RESEARCH PAPER

Social organization in ungulates: Revisiting Jarman's hypotheses

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Abstract

Ungulates (antelopes, deer and relatives) have some of the most diverse social systems among mammals. To understand the evolution of ungulate social organization, Jarman (1974) proposed an ecological scenario of how distribution of resources, habitat and feeding style may have influenced social organization. Although Jarman's scenario makes intuitive sense and remains a textbook example of social evolution, it has not been scrutinized using modern phylogenetic comparative methods. Here we use 230 ungulate species from ten families to test Jarman's hypotheses using phylogenetic analyses. Consistent with Jarman's proposition, both habitat and feeding style predict group size, since grazing ungulates typically live in open habitats and form large herds. Group size, in turn, has a knock-on effect on mating systems and sexual size dimorphism, since ungulates that live in large herds exhibit polygamy and extensive sexual size dimorphism. Phylogenetic confirmatory path analyses suggest that evolutionary changes in habitat type, feeding style and body size directly (or indirectly) induce shifts in social organization. Taken together, these phylogenetic comparative analyses confirm Jarman's conjectures, although they also uncover novel relationships between ecology and social organization. Further studies are needed to explore the relevance of Jarman (1974) scenario for mammals beyond ungulates.

KEYWORDS
artiodactyla, feeding style, group size, habitat, mating system, phylogenetic generalized least squares, phylogenetic path analysis, social evolution

1 | INTRODUCTION

One of the core tenets in behavioural ecology and sociobiology is that spatial and temporal distribution of resources influence social organization (Alcock, 2013; Crook, 1964; Davies et al., 2012; Wilson, 1975). Thus, the availability of food resources, breeding sites along with predators and parasites are expected to influence territoriality, group formation and colonial breeding (Clutton-Brock, 2016; Estes, 1974; Krause & Ruxton, 2002). Specifically, group formation and group size are thought to be influenced by various costs and benefits of group living in a particular environment. Benefits of group formation, for instance enhanced feeding efficiency, defence

against predators, access to potential mates, may be negated by the cost of group living such as increased competition for food and mates, increased detectability by predators, and a higher chance of infections by diseases and parasites (Clutton-Brock, 2016; Davies et al., 2012; Krause & Ruxton, 2002).

Artiodactyla (antelopes, deer, bovids and relatives, approx. 250 species; ungulates henceforth) is one of the most diverse mammalian order, since body size vary several magnitudes between species, they inhabit six continents and they live in diverse habitats that include deserts, grasslands and forests. In addition, their social behaviour, breeding system and associated traits such as sexual size dimorphism (SSD) are also highly variable (Clutton-Brock, 2016; Jarman, 1974;

Pérez-Barbería et al., 2002; Wilson & Mittermeier, 2011). In a seminal study, Jarman (1974) conjectured that interspecific variation in ecology and social organization of ungulates are associated. Following Crook's (1964) pioneering work on social organization in weaverbirds (*Ploceidae*), Jarman (1974) laid the foundations of behavioural ecology and sociobiology by adopting an ecological cross-species thinking that has became known as the comparative approach (Felsenstein, 1985; Harvey & Pagel, 1991).

Jarman (1974) focused on African antelopes, and he recognized five groups based on their ecology, primarily habitat and feeding style. He noticed that body size, mating systems, sexual size dimorphism and anti-predator behaviour tend to match the ecological conditions. He argued that body size should be associated with metabolic rate since metabolic requirement per unit weight is higher in small-bodied species. Therefore, small-bodied ungulates are expected to select more nutritious and higher calorie content food items such as fresh leaves and berries. Since these items are often scarce and dispersed, small-bodied ungulates are expected to hold territories alone or in pairs to monopolize food resources. In contrast, large-bodied species can feed on lower quality food in bulk such as grasses, and since this type of food is less defensible economically the large-bodied ungulates roam in herds. Jarman (1974) synthetized these relationships into an evolutionary scenario whereby polygamy and sexual size dimorphism was a consequence of habitats (i.e. closed forests versus open savannah) and feeding styles (i.e. browsers versus grazers) via metabolic demands of having a small or large body size (Figure 1a). Jarman's arguments were based on the idea that habitat types and feeding styles influence the spatial distribution of females, that in turn have knock-on effect on males' strategy to secure mating rights. Females' tendency to aggregate seasonally or all-year-round create an opportunity for males to monopolize mating rights and thus facilitate the evolution of polygamous matings. Given the high mating stakes in polygamous systems, male-male conflicts are expected to intensify leading to increased male body size, and ultimately, to extensive sexual size dimorphism

and elaboration of different weaponries including horns and antlers (Geist, 1966; Jarman, 1974).

