Evolutionary Ecology Research, 1999, **1**: 611–633

What factors shape sexual size dimorphism in ungulates?

Anne Loison,‡ Jean-Michel Gaillard,* Christophe Pélabon and Nigel Gilles Yoccoz§

Laboratoire de Biométrie, Génétique et Biologie des Populations, UMR CNRS 5558, Université Claude Bernard Lyon 1, F-69622 Villeurbanne Cedex, France

ABSTRACT

Studies of sexual size dimorphism among mammals have in the main focused on whether body weight, level of polygyny or ecological variables account for dimorphism patterns. Unfortunately, the use of different methods and indices of dimorphism has led to confusion and a failure to assess the relative role of the variables. We studied the effect of body weight, level of polygyny, feeding type and habitat type on sexual size dimorphism in ruminants. Three patterns emerged: first, dimorphism increases with body weight; second, this positive relationship is accounted for by the positive association between level of polygyny and weight; and third, the effect of feeding type is weak, and habitat type has no detectable effect. These results demonstrate that allometry is unimportant for shaping sexual size dimorphism in ungulates, and that degree of polygyny alone can almost entirely account for the phenomenon that sexual size dimorphism increases with increasing body size in ungulates. Level of polygyny increases with weight and this correlation leads to the observed positive correlation between weight and dimorphism when polygyny is not accounted for. The possibility that the relationship between weight and level of polygyny can be explained by density and spacing systems is discussed, and some other hypotheses concerning mechanisms of selection are presented.

Keywords: allometry, feeding habits, habitat, level of polygyny, sexual size dimorphism, ungulates.

INTRODUCTION

Sexual dimorphism in size is widespread among vertebrates (Short and Balaban, 1994). In mammals and birds, males are generally larger than females (Andersson, 1994; but see exceptions in Ralls, 1976). However, the degree to which the sexes differ in size varies tremendously across taxa, and several hypotheses have been proposed to account for this variability (Ralls, 1977; Hedrick and Temeles, 1989). Perhaps the best known is the theory of sexual selection (Darwin, 1871), whereby inter-male competition over access to females

* Author to whom all correspondence should be addressed. e-mail: gaillard@biomserv.univ-lyon1.fr
‡ *Present address*: Norwegian Institute for Nature Research, Tungasletta 2, N-7005 Trondheim, Norway.
§ *Present address*: Norwegian Institute for Nature Research, Department of Arctic Ecology, Storgata 25, N-9005 Tromsø, Norway.

means that larger males are more likely to obtain mates than smaller males. This results in selection for large male size, and could lead to subsequent divergence in male and female sizes, if no corresponding selection acts on females. The strength of selection for size dimorphism would depend on the intensity of competition among males (e.g. level of polygyny) and, accordingly, correlations between level of polygyny and dimorphism have been described in several groups of mammals (ungulates, Jarman, 1974, 1983; primates, Clutton-Brock, 1985; pinnipeds, Alexander *et al.*, 1979; rodents, Bondrup-Nielsen and Ims, 1990). However, other factors may also shape sexual size dimorphism (for reviews, see Hedrick and Temeles, 1989; Shine, 1989; Andersson, 1994): some may constrain size dimorphism (e.g. genetic correlation, energetic or feeding constraints), whereas others may favour increases in dimorphism (e.g. inter-sexual competition for food, increase in body weight).

Although hypotheses explaining dimorphism are not new, empirical results from mammals are still unclear. Many studies have been conducted in primates, but the results have been contradictory. For example, Leutenegger and Cheverud (1985) concluded that variation in dimorphism was primarily an allometric effect of evolutionary changes in body size (larger body size is associated with greater dimorphism), whereas Clutton-Brock (1985) emphasized the effect of level of polygyny (a higher level of polygyny is associated with greater dimorphism). In a recent review, Martin *et al.* (1994) adopted an intermediate position, finding that level of polygyny accounts for dimorphism when controlling for an unexplained allometric effect of body size (both larger body size and a higher level of polygyny are associated with greater dimorphism). In another group of large mammals, the ungulates, results have been equally inconsistent. While no quantitative studies on large data sets have yet been performed, reviews of dimorphism in ungulates have pointed to high correlations among ecological variables (e.g. habitat openness, diet), body size, size dimorphism and mating systems (Estes, 1974; Jarman, 1974, 1983; Leuthold, 1977). However, no single variable has been shown to contribute disproportionately to variation in sexual size dimorphism. These studies differed from those of primates in that they included a consideration of the role of habitat, as well as sexual selection (polygyny) and body weight (e.g. Geist and Bayer, 1988).

The use of different methods (Ranta *et al.*, 1994), and the lack of studies considering all variables simultaneously (Reiss, 1989; Webster, 1992), prevent a comprehensive assessment (e.g. in mammals) of the respective roles of allometry, level of polygyny and ecological variables in influencing the evolution of sexual size dimorphism. Hence, one cannot define and test specific mechanistic hypotheses which may explain how dimorphism patterns have evolved. Therefore, we assessed the relative influence on sexual size dimorphism of allometry, level of polygyny and certain ecological variables that are commonly used to explain dimorphism patterns. We restricted ourselves to ungulate species whose morphological attributes and other biological features have been studied extensively. We specifically addressed two questions: First, is dimorphism related to body weight? Second, can the relationship between dimorphism and weight be explained or modified when level of polygyny, feeding habits and/or habitat type are taken into account? We discuss our choice of methods as well as possible hypotheses concerning the evolution of sexual size dimorphism.

METHODS

Data and variables

We gathered data on 100 species (or subspecies) belonging to 54 genera, 25 tribes, 12 subfamilies and four families of the ruminant suborder (Appendix 1). Five variables, previously cited as possible causes of size dimorphism, were recorded: adult male body weight (MW), adult female body weight (FW), breeding group size (BGS; i.e. level of polygyny), feeding type (FED) and habitat type (HAB). We included body weight in our data set only when it was clearly stated in a paper that it was adult weight that was measured. Following Clutton-Brock *et al.* (1980), breeding group size was divided into three categories: breeding group size of 1 or 2 for monogamous species, breeding group size between 3 and 5 for weakly polygynous species, and breeding group size greater than 5 for highly polygynous species. For several species, level of polygyny varies across populations, over space or over time (Lott, 1991), and thus we classified species reported to have a breeding group size varying between 1 and 6 as weakly polygynous (BGS = 2). Values of breeding group size were based on the number of mates per male, the number of females per harem, or the number of females in mixed groups during the breeding period, depending upon the species and information given. Following Hoffmann (1989), whose classification was based on rumen morphology, three feeding types were distinguished: grazers, intermediate feeders and browsers. Similarly, we used the classification proposed by Jarman (1974) to attribute species to one of three categories of habitats: open, semi-open and closed. Species that were classified in the semi-open habitat use both open and closed habitat depending on the hour of the day or the season. When we had data for several populations of the same species, we took the mean for male and female weight in all but five cases; in these five cases, we used data from different subspecies (*Alcelaphus buselaphus*: three subspecies; *Antidorcas marsupialis*, *Cervus unicolor*, *Oryx gazella*, *Ovis canadensis*: two subspecies). We treated these subspecies as species in our study.

Analysis of dimorphism: Choice of method

First, we described patterns of dimorphism in two ways. (1) We recorded the distribution of male to female weight ratio at the generic level for the four families (Bovidae, Tragulidae, Antilocapridae and Cervidae) to describe the range of variation of dimorphism among ruminants. (2) We plotted the natural logarithm of male weight against the natural logarithm of female weight to analyse whether size dimorphism increased with female weight (see Martin *et al.*, 1994, for a similar approach) and we examined in each case which function (linear or quadratic) best described the observed patterns. We also used Spearman correlation coefficients to investigate if breeding group size, habitat type, feeding type and female weight were correlated.

Second, we assessed the relative contributions of variance in each of the four variables (breeding group size, weight, habitat and feeding types) to the variance in sexual size dimorphism. To do this, we had to decide how to measure dimorphism, because several measures are found in the literature. Recently, Ranta *et al.* (1994) recommended plotting male versus female weight on a log-transformed scale, and using the residuals from the regression between these two variables as a measure of size dimorphism. For example, to test the effect of level of polygyny on dimorphism, one could use a one-way analysis of

variance of residuals by categories of level of polygyny (see Martin *et al.*, 1994, for an application). Although this corresponds to the standard method in comparative studies of life history in which allometry has to be removed for scaling data (Western, 1979; Calder, 1984), it can be misleading for analyses of dimorphism, because (1) there is no functional relationship between weight and dimorphism (e.g. neither Calder, 1984, nor Peters, 1983, addressed this possible relationship in their reviews of allometry) and (2) this method does not take into account the possible interaction between weight and level of polygyny for shaping dimorphism. Because level of polygyny was a discrete variable with three modalities in this study, an effect of polygyny would not be detected by an analysis of residuals. Indeed, using residuals of the regression between male and female weight would not allow one to distinguish between the four evolutionary scenarios presented in Fig. 1. These four scenarios illustrate different ways by which weight and level of polygyny may account for size dimorphism. In three of the four evolutionary scenarios presented in Fig. 1 (b, c and d), polygyny is actually required to account for dimorphism. In Fig. 1a, weight alone accounts for body size dimorphism: whatever the level of polygyny, the relationship between male and female weight has the same slope and intercept. Thus weight is the only variable required to predict dimorphism. In Fig. 1b, polygyny alone accounts for body size dimorphism, and there is no effect of body size once level of polygyny is accounted for. For each level of polygyny, the line describing the relationship of male and female weight has a slope of 1. This corresponds to a 'grade effect' (Martin and Harvey, 1985), where there are different intercepts for each modality of the level of polygyny. In Fig. 1c and d, both weight and level of polygyny shape dimorphism patterns. In Fig. 1c, weight has the same effect at each level of polygyny, but the slope of the lines for each level is different from 1. As in Fig. 1b, this corresponds to a 'grade effect'. In Fig. 1d, the weight effect on dimorphism depends on the level of polygyny (the slopes of the lines differ between levels of polygyny; i.e. there is an interaction effect). We considered an observed relationship with a slope greater than 1 (bold line) to represent size dimorphism (e.g. Martin *et al.*, 1994).

