contrast, the results when using group size, a commonly used surrogate for the potential for polygyny in space, were non-significant in all the analyses. More specifically, the potential for polygyny in time predicted dimorphism in pedicel height and skull weight, especially after accounting for similarity across taxa due to common ancestry, and exhibited a negative trend with horn circumference. In hartebeest the pedicel, bringing the point of impact farther away from the braincase, might play an important role as a defensive structure during fighting (Gosling, 1975). Thus, if the pedicel is sexually selected, as our results suggest, this might also explain why dimorphism in horn circumference exhibited a tendency to increase with the length of the breeding season (although the correlation did not achieve significance). In fact, since the pedicel may have an additive effect to that of the horns in absorbing and dispersing the forces released during a blow, the presence of the pedicel might reduce the selective pressures for larger horn bases in these antelopes.

The hypothesis that skull robustness increases when sexual selection is more intense is also supported by the results pertaining to the length of the breeding season. Heavier skulls are thought to evolve in response to sexual selection because more robust skulls would be better able both to resist violent clashes and to deliver more forceful blows during fights



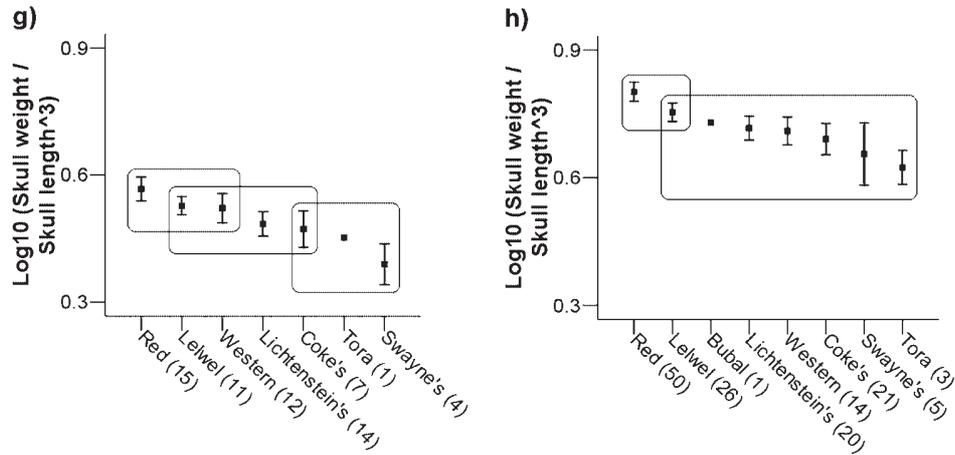


Fig. 2. Horn circumference (a, b), horn length (c, d), pedicel height (e, f), and skull weight (g, h) in female (left) and male (right) hartebeest (mean \pm 2 standard errors). Grouping follows the results of *post-hoc* testing: significant differences ($P < 0.05$) lie between groups but not within. Subspecies with small sample sizes are represented in the figures, although not included in the statistical analyses. Sample sizes are shown in parentheses.

Table 2. Dimorphism in fighting structures in each hartebeest subspecies

Subspecies	Horn circumference		Horn length	
Bubal	1.29	—	1.05	—
Red hartebeest	1.39	$t = 18.50, d.f. = 69, P < 0.001$	1.19	$t = 6.38, d.f. = 28, P < 0.001$
Coke's hartebeest	1.22	$t = 9.89, d.f. = 36, P < 0.001$	1.25	$t = 4.83, d.f. = 8, P = 0.001$
Lelwel hartebeest	1.38	$t = 10.30, d.f. = 38, P < 0.001$	1.32	$t = 6.24, d.f. = 21, P < 0.001$
Lichtenstein's hartebeest	1.48	$t = 15.35, d.f. = 33, P < 0.001$	1.43	$t = 8.02, d.f. = 22, P < 0.001$
Western hartebeest	1.31	$t = 9.90, d.f. = 28, P < 0.001$	1.19	$t = 2.98, d.f. = 13, P = 0.011$
Swayne's hartebeest	1.27	$t = 3.93, d.f. = 7, P = 0.006$	1.25	$t = 3.64, d.f. = 3, P = 0.036$
Tora hartebeest	1.26	—	—	—
Subspecies	Pedicel height		Skull weight	
Bubal	1.16	—	—	—
Red hartebeest	1.16	$t = 4.69, d.f. = 67, P < 0.001$	1.88	$t = 10.61, d.f. = 63, P < 0.001$
Coke's hartebeest	1.09	$t = 2.57, d.f. = 26, P < 0.001$	1.63	$t = 6.35, d.f. = 26, P < 0.001$
Lelwel hartebeest	1.15	$t = 4.04, d.f. = 36, P < 0.001$	1.92	$t = 12.49, d.f. = 35, P < 0.001$
Lichtenstein's hartebeest	1.18	$t = 6.54, d.f. = 33, P < 0.001$	1.85	$t = 11.22, d.f. = 32, P < 0.001$
Western hartebeest	1.11	$t = 2.40, d.f. = 28, P = 0.025$	1.70	$t = 7.86, d.f. = 24, P < 0.001$
Swayne's hartebeest	1.16	$t = 2.47, d.f. = 6, P = 0.049$	1.97	$t = 5.73, d.f. = 7, P = 0.001$
Tora hartebeest	1.08	—	1.69	—