Jarman (1974) stimulated much follow up studies and it became one of the best-cited examples of the impact of resource distribution on social organization (Bravo et al., 2019; Clutton-Brock, 1989, 2016; Emlen & Oring, 1977; Greenwood, 1980; Jaeggi et al., 2020; Lukas & Clutton-Brock, 2020; Shultz et al., 2011; Winternon et al., 2020; Wittenberger, 1981). As a result, the ungulates became a prime example of comparative approach (Clutton-Brock, 2016; Davies et al., 2012; Harvey & Pagel, 1991; Wittenberger, 1981). Consistently, it is a well-cited study as indicated by 1,484 citations in Web of Science and 2,359 citations in Google Scholar (accessed on 24.02.2021).

However, Jarman's study has limitations (Davies et al., 2012). First, the core hypotheses are limited to African ungulates, and thus the validity of his arguments for ungulates as whole has remained uncovered. Second, Jarman did not use statistical analysis to test the putative associations between ecology and social organization. Third, phylogenetic history can create erroneous impressions about trait evolution and can create statistical artefacts, and therefore, we need to incorporate phylogenetic signals in statistical analyses. As yet, Jarman's hypotheses have not been evaluated by modern phylogenetic comparative analyses except Pérez-Barbería et al. (2002) that investigated the origin of sexual size dimorphism among ungulates using a binary character evolution analysis. Although Pérez-Barbería et al. (2002) uncovered important associations, they (i) have not included ecological variables in their analyses although the ecological variables were key components of Jarman's scenario, and (ii) assessed bivariate associations only, and therefore, the overall fit of data to Jarman's scenario has remained untested.

Here we revisit Jarman's (1974) hypotheses using phylogenetically controlled analyses. Using data from 230 ungulate species worldwide from 10 families, recent phylogenetic hypotheses and modern phylogenetic methods, we investigate (1) whether habitat type and feeding style predict body size, (2) whether habitat and
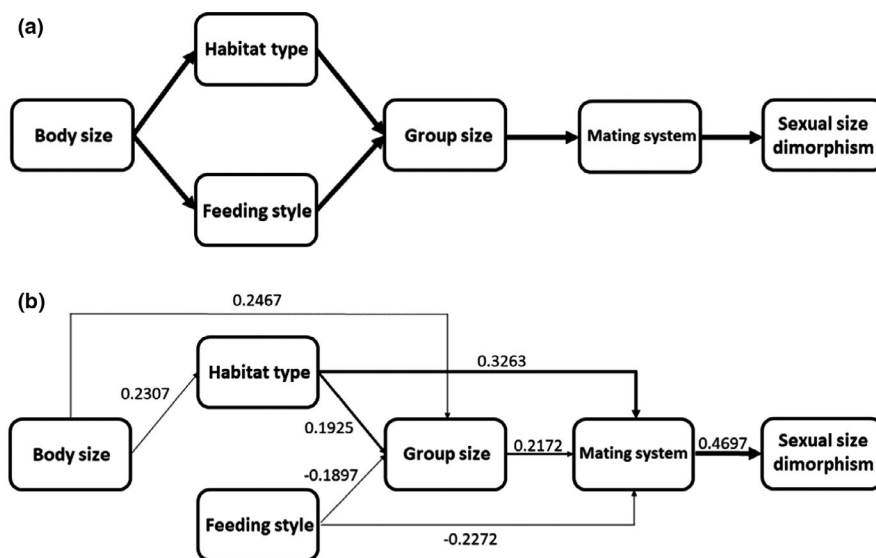
FIGURE 1 Social evolution in ungulates. (a) An ecological scenario proposed by Jarman (1974) and (b) best-fit model in phylogenetic confirmatory analyses (Fisher's $C = 15.689$, $df = 12$, $p = .206$). We provide path coefficients for each pathway. Wider arrows indicates stronger relationships