To distinguish among these four cases, we used either analyses of covariance or multiple regression, depending on whether levels of discrete variables were considered qualitative or quantitative. These methods allowed us to take account of the possible effects of the variables, as well as possible interactions among these effects. We thus sought to account for variability in lnMW using four variables (one continuous, lnFW; and three discrete, BGS, FED and HAB), and the interaction between lnFW and BGS. We only investigated the effect of the interaction between female weight and breeding group size, because none of the other interactions were significant when tested. Our analysis followed three steps (Table 1). We first fitted a general linear model including all the variables as well as the interaction between lnFW and BGS. Second, we used a backward procedure, successively removing the interaction and then the main effects of factors except FW. Indeed, FW is required to measure the degree of sexual size dimorphism. Third, when significant, we tested for linearity of the effects of BGS, FED and/or HAB (for BGS, for example, we compared the model in which male weight is related to the three modalities of BGS with the model in which male weight increases linearly with increasing BGS). When these two models did not differ, we selected the linear model that was the most parsimonious. Finally, we tested whether dimorphism depends on weight (i.e. whether the slope of the regression between male and female weights differs from 1 when the effects of other variables are taken into account).

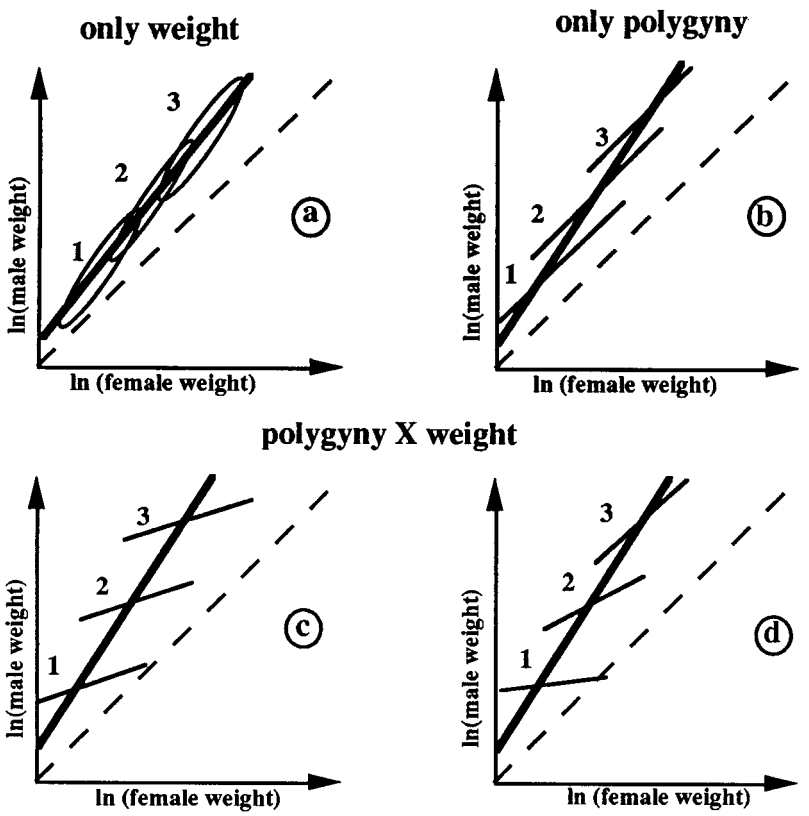

Fig. 1. Four situations representing possible relationships between male and female body weight. Monomorphism is represented by the dashed line (same weight for males and females) and the observed relationship by the bold line. If the slope is greater than 1, then male weight increases faster than female weight, which means that size dimorphism increases with weight. If the slope equals 1, then dimorphism is independent of weight. Level of polygyny is considered a categorical variable with three modalities, designated 1, 2 and 3 (see text for more details).

Comparative method

Because some species share a common phylogenetic history, their traits may be correlated, possibly leading to biased tests (e.g. Purvis *et al.*, 1994; Martins and Hansen, 1995). The dependence between points can artificially create clusters of points (i.e. species sharing the same traits because of close phylogenetic relatedness), and result in a misleading small estimate of variance causing the null hypotheses to be rejected too often. Nevertheless, this dependence does not result in biased estimates (e.g. Royall, 1986). One solution is to consider phylogenetic relatedness as a measure of point dependence (Felsenstein, 1985; see Gittleman and Luh, 1992, for a review of methods). One of the most useful methods (the independent contrast analysis method; Garland *et al.*, 1992) is derived from this concept. However, in our analysis, we did not use independent contrasts because regressions performed on contrasts must pass through the origin (e.g. Garland *et al.*, 1992) and so the intercept concept is lost. Therefore, using independent contrasts, it would not be possible to

Table 1. Procedure for selecting the model[a]

Analysis stage	Models compared
1. Test for an interaction between lnFW and (BGS)	lnFW + (BGS) + (FED) + (HAB) + lnFW·(BGS) *vs* lnFW + (BGS) + (FED) + (HAB)
2. Test for single effect	
(BGS)	lnFW + (BGS) + (FED) + (HAB) *vs* lnFW + (FED) + (HAB)
(FED)	lnFW + (BGS) + (FED) + (HAB) *vs* lnFW + (BGS) + (HAB)
(HAB)	lnFW + (BGS) + (FED) + (HAB) *vs* lnFW + (BGS) + (FED)
3. Test for linearity	
(BGS)	lnFW + (BGS) + (FED) *vs* lnFW + BGS + (FED)
(FED)	lnFW + BGS + (FED) *vs* lnFW + BGS + FED

[a] Discrete variables are in parentheses when their three modalities are used. Otherwise, variables are linearly related. lnFW·(BGS) designates the interaction between the natural logarithm of female weight and breeding group size.

discriminate between the four situations shown in Fig. 1. In particular, the 'only weight' model (Fig. 1a) would be non-dissociable from the 'only polygyny' model (Fig. 1b). Thus, to allow us to distinguish statistically between the four models in Fig. 1, we chose to use analysis of covariance to analyse our data (Bell, 1989; Harvey and Pagel, 1991). To avoid both overly inflated sample sizes at lower taxonomic levels (leading us to reject the null hypothesis too often) and drastic loss of degrees of freedom at higher taxonomic levels (making the tests too conservative), we chose to replicate the analyses at the three intermediate levels (genus, tribe and subfamily). These three levels are the best compromises between avoiding redundancy in the data and performing tests without enough degrees of freedom. Nested analyses of variance (Harvey and Pagel, 1991; Gittleman and Luh, 1992) were performed on male and female weight, habitat, feeding type and breeding group size, for five taxonomic levels (species, genus, tribe, subfamily and family), to check if most of the variability in these traits occurred at these three intermediate levels. We chose a taxonomy-based method rather than a phylogeny-based one because mammalian phylogeny is poorly understood (Benton, 1988), especially below the tribe level (see Geraads, 1992, for an example of several possible phylogenies below the tribe level in the Bovini). Moreover, we conducted an *a posteriori* check of our results against possible biases due to errors in taxonomy (see below).

Checking the validity of the analysis

We checked the validity of the analysis for possible biases due to taxonomy. In particular, we checked that residuals were randomly distributed across taxonomic levels (i.e. that the model was valid for each single taxonomic category), and that the relationship was not due to a few points from only a small number of taxonomic groups. We thus controlled for the validity of the model selected at each taxonomic level by analysing residuals and Cook's distances (Francis *et al.*, 1993). Residual analysis also allowed us to check the assumptions of the model (in particular, the linearity and normality of the residuals). To check that each

taxonomic group was correctly fitted, we tested whether residuals significantly differed among the taxonomic groups using one-way analysis of variance. For example, we tested whether the residuals of the selected model at the generic level differed significantly among tribe groups or subfamily groups. Cook's distance is a measure of the contribution of each point to parameter estimation and allowed us to control for effects due to influential points (Francis *et al.*, 1993). When a point had a high Cook's distance value relative to the others, we repeated the analysis without this point to determine if the model selected was the same. All analyses were performed with GLIM4 software (Francis *et al.*, 1993).