Note: Dimorphism in horn circumference, horn length (only prime age individuals), pedicel height, and skull weight was first estimated as a ratio of male on female size (given here before log-transformation), while independent sample *t*-tests were carried out on the logged ratio of trait size on skull length.

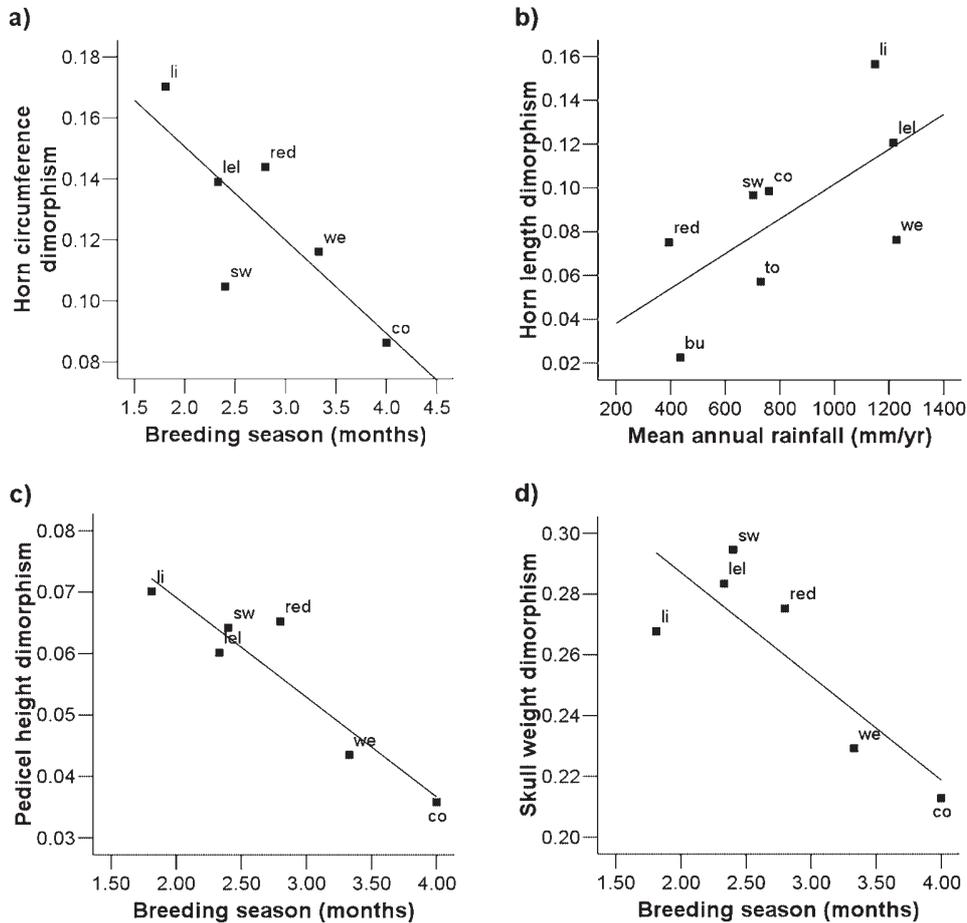


Fig. 3. Dimorphism in horn circumference with the length of the breeding season (a); horn length dimorphism in prime age individuals with mean annual rainfall (b); and dimorphism in pedicel height (c) and skull weight (d) with the length of the breeding season. Subspecies are indicated as follows: bu = Bubal; we = Western hartebeest; lel = Lelwel hartebeest; to = Tora hartebeest; sw = Swayne's hartebeest; co = Coke's hartebeest; li = Lichtenstein's hartebeest; red = Red hartebeest.