feeding style predict group size, and (3) the associations between group size, mating system and sexual size dimorphism. By using phylogenetic confirmatory path analyses (Gonzalez-Voyer & von Hardenberg, 2014; Santos, 2012; Santos & Cannatella, 2011), (4) we also test the fits of several evolutionary hypotheses—including Jarman's scenario—to the data.

2 | MATERIAL AND METHODS

2.1 | Data collection

We collected ecological and behavioural data from textbooks including the Handbook of the Mammals of the World (part 2, Hoofed Mammals; Wilson & Mittermeier, 2011), peer-reviewed papers and books, published IUCN reports on ungulate ecology and life history (Data S1; distribution of the data among ungulate families is given in Table S1). We targeted all ungulate species listed in the Handbook of the Mammals of the World (Wilson & Mittermeier, 2011) except (1) species that were extinct or extinct in the wild according to their IUCN categories, and (2) domesticated species and subspecies. In total, we obtained data on 230 Artiodactyla species representing all ten extant families.

We used group size as one of the indicators of social organization defined as the mean number of individuals in a group. For species where there were no available data for mean number of individuals, we calculated it as the mean value of minimum and maximum group size. We used mating system as a further proxy of social organization, defined as a binary variable: we considered a species polygamous if the individuals typically have more than one mate per breeding season and monogamous if individuals of both sexes have only one mate per breeding season. Habitat types were classified as open or closed: open-habitat dwelling species were those that spend most of the year in habitats with low vegetation like grasses, whereas closed-habitat dwelling species were those that live in dense habitats such as forests. Feeding style was scored as a binary trait: grazer or nongrazer. Grazers were those species that predominantly feed on grasses, whereas nongrazers feed on the leaves and branches of trees and shrubs and may also consume fruits, mushrooms or even some animals. Male and female body size were expressed in kg, and we calculated average body size as the average of female and male mass. We calculated sexual size dimorphism (SSD) as $\log_{10}$ (male body size / female body size) following Fairbairn et al. (2007).

2.2 | Statistical analyses

2.2.1 | Phylogenetic generalized least squares models

We analysed the relationships between the variables using phylogenetic generalized least squares (PGLS, Freckleton et al., 2002), that controls for the phylogenetic nonindependence among species. The

analyses were conducted in the R software (version 3.5.3.; R Core Team, 2016), with package 'caper' (Orme & Freckleton, 2013). We used the phylogenetic tree published by Bininda-Emonds et al. (2007) to represent phylogenetic relationships between species, because this is the most complete phylogenetic tree for mammals.

To test specific hypotheses, we conducted eight bivariate (with one response variable and one explanatory variable in each model) PGLS models. We grouped the models into three sets, according to the structure of relationships proposed by Jarman (Figure 1a). The first set of analyses investigated the putative factors related to body size. The bivariate models included habitat type and feeding style as explanatory variables (one predictor in each model) and body size as response variable. The second set of models focused on group size: here we had three bivariate models in which group size was the response variable and body size, feeding style and habitat type were the explanatory variables. The third set of PGLS analyses comprised of three bivariate models. The first model included group size as response variable and SSD as explanatory variable. In the second model, group size was the response variable and mating system appeared as explanatory variable. The third model investigated the association between mating system and SSD where SSD was included as response variable and mating system as explanatory variable. Group size and body size were log-transformed prior to the analysis.

2.2.2 | Phylogenetic path analysis

To investigate further the structure of relationships between ecological factors and components of social organization, we applied phylogenetically controlled path analyses, a method that was suggested for testing direct and indirect relationships among a set of variables (Gonzalez-Voyer & von Hardenberg, 2014).