RESULTS

Taxonomic levels

For all variables, most variability is expressed among subfamilies within families (between 39% and 52%), and least variability among species within genera (Table 2). Intermediate amounts of variability can be partitioned into the family (about 15%), tribe (about 15%) and generic levels (about 17%). Although the appropriate level is at that of the subfamily, we also used genus and tribe because the subfamily level offers too few degrees of freedom to assess our biological problem. All subsequent analyses were therefore performed at the subfamily, tribe and genus levels.

Dimorphism patterns

The MW/FW ratios (Fig. 2) showed that, for a small number of genera, females are larger than males ($n = 8$, Appendix 1), and that for most genera, males are larger than females ($n = 43$). Dimorphism varied from 0.8 to 2.1. Both Bovidae and Cervidae show a large range of dimorphism values. The larger range observed for Bovidae may be due to the larger number of species studied.

At all three taxonomic levels, the relationship between lnMW and lnFW was significantly different from a linear relationship with a slope of 1 (Fig. 3). The hypothesis that dimorphism does not depend on weight can thus be rejected. At the generic level, the relationship is quadratic ($t_{51} = -2.67$, $P = 0.010$), whereas at the tribe and subfamily levels, the relationship is linear (tests for the quadratic relationship; tribe: $t_{22} = -1.34$, $P = 0.19$;

Table 2. Percent total variability in breeding group size (BGS), feeding type (FED), habitat (HAB), natural logarithm of male weight (lnMW) and natural logarithm of female weight (lnFW), expressed at each taxonomic level, and resulting from nested analyses of variance (each variance component was multiplied by 100 and divided by the total variance)

	BGS	FED	HAB	lnMW	lnFW
Among families	14.8	6.1	25.0	14.6	14.4
Among subfamilies	41.1	48.2	38.8	52.0	48.2
Among tribes	19.2	11.7	10.8	14.8	16.3
Among genera	15.1	22.2	20.8	12.0	13.2
Among species	9.8	11.8	4.6	6.6	7.9

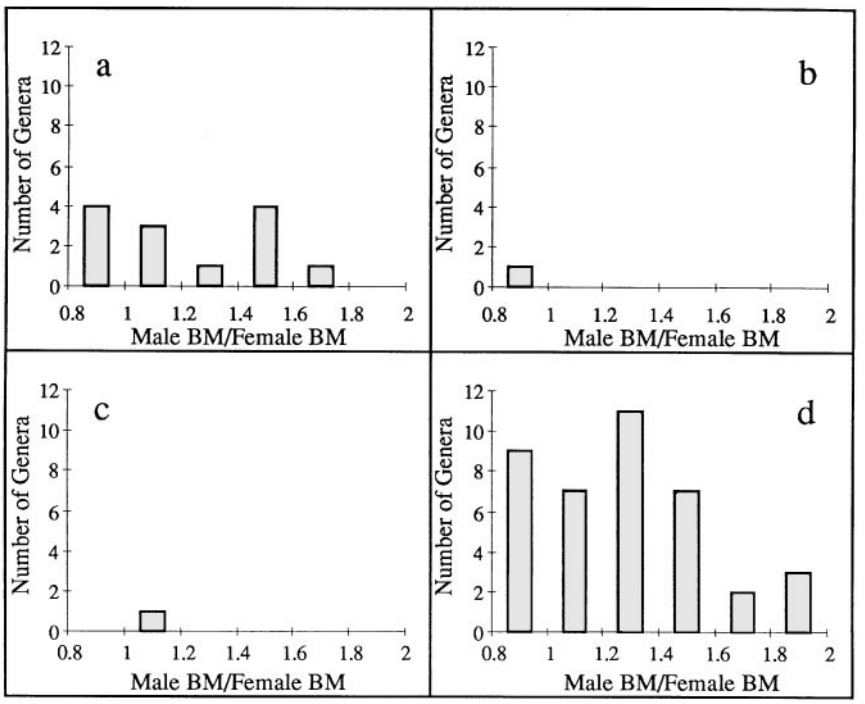

Fig. 2. Frequency distribution of male weight to female weight ratio for (a) Cervidae, (b) Tragulidae, (c) Antilocapridae and (d) Bovidae genera.

subfamily: $t_9 = 1.18$, $P = 0.27$), with slopes of 1.10 (95% CI = 1.04–1.16) and 1.12 (95% CI = 1.06–1.18) respectively. Dimorphism increases with increasing body size.

The correlation matrix (Table 3) shows that feeding habits and habitat types were negatively correlated with female weight at all taxonomic levels (as weight increased, feeding habits changed from browsing to grazing, and habitat type from closed to open). Breeding group size was positively correlated with female weight at these same taxonomic levels (as weight increased, breeding group size also increased). Moreover, habitat changed from closed to open with a change in feeding type from browser to grazer, and breeding group size changed from small BGS to large BGS. These correlations justify an approach in which all these variables are taken into account simultaneously.

Effects of variables on dimorphism

The interaction between female weight and breeding group size was not significant (first step of the analysis, Table 1) at any taxonomic level (genus: $F_{2,41} = 0.80$, $P = 0.46$; tribe: $F_{2,14} = 0.81$, $P = 0.47$; subfamily: $F_{2,2} = 1.59$, $P = 0.39$). Main effects (second step of the analysis) differed according to the variable considered. The effect of habitat was never significant (genus: $F_{2,43} = 0.04$, $P = 0.96$; tribe: $F_{2,16} = 0.50$, $P = 0.61$; subfamily: $F_{2,4} = 2.17$, $P = 0.23$). Feeding type was significant only at the generic level (genus: $F_{2,43} = 3.88$, $P = 0.03$; tribe: $F_{2,16} = 1.34$, $P = 0.29$; subfamily: $F_{2,4} = 0.26$, $P = 0.78$). Breeding group size was

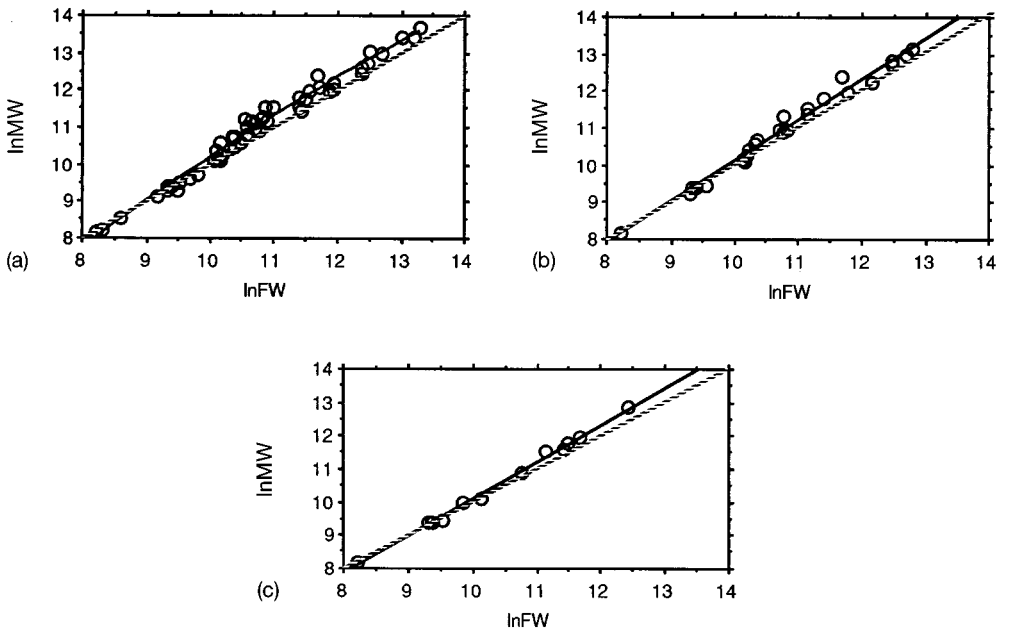

Fig. 3. Male weight (MW) plotted against female weight (FW) on a natural logarithmic scale, at the (a) generic, (b) tribe and (c) subfamily levels. The dashed line represents monomorphism (i.e. MW = FW). (a) $\ln MW = -5.11 + 1.90\ \ln FW - 0.04\ (\ln FW)^2$; (b) $\ln MW = -0.88 + 1.10\ \ln FW$; (c) $\ln MW = -1.09 + 1.10\ \ln FW$.

Table 3. Spearman correlation coefficients between the variables, at each taxonomic level (FED = feeding type, HAB = habitat type, BGS = breeding group size, lnFW = natural logarithm of female weight)[a]

	FED	HAB	lnFW
Generic level			
BGS	–0.586 (51); *0.0001*	–0.613 (51); *0.0001*	0.655 (51); *0.0001*
FED		0.615 (51); *0.0001*	–0.425 (51); *0.0001*
HAB			–0.436 (51); *0.002*
Tribe level			
BGS	–0.643 (24); *0.002*	–0.690 (25); *0.0007*	0.713 (25); *0.0005*
FED		0.648 (24); *0.002*	–0.482 (24); *0.021*
HAB			–0.451 (25); *0.027*
Subfamily level			
BGS	–0.700 (12); *0.020*	–0.767 (12); *0.011*	0.745 (12); *0.014*
FED		0.495 (12); *0.101*	–0.631 (12); *0.036*
HAB			–0.592 (12); *0.050*

[a] Sample sizes are given in parentheses (they differed according to the variables considered because of some missing data; see Appendix 1). *P*-values are in *italics*.

significant at the generic and tribe levels (genus: $F_{2,43} = 10.1$, $P = 0.00025$; tribe: $F_{2,16} = 4.14$, $P = 0.04$), but not at the subfamily level ($F_{2,4} = 2.45$, $P = 0.20$). However, male weight tended to increase with increasing breeding group size at the subfamily level. Since this test had low power due to a low number of observations ($n = 12$), we retained the effect of breeding group size in the model for subsequent analysis.