(Geist, 1966; Grubb, 2000). To our knowledge, no study has tested this hypothesis to date. However, in red deer (*Cervus elaphus*) antler weight correlates with fighting and mating success (Clutton-Brock *et al.*, 1982), even though such findings could be due to an intercorrelation between antler weight, body size, and body weight.

Contrary to our prediction, the potential for polygyny in space did not explain dimorphism in any trait. When testing similar hypotheses on the evolution of fighting structures across the bovids (Popp, 1985; Roberts, 1996) and cervids (Clutton-Brock and Albon, 1980), group size proved to be a good predictor of the differential investment in fighting structures across species and sex. The non-significance of group size in our study could be due to several factors. First, the quality of the data available in the literature was very variable. For example, although there is detailed modern information for Coke's and Swayne's

Table 3. Conventional cross-taxa analysis

	Group size	Length of breeding season (months)	Mean annual rainfall (mm · year ⁻¹)	Index of seasonality	Log female skull length
Horn circumference	$F_{1,7} = 0.07$ $R^2 = 0.01$ $P = 0.80$ —	$F_{1,5} = 11.50$ $R^2 = 0.74$ $P = 0.03$ Negative	$F_{1,7} = 0.30$ $R^2 = 0.01$ $P = 0.87$ —	$F_{1,7} = 1.97$ $R^2 = 0.25$ $P = 0.21$ Negative	$F_{1,7} = 0.33$ $R^2 = 0.05$ $P = 0.59$ —
Horn length	$F_{1,7} = 3.26$ $R^2 = 0.35$ $P = 0.12$ Positive	$F_{1,5} = 2.43$ $R^2 = 0.38$ $P = 0.19$ Negative	$F_{1,7} = 5.40$ $R^2 = 0.47$ $P = 0.06$ Positive	$F_{1,7} = 0.31$ $R^2 = 0.05$ $P = 0.60$ —	$F_{1,7} = 1.13$ $R^2 = 0.16$ $P = 0.33$ Positive
Pedicle height	$F_{1,7} = 0.36$ $R^2 = 0.06$ $P = 0.57$ —	$F_{1,5} = 12.87$ $R^2 = 0.76$ $P = 0.02$ Negative	$F_{1,7} = 0.20$ $R^2 = 0.03$ $P = 0.67$ —	$F_{1,7} = 1.16$ $R^2 = 0.16$ $P = 0.32$ Negative	$F_{1,7} = 0.04$ $R^2 = 0.01$ $P = 0.85$ —
Skull weight	$F_{1,7} = 1.54$ $R^2 = 0.24$ $P = 0.27$ Positive	$F_{1,5} = 7.27$ $R^2 = 0.65$ $P = 0.05$ Negative	$F_{1,7} = 0.11$ $R^2 = 0.02$ $P = 0.75$ —	$F_{1,7} = 0.20$ $R^2 = 0.04$ $P = 0.67$ —	$F_{1,7} = 0.02$ $R^2 = 0.01$ $P = 0.91$ —

Note: Simple linear regression of dimorphism in horn circumference, horn length, pedicle height, and skull weight with group size, length of the breeding season (months), mean annual rainfall (mm · year⁻¹), index of seasonality, and female skull length before applying phylogenetic correction. Variables highlighted in bold are included in the best model when using stepwise multiple regressions. All regressions were weighted by sample size.

hartebeest, in the case of Bubal and Tora hartebeest the data are restricted to records by early explorers. Such factors may have little effect on analyses at the family level where both morphological differences and variation in mating system and group size across taxa are large; but they could have a relatively strong effect in studies of intra-specific differences where such variation is smaller. More importantly, group size might not be the best surrogate of the potential for polygyny. In fact, although it is possible that the percentage of females within a group is similar across all hartebeest subspecies, group composition might vary significantly. Thus, detailed information on female numbers, which are not available at present for all hartebeest taxa, might be more appropriate. Similarly, better information about female movements between male territories and patterns of receptivity would improve estimates of polygyny potential. Finally, as suggested by Plavcan *et al.* (1995), group size might not adequately quantify the intensity of sexual selection acting on fighting structures. The frequency and intensity of fighting encounters are better predictors and have been used to explain the evolution of canine size dimorphism across primates (Plavcan *et al.*, 1995). Unfortunately, this kind of information, with rare exceptions, is not available for ungulates.