To find the best fitting path model to the data, we followed the method proposed by Santos and Cannatella (2011) and Santos (2012), using the R package 'piecewieseSEM' (Lefcheck, 2016). Before the path analysis, we transformed the data phylogenetically, so we were able to control for phylogenetic relatedness among species (Santos, 2012). For the latter purpose, we (1) determined Pagel's λ (a measure of the strength of phylogenetic signal in the data) separately for each variable by PGLS models using maximum likelihood, (2) used this variable-specific λ value to re-scale the phylogenetic tree to a unit tree and (3) used the transformed tree to calculate phylogenetically independent contrasts for the variable by the 'pic' function of the 'ape' R package (Paradis, 2012). We repeated this process for each variable (body size, feeding style, habitat type, group size, mating system and SSD), and the resulting phylogenetically transformed values were used for fitting path models (see Santos (2012) for a similar approach; R. P. Freckleton, personal communication).

Our approach for finding the best fitting model was based on a model selection procedure proposed by Santos and Cannatella (2011) and Santos (2012). We used Jarman's (1974) hypothesis as a starting model (Figure 1a). According to this model, we created a full initial (i.e. just-identified) model which included all the

pathways between the variables (Figure S1). After fitting the full initial model, we excluded the nonsignificant pathways from the model one-by-one. In each step, we eliminated the path which had the path coefficient with the highest p value and then re-fitted the new, reduced model to the data. We had seven steps until a model with the acceptable fit was reached. Model fit was evaluated by Fisher C statistics. The C statistic tests the goodness of fit of the whole path model, and the model is rejected, that is it does not provide a good fit to the data, if the result of this C statistic is statistically significant (and conversely, a statistically nonsignificant result means acceptable fit; Lefcheck, 2016). In the accepted model, all the pathways had path coefficient with less than .05 p value (Table S2).

3 | RESULTS

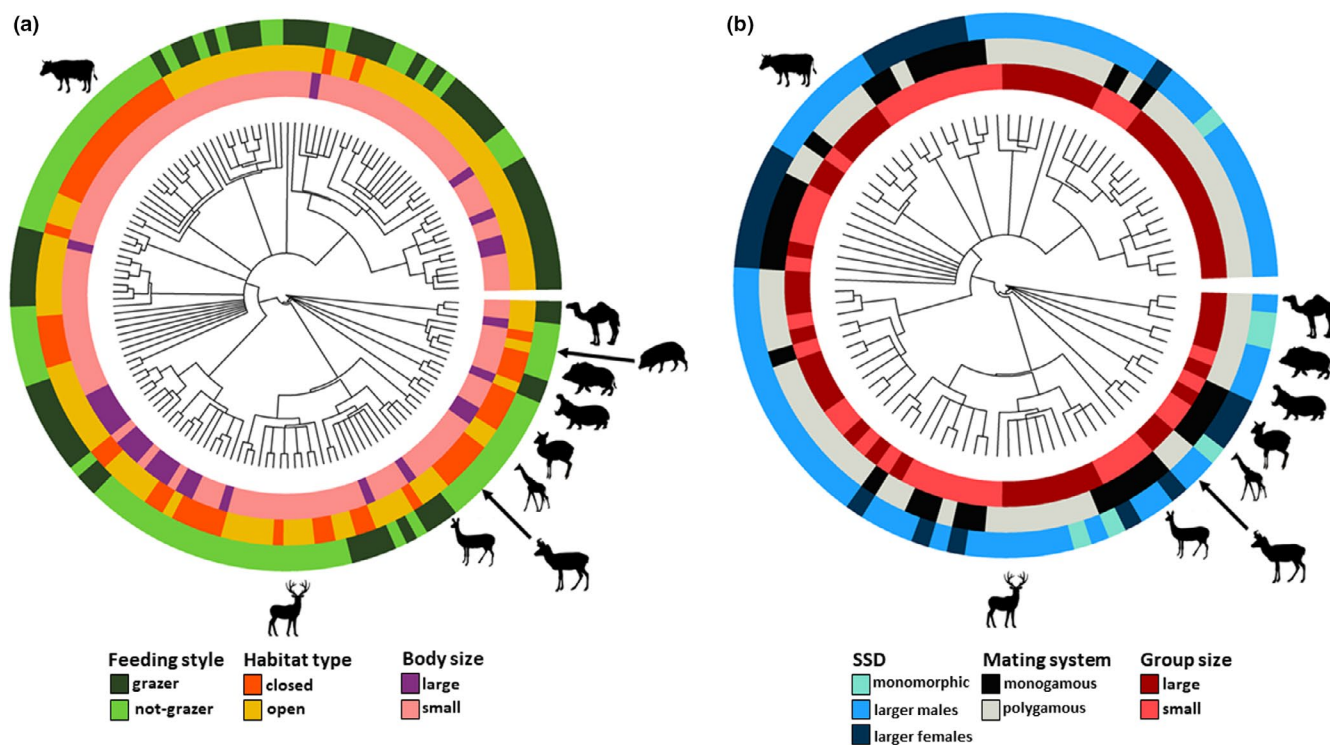### 3.1 | Diversity in ecology and social organization of ungulates