Whatever the taxonomic level, the model of a linear increase of male weight relative to female weight in relation to breeding group size can be selected (no significant differences between the model with three modalities in BGS and the linear model; genus: $F_{1,45} = 6.35$, $P = 0.18$; tribe: $F_{1,20} = 1.34$, $P = 0.26$; subfamily: $F_{1,4} = 1.36$, $P = 0.31$). Relative male weight (lnMW) increased linearly with breeding group size with a slope of 0.18 (95% CI = 0.10–0.26) at the generic level, 0.16 (95% CI = 0.08–0.24) at the tribe level and 0.10 (95% CI = –0.02 to 0.20) at the subfamily level. In contrast, the effect of feeding type (generic level) on relative male weight was not linear and has to be considered with three modalities ($F_{1,46} = 6.35$, $P = 0.015$). Indeed, intermediate feeders have the highest relative male weight at the generic level: the lnMW difference is 0.146 ± 0.050 between browsers and intermediate feeders, and 0.11 ± 0.07 between browsers and grazers. Thus, the final model selected is lnFW + BGS + (FED) at the generic level (see Table 1 for model notations), and lnFW + BGS at the tribe and the subfamily levels.

The partial regression between lnMW and lnFW had a slope of 1 at every taxonomic level (genus: 1.02, 95% CI = 0.98–1.06; tribe: 1.01, 95% CI = 0.95–1.07; subfamily: 1.06, 95% CI = 0.96–1.15). This means that male weight is isometric to female weight (MW = aFW) when other variables are taken into account (Fig. 1). We can thus accept the null hypothesis that variation in sexual size dimorphism (i.e. male weight for a given female

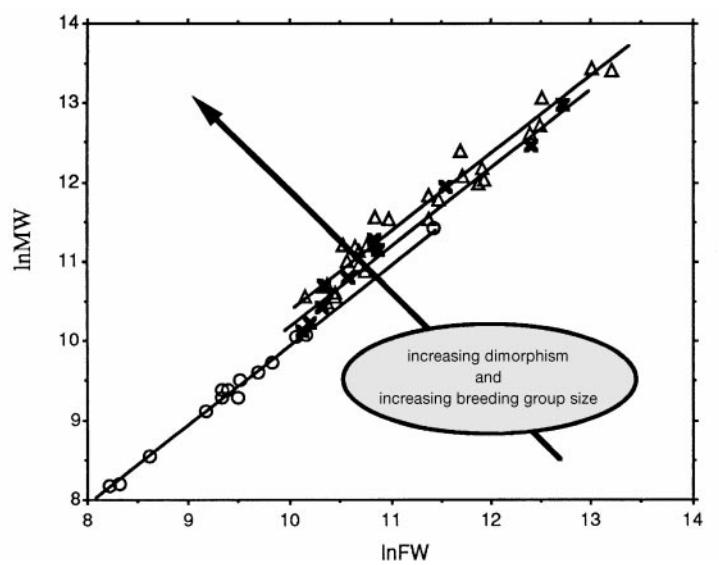

Fig. 4. Grade effect due to breeding group size at the generic level. Although the model selected considers breeding group size as a continuous variable, we represented it as a categorical variable because it is easier to see the consequences of the grade effect. All three lines have a slope equal to 1. Therefore, once the effect of breeding group size is accounted for, males increase in size in direct proportion to increases in female size. ○, BGS = 1; ×, BGS = 2; △, BGS = 3.

weight) does not depend on weight of the female, when breeding group size and feeding variables are taken into account. We conclude that previous studies reporting the relationship between female and male weight to have a slope greater than 1 could be explained by breeding group size and feeding type variables (Fig. 1b). This corresponds to what Martin and Harvey (1985) described as a grade effect (Fig. 4). For a given female weight, size dimorphism depends only on breeding group size, and for a given breeding group size, female weight has no effect on dimorphism. Since groups that are monogamous are smaller than polygynous groups (Fig. 5), we performed the analysis without the monogamous group. This analysis confirmed that the grade effect is not simply due to a contrast between small monomorphic and monogamous groups and larger and more polygynous groups (for example, at the generic level: no interaction between BGS and ln(FW): $F_{1,29} = 1.16$, $P = 0.29$; no effect of HAB: $F_{2,30} = 0.06$, $P = 0.95$; effect of FED approaching significance: $F_{2,30} = 2.72$, $P = 0.08$; highly polygynous genera with higher level of sexual size dimorphism (+0.1314, S.E. = 0.073) than weakly polygynous genera: $t = 1.80$, $P = 0.041$).

Checking assumptions

Models selected at each taxonomic level were adequately fitted, since no patterns occurred when residuals were plotted against female weight, breeding group size or feeding type: the linearity was acceptable and residuals were normally distributed. Moreover, residuals did not depend significantly on taxonomic group (see Table 4 for tests). No genus had a large

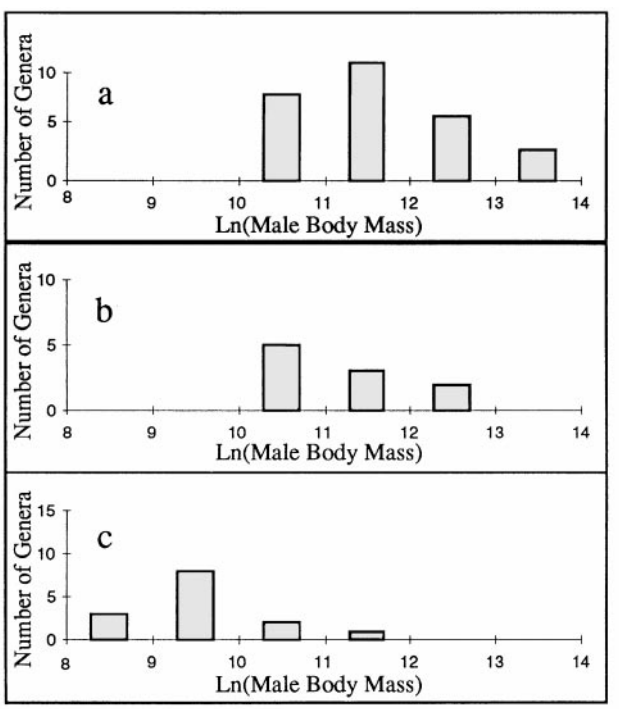

Fig. 5. Frequency distribution of male body weight according to three modalities of breeding group size (a = highly polygynous, b = weakly polygynous, c = monogamous) for ungulate genera.

Table 4. Results of analyses of variance (ANOVA) performed on the residuals of the selected model for each taxonomic group

Residuals from the model at:	ANOVA/tribe	ANOVA/subfamily	ANOVA/family
Generic level	$F_{21,27} = 1.738$ *P = 0.085*	$F_{11,39} = 1.205$ *P = 0.316*	$F_{3,47} = 1.402$ *P = 0.254*
Tribe level		$F_{11,12} = 1.208$ *P = 0.374*	$F_{3,21} = 2.408$ *P = 0.096*
Subfamily level			$F_{3,8} = 1.263$ *P = 0.350*

Cook's distance, but two tribes (Alcini and Caprini) and one subfamily (Tragulinae) had high Cook's distance values relative to other groups of the same taxonomic level. However, the results were unchanged when the same analysis was performed without these groups (same model selected, same slope for the partial regression between lnMW and lnFW).

DISCUSSION

The main results of this study are as follows: (1) Size dimorphism increases with female body weight. (2) The increase in dimorphism with weight is explained by an increase in level of polygyny. Male weight was isometric with female weight once the effect of breeding group size was included. (3) Ecological variables (feeding and habitat types) have only slight effects on dimorphism once breeding group size is taken into account.

After discussing methodological aspects, we focus on the biological interpretation of our results, and on the hypotheses that have still to be tested.

Methodology

Two consequences of the methods used may have influenced our results: the use of analysis of covariance to account for correlations between variables, and the use of taxonomy to account for phylogenetic problems. In previous studies, the use of various indices of size dimorphism and different methods for analysing relationships between dimorphism and other variables led to confusion or possible misinterpretation of patterns (Ranta *et al.*, 1994). The effect of breeding group size observed here (i.e. the increase in dimorphism with breeding group size, for a given female weight) was detected only because we took all variables into account in the analysis of covariance. An analysis of residuals of the relationship between male and female weight would remove statistically the effects of body size, but would also fail to highlight such a grade effect and, as in Martin *et al.* (1994), could have attributed part of the variability in size dimorphism to an unexplained allometric relationship. In line with our results, Webster (1992) found in New World blackbirds that 'the positive correlation between body size and size dimorphism is due to a correlation between body size and mating system'. Similarly, Reiss (1989) found no convincing evidence in studies of birds or mammals that weight effects remained after accounting for the

correlation between level of polygyny and weight. It thus appears based on existing evidence that the unexplained 'allometric effect' of size on dimorphism is actually a consequence of methodological problems. Reanalysis of available data is required to confirm the generality of the grade effect described here and the predominance of level of polygyny for explaining patterns of dimorphism.