The hypothesis that natural selection would also influence the evolution of fighting structures found support in the analysis on horn length. In fact, contrary to the results at

Table 4. Phylogenetic analysis with independent contrasts

	Group size	Length of breeding season (months)	Mean annual rainfall (mm · year ⁻¹)	Index of seasonality	Log female skull length
Horn circumference	$F_{1,6} = 0.19$ $R^2 = 0.03$ $P = 0.68$ —	$F_{1,4} = 4.50$ $R^2 = 0.53$ $P = 0.10$ Negative	$F_{1,6} = 2.40$ $R^2 = 0.29$ $P = 0.17$ Positive	$F_{1,6} = 0.01$ $R^2 = 0.00$ $P = 0.93$ —	$F_{1,6} = 0.63$ $R^2 = 0.09$ $P = 0.46$ —
Horn length	$F_{1,6} = 0.13$ $R^2 = 0.02$ $P = 0.73$ —	$F_{1,4} = 1.07$ $R^2 = 0.21$ $P = 0.36$ Negative	$F_{1,6} = 12.79$ $R^2 = 0.68$ $P = 0.01$ Positive	$F_{1,6} = 0.00$ $R^2 = 0.00$ $P = 0.99$ —	$F_{1,6} = 3.00$ $R^2 = 0.33$ $P = 0.13$ Positive
Pedicle height	$F_{1,6} = 0.00$ $R^2 = 0.00$ $P = 0.98$ —	$F_{1,4} = 47.89$ $R^2 = 0.92$ $P = 0.02$ Negative	$F_{1,6} = 0.13$ $R^2 = 0.02$ $P = 0.73$ —	$F_{1,6} = 1.28$ $R^2 = 0.18$ $P = 0.30$ Negative	$F_{1,6} = 1.28$ $R^2 = 0.18$ $P = 0.30$ Positive
Skull weight	$F_{1,6} = 0.55$ $R^2 = 0.10$ $P = 0.49$ —	$F_{1,4} = 18.87$ $R^2 = 0.83$ $P = 0.01$ Negative	$F_{1,6} = 0.01$ $R^2 = 0.00$ $P = 0.94$ —	$F_{1,6} = 0.04$ $R^2 = 0.01$ $P = 0.85$ —	$F_{1,6} = 0.07$ $R^2 = 0.01$ $P = 0.81$ —

Note: Simple linear regression of phylogenetic independent contrasts of dimorphism in horn circumference, horn length, pedicle height, and skull weight with contrasts of group size, length of the breeding season (months), mean annual rainfall (mm · year⁻¹), index of seasonality, and female skull length. Variables highlighted in bold were the significant predictors. All phylogenetic regressions were forced through the origin (Harvey and Pagel, 1991; Garland *et al.*, 1992; Nunn and Barton, 2001).

the family level among bovids (Popp, 1985), horn length was not explained by either group size or length of the breeding season within the hartebeest group, but by mean annual rainfall, a surrogate of habitat primary production. This suggests that reduced trophic resource availability in poorer savannahs limits the investment in horn length, as observed within populations of bighorn sheep [*Ovis canadensis* (Le Blanc *et al.*, 2001; Festa-Bianchet *et al.*, 2004)] and Alpine ibex [*Capra ibex ibex* (Toigo *et al.*, 1999)]. In our study, we predicted that seasonality would show a negative correlation with dimorphism in fighting structures, since natural selection should facilitate investment in horns by males in subspecies living in less seasonal savannahs where grass availability is more consistent over the year. However, seasonality was always a poor predictor of dimorphism in all traits. Although it is possible that the index employed does not fully represent variation in seasonality across regions, it is more likely that seasonality has contrasting effects on the investment in weaponry. More seasonal habitats provide a less consistent food supply over the year, hence opposing the evolution of more massive fighting structures. On the other hand, the breeding season is shorter in more seasonal environments because trophic resources, important for lactating females, are limited in time (Gosling, 1969, 1986). Therefore, intra-sexual competition among males and

sexual selection may tend to increase in more seasonal savannahs, thus promoting investment in weaponry.

In conclusion, sexual selection appears to drive the evolution of horn circumference, pedicel height, and skull robustness in response to the potential for polygyny in time, which affects the intensity of intra-sexual competition among males. The pedicel is probably a morphological adaptation to increase the protection to the head during fighting and represents an alternative, or additional, defensive solution to the enlargement of the horn bases. Thus, selective pressures for larger horns might be less intense in the hartebeest than in bovid groups that lack a pedicel. Conversely, horn length appears to respond to variation in trophic resource availability, suggesting that natural selection has an important role in the evolution of horn dimensions. Group size is probably not a good predictor of the intensity of sexual selection when testing the hypothesis at the species level, and more detailed data are needed to help quantify the potential for polygyny in space and levels of male intra-sexual competition. Environmental seasonality probably generates opposing selective pressures and, overall, seasonality does not appear to influence the evolution of weaponry in this clade.

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