Taxonomy does not appear to bias our results. Regardless of taxonomic levels, a given level of dimorphism is expected for a given level of polygyny. The importance of level of polygyny relative to body size or taxonomy in explaining size dimorphism is confirmed by the high variability of dimorphism found among most taxonomic groups. For example, although both the serow (*Capricornis sumatrensis*) and the chamois (*Rupicapra rupicapra*) are in the Rupicaprini, the chamois is one third the size, more polygynous and more dimorphic than the serow, a species that is monogamous and monomorphic. Similarly, moose (*Alces alces*) and reindeer (*Rangifer tarandus*) are both in the Odocoilinae, but although the moose is larger, it is less polygynous and less dimorphic than the reindeer. These patterns are explained by our model, which highlights the role of level of polygyny rather than weight or phylogeny in shaping sexual size dimorphism. Note that the main problem that arises when the dependence between points is not taken into account is that confidence intervals are underestimated (Martins and Hansen, 1995), which leads to a rejection of the null hypothesis too often. Because we never rejected the null hypothesis, whatever the taxonomic level being considered (i.e. dimorphism does not depend on weight when polygyny is taken into account), our results cannot be questioned in relation to phylogenetic dependence between observations.

Effect of ecological variables

Ecological factors appear to play a minor role in the evolution of ungulate sexual size dimorphism. We observed only a slight effect of feeding type, since at the generic level intermediate feeders and grazers are more dimorphic in size than browsers, after accounting for other variables. Contrary to the hypothesis proposed by Geist and Bayer (1988), we did not observe any significant effect of habitat. Habitat has no independent effect on size dimorphism when breeding group size is accounted for. Two reasons may explain this small effect of ecological variables, the first a technical one, the second a biological one. Our categories may be too broadly defined and the ecological variables may be too closely related either to weight or to level of polygyny to have an independent effect (Emlen and Oring, 1977). In contrast to several other studies (e.g. Estes, 1974; Sæther and Gordon, 1994), we defined an additional category (intermediate) for both ecological variables, to take account of the large between-species and intra-species variability. Nevertheless, this classification still restrains the variability to only three categories, and decreases the probability of detecting a significant effect of ecological variables on size dimorphism. More generally, the use of broad classifications may be the main factor underlying this lack of detection of ecological effects, which is generally the case in comparative studies (e.g. Harvey and Clutton-Brock, 1985; Gittleman, 1986; Partridge and Harvey, 1988). However, we emphasize other possible explanations. The relatively pronounced similarity among species of ruminants (all are terrestrial, adapted to cursorial locomotion and have the same digestive system) may account for the strong relationship between level of polygyny and size dimorphism. In contrast, this relationship is weaker in primates and pinnipeds. Weddel seals (*Leptonychotes weddellii*), for example, exhibit reversed sexual dimorphism although they

are polygynous: presumably, the advantage of small size is agility in water, which determines the outcome of male contests (e.g. Alexander *et al.*, 1979). Constraints on body weight could also be stronger in primates and pinnipeds because of the necessity to move in a three-dimensional environment (Clutton-Brock and Harvey, 1978; Alexander *et al.*, 1979; Martin *et al.*, 1994).

Size dimorphism and sexual selection

The most important results of this study are that the degree of dimorphism does not increase with increasing body weight of females within a given level of polygyny (e.g. small, highly polygynous species are as dimorphic as large, highly polygynous species), and that dimorphism can be explained by level of polygyny in ruminants (see Fig. 4). Because slopes were equal to 1 for a given breeding group size, males increase in size in direct proportion to an increase in female size. This pattern implies that sexual size dimorphism does not increase with species size. The increase in size dimorphism with increasing breeding group size is predicted by the sexual selection theory. Our results are in line with those of studies that support the role of level of polygyny (e.g. Clutton-Brock, 1982) rather than the role of body weight (e.g. Leutenegger and Cheverud, 1985) to explain size dimorphism. Our results allow us to disentangle the respective roles of allometry and sexual selection for ungulates. Thus the primary mechanism underlying variation in size dimorphism in ungulates could be differences in the level of male–male competition resulting from variation in breeding group size. Breeding group size could therefore be a good index of the intensity of sexual selection at the interspecific level, although it may be a poor measure of sexual selection at the intraspecific level (see Clutton-Brock, 1987, on red deer, *Cervus elaphus*, for an example of a weak relationship between harem size during one year and lifetime reproductive success of males).

Weight and level of polygyny

In addition to the strong correlation between breeding group size and size dimorphism, we observed that larger species are more dimorphic than smaller ones, because an apparent increase in dimorphism with weight occurs when level of polygyny is excluded. This implies that body weight and level of polygyny are correlated: level of polygyny increases when body size increases (Fig. 5). This is especially clear for small ruminant species, since no species under 20–30 kg is polygynous. Similarly, no species over 90 kg is monogamous. Thus, dimorphism is related to level of polygyny, and level of polygyny is related to weight.

To understand why larger species are more polygynous and consequently more dimorphic than smaller ones, the relationship between level of polygyny and weight has to be explored. The scarcity of field studies on small ruminants, which usually have discrete habits and live in closed habitats, may cast doubt on the reliability of our current knowledge of mating systems for these species (but see Arcese *et al.*, 1995). However, biological reasons may also be involved. As pointed out previously (Jarman, 1974, 1983; Emlen and Oring, 1977; Clutton-Brock and Harvey, 1978; Alexander *et al.*, 1979; Gosling, 1986; Ims, 1987), the male mating system depends on female dispersion, which itself depends on resource dispersion and predation. One hypothesis could thus be that small species are not polygynous because females do not occur at a sufficient local density and that large species are usually polygynous because they occur at a high local density. The relationship between local

density and weight may itself result from different factors that are often confounding (e.g. predation, habitat, feeding type). For most species, however, mating and spacing systems vary with ecological conditions (see Lott, 1991, for a review), especially with local density. Thus, to test whether local density, spacing systems or other ecological factors constrain the evolution of polygyny, further long-term studies at the intraspecific level are required.

Complementary hypotheses

Although we suggest that sexual size dimorphism results primarily from sexual selection rather than allometry, other mechanisms of natural selection may interact with sexual selection to reinforce the relationship between breeding group size and size dimorphism (Andersson, 1994). Male and female weight differ in most ruminants to an extent that breeding group size can predict. Depending on the level of polygyny, selection engenders size dimorphism (Clutton-Brock, 1991), but may act on male and female weight via different mechanisms (e.g. Martin *et al.*, 1994). Among small ruminants (<13 kg; Appendix 1), for example, species often show reversed sexual dimorphism (females are slightly larger than males). The cost of gestation and lactation for females may explain this pattern in small species (see Ralls, 1976, for a review of reversed sexual dimorphism in mammals). For large species, size dimorphism could increase through selection for a smaller body weight of females, favouring an earlier age of first reproduction (e.g. Clutton-Brock and Harvey, 1978; see Martin *et al.*, 1994, on primates). This mechanism is not very likely in ungulates, since their age at maturity is among the earliest in large mammals (Wooton, 1987). A decrease in this parameter would therefore not be as influential on female fitness in ungulates as in primates, in which selection for a decrease in female weight has been found (Martin *et al.*, 1994).

ACKNOWLEDGEMENTS

We thank M. Björklund, M. Boyce, P. Duncan, L. Ellisson, M. Hewison, R. Ims, X. Lambin, D. Pontier, N. Rioux and N.C. Stenseth for their constructive comments on earlier drafts of the manuscript. We thank M. Hewison for checking the English language.

REFERENCES

Alados, C.L. 1986. Aggressive behaviour, sexual strategies and their relation to age in male Spanish ibex (*Capra pyrenaica*). *Behav. Processes*, **12**: 145–158.

Alexander, R.D, Hoogland, J.L., Howard, R.D., Noonan, K.M. and Sherman, P.W. 1979. Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates and humans. In *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective* (N.A. Chagnon and W. Irons, eds), pp. 402–435. N. Scituate, MA: Duxbury Press.

Andersson, M. 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.

Arcese, P., Jongejean, G. and Sinclair, A.R.E. 1995. Behavioural flexibility in a small African antelope: Group size and composition in the oribi (*Ourebia ourebi*, Bovidae). *Ethology*, **99**: 1–23.

Balmford, A. and Blakeman, S. 1992. Horn size and body size of topi in relation to a variable mating system. *Afr. J. Ecol.*, **29**: 37–42.

Balmford, A., Bartos, L., Brotherton, P., Herrmann, H., Lancingerova, J., Mika, J. and Zeeb, U. 1993. When to stop lekking: Density-related variation in the rutting behaviour of sika deer. *J. Zool.* (*Lond.*), **231**: 652–656.

Barrett, M.W. 1982. Distribution, behavior, and mortality of pronghorns during a severe winter in Alberta. *J. Wildlife Manage.*, **46**: 991–1002.

Barrette, C. 1987. The comparative behavior and ecology of chevrotains, musk deer, and morphologically conservative deer. In *Biology and Management of the Cervidae* (C.M. Wemmer, ed.), pp. 200–213. Washington, DC: Smithsonian Institution Press.

Bell, G. 1989. A comparative method. *Am. Nat.*, **133**: 553–571.

Benton, M.J. 1988. *The Phylogeny and Classification of the Tetrapods*, *Vol. 2*: *Mammals*. Oxford: Clarendon Press.

Blaxter, K.L. and Hamilton, W.J. 1980. Reproduction in farmed red deer. 2. Calf growth and mortality. *J. Agric. Sci.*, *Cambridge*, **95**: 275–284.

Blood, D.A., Flook, D.R. and Wishart, W.D. 1970. Weights and growth of Rocky Mountain bighorn sheep in western Alberta. *J. Wildlife Manage.*, **34**: 451–455.

Bondrup-Nielsen, S. and Ims, R.A. 1990. Reversed sexual size dimorphism in microtines: Are females larger than males or are males smaller than females? *Evol. Ecol.*, **4**: 261–272.

Boyce, M.S. 1989. *The Jackson Elk Herd*. Cambridge: Cambridge University Press.

Bunnell, F.L. 1987. Reproductive tactics of Cervidae and their relationships to habitat. In *Biology and Management of the Cervidae* (C.M. Wemmer, ed.), pp. 145–167. Washington, DC: Smithsonian Institution Press.

Calder, W.A. 1984. *Size*, *Function and Life History*. Cambridge, MA: Harvard University Press.

Child, G. 1965. Growth and ageing criteria of impala, *Aepyceros melampus*. *Occas. Paper, Nat. Mus. S. Rhodesia B*, **4**: 128–135.

Clutton-Brock, T.H. 1982. The functions of antlers. *Behaviour*, **70**: 108–125.

Clutton-Brock, T.H. 1985. Size, sexual dimorphism, and polygyny in primates. In *Size and Scaling in Primate Biology* (W.L. Jungers, ed.), pp. 51–60. New York: Plenum Press.

Clutton-Brock, T.H. 1987. Sexual selection in the Cervidae. In *Biology and Management of the Cervidae* (C.M. Wemmer, ed.), pp. 110–122. Washington, DC: Smithsonian Institution Press.

Clutton-Brock, T.H. 1991. The evolution of sex differences and the consequences of polygyny in mammals. In *The Development and Integration of Behavior* (P. Bateson, ed.), pp. 229–253. Cambridge: Cambridge University Press.

Clutton-Brock, T.H. and Harvey, P.H. 1978. Mammals, resources and reproductive strategies. *Nature*, **273**: 191–195.

Clutton-Brock, T.H., Albon, S.D. and Harvey, P.H. 1980. Antlers, body size and breeding group size in the Cervidae. *Nature*, **285**: 565–566.

Clutton-Brock, T.H., Green, D., Hiraiwa-Hasegawa, M. and Albon, S.D. 1988. Passing the buck: Resource defence, lek breeding and mate choice in fallow deer. *Behav. Ecol. Sociobiol.*, **23**: 281–296.

Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. London: John Murray.

Dhungel, S.K. and O'Gara, B.W. 1991. Ecology of the hog deer in Royal Chitwan National Park, Nepal. *Wildlife Monogr.*, **119**.

Dubost, G. 1980. L'écologie et la vie sociale du Céphalophe bleu (*Cephalophus monticola* Thunberg), petit ruminant forestier africain. *Zeitschrift für Tierpsychologie*, **54**: 205–266.

Dubost, G. and Feer, F. 1981. The behavior of the male *Antelope cervicapra* L., its development according to age and social rank. *Behaviour*, **76**: 62–127.

Dunbar, R.I.M. and Dunbar, P. 1974. Social organisation and ecology of the klipspringer in Ethiopia. *Zeitschrift für Tierpsychologie*, **35**: 481–493.

Eisenberg, J.F. 1989. *Mammals of the Neotropics*: *The Northern Neotropics*. Chicago, IL: University of Chicago Press.

Emlen, S.T. and Oring, L.W. 1977. Ecology, sexual selection and the evolution of mating systems. *Science*, **197**: 215–223.

Estes, R.D. 1974. Social organisation of the African Bovidae. In *The Behavior of Ungulates and its Relation to Management* (V. Geist and F. Walther, eds), pp. 14–55. Morges, Switzerland: IUCN.

Estes, R.D. 1991. *The Behavior Guide to African Mammals*. Berkeley, CA: University of California Press.

Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.*, **125**: 1–15.

Francis, B., Green, M. and Payne, C. 1993. *The GLIM System, Release 4 Manual.* Oxford: Clarendon Press.

Garland, T., Harvey, P.H. and Ives, A.R. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.*, **41**: 18–32.

Geist, V. and Bayer, M. 1988. Sexual dimorphism in Cervidae and its relation to habitat. *J. Zool.* (*Lond.*), **214**: 45–53.

Geraads, D. 1992. Phylogenetic analysis of the tribe Bovini (Mammalia: Artiodactyla). *Zool. J. Linn. Soc.*, **104**: 193–207.

Gittleman, J.L. 1986. Carnivore life history patterns: Allometric, phylogenetic, and ecological associations. *Am. Nat.*, **127**: 744–771.

Gittleman, J.L. and Luh, H.-K. 1992. On comparing comparative methods. *Ann. Rev. Ecol. Syst.*, **23**: 383–404.

Gosling, L.M. 1986. The evolution of the mating strategies in male antelopes. In *Ecological Aspects of Social Evolution* (D.I. Rubenstein and R.W. Wrangham, eds), pp. 244–281. Princeton, NJ: Princeton University Press.

Harvey, P.H. and Clutton-Brock, T.H. 1985. Life history variation in primates. *Evolution*, **39**: 559–581.

Harvey, P.H. and Pagel, M.D. 1991. *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.

Hedrick, A.V. and Temeles, E.J. 1989. The evolution of sexual dimorphism in animals: Hypotheses and tests. *Trends Ecol. Evol.*, **4**: 136–138.

Heptner, V.G., Nasimovitch, A.A. and Bannikov, A.G. 1989. *Mammals of the Soviet Union.* Leiden: Brill.

Hoffmann, R.R. 1989. Evolutionary steps of ecophysiological adaptations and diversification of ruminants: A comparative view of their digestive systems. *Oecologia*, **78**: 443–457.

Hogg, J.T. 1988. Copulatory tactics in relation to sperm competition in Rocky Mountain bighorn sheep. *Behav. Ecol. Sociobiol.*, **22**: 49–59.

Ims, R.A. 1987. Male spacing systems in microtine rodents. *Am. Nat.*, **130**: 475–484.

Jarman, P.J. 1974. The social organisation of antelope in relation to their ecology. *Behaviour*, **48**: 215–266.

Jarman, P.J. 1983. Mating system and sexual dimorphism in large, terrestrial, mammalian herbivores. *Biol. Rev.*, **58**: 485–520.

Kattel, B. and Alldredge, A.W. 1991. Capturing and handling of the Himalayan musk deer. *Wildlife Soc. Bull.*, **19**: 397–399.

Kingdon, J. 1989. *East African Mammals. An Atlas of Evolution in Africa*: *Bovids.* Chicago, IL: University of Chicago Press.

Krebs, C.J. and Cowan, I.McT. 1962. Growth studies of reindeer fawns. *Can. J. Zool.*, **40**: 863–869.

Leader-Williams, N. 1988. *Reindeer on South Georgia.* Studies in Polar Research. Cambridge: Cambridge University Press.

Lepetit, T., Poilane, A., Poilane, J.F., Seitre, J. and Seitre, R. 1989. Croissance de l'oryx d'Arabie. *Mammalia*, **53**: 97–108.

Leutenegger, W. and Cheverud, J.M. 1985. Sexual dimorphism in primates: The effects of size. In *Size and Scaling in Primate Biology* (W.L. Jungers, ed.), pp. 33–50. New York: Plenum Press.

Leuthold, W. 1977. *African Ungulates: A Comparative Review of Their Ecology and Behavioral Ecology.* Berlin: Springer-Verlag.

Linnell, J.D.C. 1994. Reproductive tactics and parental care in Norwegian roe deer. Doctoral dissertation, University of Cork, Ireland.

Lott, D.F. 1979. Dominance relations and breeding rate in mature male American bison. *Zeitschrift für Tierpsychologie*, **49**: 418–432.

Lott, D.F. 1991. *Intraspecific Variation in the Social Systems of Wild Vertebrates.* Cambridge: Cambridge University Press.

Lovari, S. 1984. Herding strategies of male Abbruzzo chamois on the rut. *Acta Zool. Fenn.*, **172**: 91–92.

Lovari, S. and Apollonio, M. 1994. On the rutting behaviour of the Himalayan goral *Nemorhaedus goral* (Hardwicke, 1825). *J. Ethol.*, **12**: 25–34.

MacDonald, D. 1984. *The Encyclopedia of Mammals*. New York: Facts on File, Inc.

Martin, R.D. and Harvey, P.H. 1985. Brain size allometry: Ontogeny and phylogeny. In *Size and Scaling in Primate Biology* (W.L. Jungers, ed.), pp. 147–173. New York: Plenum Press.

Martin, R.D., Willner, L.A. and Dettling, A. 1994. The evolution of sexual dimorphism in primates. In *The Differences Between the Sexes* (R.V. Short and E. Balaban, eds), pp. 159–200. Cambridge: Cambridge University Press.

Martins, E.P. and Hansen, T.F. 1995. The statistical analysis of interspecific data: A review of phylogenetic comparative methods. In *Phylogenies and the Comparative Methods in Animal Behavior* (E.P. Martins, ed.), pp. 22–75. Oxford: Oxford University Press.

Mitchell, G.J. 1980. *The Pronghorn Antelope in Alberta.* Regina: G.J. Mitchell.

Miura, S. and Tokida, K. 1992. Demographic parameters of Japanese serow population in Japan. In *Global Trends in Wildlife Management* (B. Bobek, K. Perzanovski and W. Regelin, eds), pp. 423–426. Krakow-Warszawa: Swiat Press.

Niethammer, J. and Krapp, F. 1986. *Handbuch der Saügetiere Europas. Paarhufer. Artiodactyla* (*Suidae, Cervidae, Bovidae*). Wiensbaden: AULA Verlag.

Owen-Smith, N. 1988. *Megaherbivores*: *The Influence of Very Large Body Size on Ecology*. Cambridge: Cambridge University. Press.

Partridge, L. and Harvey, P.H. 1988. The ecological context of life history evolution. *Science*, **241**: 1449–1455.

Pélabon, C. 1994. La sélection sexuelle chez le daim: une étude de l'investissement maternel et des stratégies de reproduction. Doctoral dissertation, University of Lyon, France.

Peters, R.H. 1983. *The Ecological Implications of Body Size.* Cambridge: Cambridge University Press.

Purvis, A., Gittleman, J.L. and Luh, H.K. 1994. Truth or consequences: Effects of phylogenetic accuracy on two comparative methods. *J. Theor. Biol.*, **167**: 293–300.

Qin, R. and Li, S. 1992. A study on the biological characteristics of sika deer. In *The Biology of Deer* (R.D. Brown, ed.), p. 221. Berlin: Springer Verlag.

Ralls, K. 1976. Mammals in which females are larger than males. *Quart. Rev. Biol.*, **51**: 245–276.

Ralls, K. 1977. Sexual dimorphism in mammals: Avian models and unanswered questions. *Am. Nat.*, **111**: 917–938.

Ranta, E., Laurila, A. and Elmberg, J. 1994. Reinventing the wheel: Analysis of sexual dimorphism in body size. *Oikos*, **70**: 313–321.

Redford, K.H. and Eisenberg, J.F. 1992. *Mammals of the Neotropics*: *The Southern Cone.* Chicago, IL: University of Chicago Press.

Reiss, M.J. 1989. *The Allometry of Growth and Reproduction*. Cambridge: Cambridge University Press.

Rice, C.G. 1988. Reproductive biology of Nilgiri tahr, *Hemitragus hylocrius* (Mammalia: Bovidae). *J. Zool.* (*Lond.*), **214**: 269–284.

Robinette, W.L. and Archer, A.L. 1971. Notes on ageing criteria and reproduction of Thompson's gazelle. *East Afr. Wildlife J.*, **9**: 83–98.

Rosser, A.M. 1992. Resource distribution, density, and determinants of mate access in puku. *Behav. Ecol.*, **3**: 13–24.

Royall, R.M. 1986. Model robust confidence intervals using maximum likelihood estimators. *Int. Stat. Rev.*, **54**: 221–226.

Schaller, G.B. 1977. *Mountain Monarchs*: *Wild Sheep and Goats of the Himalaya.* Chicago, IL: University of Chicago Press.

Scott, K.M. 1987. Allometry and habitat-related adaptations in the postcranial skeleton of Cervidae. In *Biology and Management of the Cervidae* (C.M. Wemmer, ed.), pp. 65–80. Washington, DC: Smithsonian Institution Press.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: A review of the evidence. *Quart. Rev. Biol.*, **64**: 419–461.

Short, R.V. and Balaban, E. 1994. *The Differences Between the Sexes.* Cambridge: Cambridge University Press.

Sæther, B.E. and Gordon, I.J. 1994. The adaptive significance of reproductive strategies in ungulates. *Proc. Roy. Soc. Lond. B*, **256**: 263–268.

Talbot, L.M. and Talbot, M.H. 1963. The wildebeest in western Masailand. *Wildlife Monog.*, **12**.

Webster, M.S. 1992. Sexual dimorphism, mating system and body size in New World Blackbirds (Icterinae). *Evolution*, **46**: 1621–1641.

Western, D. 1979. Size, life history and ecology in mammals. *Afr. J. Ecol.*, **17**: 185–204.

Wooton, J.T. 1987. The effects of body mass, phylogeny, habitat and trophic level on mammalian age at first reproduction. *Evolution*, **41**: 732–749.

Zejda, J. and Horakova, M. 1988. Three kinds of weight in Sika deer (*Cervus nippon*). *Folia Zool.*, **37**: 289–299.

APPENDIX

Species	MW (g)	FW (g)	BGS	FED	HAB	Family	Subfamily	Tribe	Reference*
Aepyceros melampus	57 216	43 970	3	it	2	1	3	8	10, 18, 20, 24
Alcelaphus buselaphus cokei	142 000	126 000	3	ge	1	1	3	7	18, 24
Acelaphus buselaphus lichtensteini	177 000	165 000	3	ge	1	1	3	7	18, 24
Alcelaphus buselaphus lelwel	183 000	167 000	3	ge	1	1	3	7	18, 24
Alces alces	440 000	330 500	2	cs	3	2	8	20	1, 20, 36, 44
Amnotragus lervia	104 000	52 000	3	it	1	1	5	14	43
Antidorcas marsupialis hofmeyri	41 000	37 000	3	it	1	1	2	5	19
Antidorcas marsupialis marsupialis	30 600	26 700	3	it	1	1	2	5	19
Antilocapra americana	53 550	46 844	3	it	1	3	6	16	4, 20, 33
Antilope cervicapra	38 000	35 000	3	ge	2	1	2	5	15, 20, 36
Axis axis	88 000	55 000	3	ge	2	2	7	17	9, 11, 36, 44
Axis porcinus	46 350	33 600	3	ge	3	2	7	17	9, 11, 13, 44
Bison bison	469 900	274 750	3	it	1	1	1	2	29, 32
Boocercus eurycerus	300 000	240 000	3	cs	3	1	1	3	18, 24
Bos gaurus	880 000	590 000	·	ge	2	1	1	2	36
Boselaphus tragocamelus	240 000	120 000	3	·	2	1	1	1	32, 36
Capra aegagrus	33 800	20 125	3	it	1	1	5	14	20, 35, 43
Capra cylindricornis	83 000	50 000	3	it	1	1	5	14	20, 43
Capra falconeri	83 000	36 500	3	it	1	1	5	14	20, 43
Capra ibex	95 000	45 000	3	it	1	1	5	14	20, 35, 43
Capra pyrenaica	70 000	37 500	3	it	1	1	5	14	1, 20, 35
Capreolus capreolus	27 680	26 730	2	cs	2	2	8	19	11, 20, 22, 28
Capricornis sumatraensis	92 000	91 000	1	cs	2	1	5	13	34, 43
Cephalophus monticola	4 400	5 050	1	cs	3	1	4	11	14, 19, 20, 36
Cephalophus natalensis	14 000	14 000	1	cs	3	1	4	11	18, 20, 36
Cervus canadensis	312 000	238 667	3	it	2	2	7	17	8, 11, 20, 36, 44
Cervus duvauceli	236 000	145 000	3	it	2	2	7	17	36
Cervus elaphus	160 000	107 500	3	it	2	2	7	17	6, 11, 20, 44

Cervus eldi	100 000	64 000	3	ge	2	2	7	17	9, 44
Cervus nippon	79 867	50 133	3	it	2	2	7	17	2, 20, 38, 44, 46
Cervus unicolor brookei	121 000	91 000	2	ge	2	2	7	17	9, 11, 44
Cervus unicolor equinus	215 000	162 000	2	ge	2	2	7	17	9, 11, 44
Connochaetes gnou	180 000	140 000	3	ge	1	1	3	7	18, 36
Connochaetes taurinus	205 000	162 500	3	ge	1	1	3	7	18, 24, 45
Dama dama	71 000	41 200	3	it	2	2	7	17	12, 20, 37, 44
Damaliscus dorca	61 000	55 000	3	ge	1	1	3	7	18, 36
Damaliscus lunatus	139 433	122 267	3	ge	1	1	3	7	3, 18, 20, 24
Gazella granti	65 000	45 000	3	it	1	1	2	5	18, 20, 24
Gazella thomsoni	24 500	19 350	3	it	1	1	2	5	19, 20, 24, 41
Hemitragus jemlahicus	101 000	59 000	3	it	1	1	5	14	40, 43
Hippotragus equinus	280 000	260 000	2	ge	1	1	3	9	18, 24
Hippotragus niger	235 000	220 000	2	ge	1	1	3	9	18, 24
Hydropotes inermis	11 900	11 900	1	cs	2	2	11	24	5, 11, 20, 44
Kobus ellipsiprimnus	238 000	183 000	3	ge	1	1	3	6	18, 24
Kobus kob	94 000	63 000	3	ge	1	1	3	6	18, 24
Kobus leche	104 000	79 500	3	ge	1	1	3	6	18, 36
Kobus vardoni	77 000	66 000	3	ge	1	1	3	6	24, 42
Lithocranius walleri	45 000	31 000	2	cs	2	1	2	5	18, 20, 24
Madoqua kirkii	5 100	5 500	1	cs	3	1	2	5	18, 20, 24
Mazama americana	29 000	29 000	1	cs	3	2	8	18	17, 44
Mazama gouazoubira	18 000	18 000	1	it	2	2	8	18	17, 44
Moschus chrysogastere	10 190	10 880	1	it	3	2	10	23	23
Moschus moschiferus	11 000	11 000	1	it	3	2	10	23	9, 44
Moschus sibiricus	15 000	12 000	1	it	3	2	10	23	5
Muntiacus bancanus	19 000	19 000	1	it	3	2	9	22	9, 11, 44
Muntiacus grandicornis	36 000	36 000	1	it	3	2	9	22	9, 11, 44
Muntiacus moschatus	25 000	25 000	1	it	3	2	9	22	9, 11, 44
Muntiacus muntjak	22 500	20 000	1	cs	3	2	9	22	5, 10, 20, 44

Species	MW (g)	FW (g)	BGS	FED	HAB	Family	Subfamily	Tribe	Reference*
Muntiacus pleihareus	16 000	16 000	1	it	3	2	9	22	9, 11, 44
Muntiacus reevesi	14 500	11 800	1	it	3	2	9	22	5, 9, 11, 44
Nemorhaedus goral	33 500	30 250	2	it	1	1	5	13	31, 32, 43
Neotragus batesi	2 200	2 800	1	cs	3	1	2	4	18, 24
Neotragus moschatus	5 000	5 400	1	cs	3	1	2	4	18, 20, 36
Odocoileus hemionus	87 500	56 000	2	cs	2	2	8	18	11, 20, 36, 44
Odocoileus virginianus	68 000	45 000	2	cs	2	2	8	18	11, 20, 44
Oreamnos americanus	69 000	53 000	2	it	1	1	5	13	20, 43
Oreotragus oreotragus	10 800	13 100	1	cs	2	1	2	4	16, 18, 36
Oryx gazella	176 000	16 000	3	ge	1	1	3	9	18, 36
Oryx gazella ssp2	205 000	186 000	3	ge	1	1	3	9	18, 36
Oryx leucoryx	92 700	87 700	3	ge	1	1	3	9	18, 27
Ourebia ourebi	15 000	16 100	1	ge	1	1	2	4	18, 20, 24
Ovibos moschatus	334 000	266 000	3	it	1	1	5	15	20, 43
Ovis aries	35 000	25 000	3	ge	1	1	5	14	20, 36
Ovis canadensis canadensis	93 875	72 107	3	ge	1	1	5	14	7, 20, 21
Ovis canadensis nelsoni	70 746	43 989	3	ge	1	1	5	14	7, 20, 21
Ovis nivicola	93 000	51 000	3	ge	1	1	5	14	19, 20
Ozotoceros bezoarcticus	40 000	35 000	3	ge	1	2	8	18	11, 39, 44
Pelea capreolus	25 000	25 000	2	it	2	1	3	10	18, 36
Procapra gutturosa	32 000	24 000	·	ge	1	1	2	5	21
Pseudois nayaur	60 000	39 000	3	ge	1	1	5	14	43
Pudu pudu	13 500	13 500	1	it	3	2	8	18	39, 44
Rangifer tarandus	136 667	88 867	3	it	1	2	8	21	9, 10, 25, 26, 44
Raphicerus campestris	10 950	11 150	1	cs	2	1	2	4	18, 36
Redunca arundinum	68 000	48 000	1	ge	1	1	3	6	18, 24
Redunca fulvorufula	30 000	29 000	3	ge	1	1	3	6	18, 24
Redunca redunca	50 000	40 000	2	ge	1	1	3	6	18, 24

Rupicapra rupicapra	38 500	26 000	3	it	2	1	5	13	20, 30, 35, 43
Saiga tatarica	43 100	30 800	3	it	1	1	5	12	19, 20
Sylvicapra grimmia	16 700	18 300	1	cs	3	1	4	11	18, 20, 24
Syncerus caffer	668 000	548 000	3	ge	2	1	1	2	18, 24
Taurotragus derbianus	680 000	440 000	3	it	1	1	1	3	18, 24
Taurotragus oryx	690 000	450 000	3	it	1	1	1	3	18, 20, 24
Tragelaphus angasi	110 500	60 500	2	it	3	1	1	3	18, 24
Tragelaphus euryceros	300 000	240 000	2	cs	3	1	1	3	18, 20
Tragelaphus imberbis	100 000	63 000	2	cs	3	1	1	3	18, 20, 24
Tragelaphus scriptus	54 000	33 000	2	cs	3	1	1	3	18, 20, 24
Tragelaphus spekei	100 000	54 000	2	it	3	1	1	3	18, 24
Tragelaphus strepticeros	257 000	170 000	3	cs	3	1	1	3	18, 20, 24
Tragulus javanicus	1 300	1 460	1	cs	3	4	b	25	5, 32
Tragulus napu	5 800	5 900	1	cs	3	4	b	25	5, 32

BGS : 1 = breeding group size of 1 or 2 (monogamous); 2 = breeding group size of 3–5 (weakly polygynous); 3 = breeding group size more than 5 (highly polygynous).
FED: ge = grass eater; it = intermediate feeder; cs = concentrate selector.
HAB: 1 = open habitat; 2 = semi-open habitat; 3 = closed habitat.
Family: 1 = Bovidae; 2 = Cervidae; 3 = Antilocapridae; 4 = Tragulidae.
Subfamily: 1 = Bovinae; 2 = Antilopinae; 3 = Hippotraginae; 4 = Cephalophinae; 5 = Caprinae; 6 = Antilocaprinae; 7 = Cervinae; 8 = Odocoilinae; 9 = Muntiacinae; 10 = Moschinae; 11 = Hydropotinae; 12 = Tragulinae.
Tribe: 1 = Boselaphini; 2 = Bovini; 3 = Tragelaphini; 4 = Neotragini; 5 = Antilopini; 6 = Reduncini; 7 = Alcelaphini; 8 = Aepycerotini; 9 = Hippotragini; 10 = Pelini; 11 = Cephalophini; 12 = Saigini; 13 = Rupicaprini; 14 = Caprini; 15 = Ovibovini; 16 = Antilocaprini; 17 = Cervini; 18 = Odocoilini; 19 = Capreolini; 20 = Alcini; 21 = Rangiferini; 22 = Muntiacini; 23 = Moschini; 24 = Hydropotini; 25 = Tragulini.
* *References*: **1** = Alados (1986), **2** = Balmford *et al.* (1993), **3** = Balmford and Blakeman (1992), **4** = Barrett (1982), **5** = Barrette (1987), **6** = Blaxter and Hamilton (1980), **7** = Blood *et al.* (1970), **8** = Boyce (1989), **9** = Bunnell (1987), **10** = Child (1965), **11** = Clutton-Brock (1987), **12** = Clutton-Brock *et al.* (1988), **13** = Dhungel and O'Gara (1991), **14** = Dubost (1980), **15** = Dubost and Feer (1981), **16** = Dunbar and Dunbar (1974), **17** = Eisenberg (1989), **18** = Estes (1991), **19** = Heptner *et al.* (1989), **20** = Hoffmann (1989), **21** = Hogg (1988), **22** = Gaillard *et al.* (unpublished data), **23** = Kattel and Alldredge (1991), **24** = Kingdon (1989), **25** = Krebs and Cowan (1962), **26** = Leader-Williams (1988), **27** = Lepetit *et al.* (1989), **28** = Linnell (1994), **29** = Lott (1979), **30** = Lovari (1984), **31** = Lovari and Apollonio (1994), **32** = MacDonald (1984), **33** = Mitchell (1980), **34** = Miura and Tokida (1992), **35** = Niethammer and Krapp (1986), **36** = Owen-Smith (1988), **37** = Pélabon (1994), **38** = Qin and Li (1992), **39** = Redford and Eisenberg (1992), **40** = Rice (1988), **41** = Robinette and Archer (1971), **42** = Rosser (1992), **43** = Schaller (1977), **44** = Scott (1987), **45** = Talbot and Talbot (1963), **46** = Zejda and Horakova (1988).