Ecology, body mass and social organization are highly variable among ungulates (Figures S2,S3): 84 species live in forests, whereas 112 species live in open habitats (we have no habitat data for 34 species, Table S1). Body size varies between 1.3 kg (smallest) and 1,600 kg (largest), and body size dimorphism ranges between male-biased SSD ($N = 133$ species, males are larger in average by 26%) and female-biased SSD ($N = 34$ species, females are larger in average by 10%) (we have no data on degree of SSD of 63 species, see in Table S1). Importantly, the variation in ecology, body size and social organization is scattered across the ungulate phylogeny (Figure 2).

3.2 | Ecology, body size and group size

Both feeding style and habitat correlate with body size, since grazers are larger than nongrazers (PGLS, $F_{159} = 6.059$, $p = .014$, $N = 148$ species; Table 1, Figure 3a), and ungulates that live in open habitats are larger than those that live in closed habitats (PGLS, $F_{147} = 23.81$, $p < .01$, $N = 148$ species; Table 1, Figure 3b). These differences are consistent with sex-specific data (Figure S4).

Feeding style and habitat also associate with group size, since grazers live in larger groups than browsers (PGLS, $F_{175} = 26.14$, $p < .001$, $N = 177$ species; Table 1, Figure 3c), and open-habitat dwelling species live in larger groups then those in closed habitats (PGLS, $F_{157} = 22.40$, $p < .001$, $N = 159$ species; Table 1, Figure 3d). Consistently, body size and group size are associated since large-bodied species live in groups, whereas small ones usually live alone or in pairs (PGLS, $F_{148} = 31.73$, $p < .01$, $N = 148$ species; Table 1, Figure 4a).

Feeding style
- grazer
- not-grazer

Habitat type
- closed
- open

Body size
- large
- small

SSD
- monomorphic
- larger males
- larger females

Mating system
- monogamous
- polygamous

Group size
- large
- small

FIGURE 2 Phylogenetic distribution of ecological and social variables in ungulates. (a) represents how different types of feeding style, habitat type and body size distirbute among Artiodactyla. (b) shows the distribution the following traits: sexual size dimorphism (SSD), mating system and group size. For illustrative purpose, continuous variables were split into binary variables as follows. For body size and group size, we calculated the mean value of these variables, and species were split whether below or above the mean for a given variable. Sexual size dimorphism (SSD) was termed monomorphic if SSD was zero, whereas species with SSD larger than zero were termed male-biased SSD and species with SSD less than zero were termed female-biased SSD. Note that Tayassuidae is represented only on (a), since we have no data on any species' mating system from this family (see distribution of variables in Table S1 and Figure S2)

Predictors	$\beta \pm SE$	adjusted R^2	t	p-value	N
1. Body size (response variable)					
Feeding style	-0.152 ± 0.061	.031	-2.4636	.014	161
Habitat type	0.371 ± 0.076	.133	4.879	<.001	149
2. Group size (response variable)					
Feeding style	-0.385 ± 0.075	.125	-5.113	<.001	176
Habitat type	0.391 ± 0.082	.119	4.732	<.001	159
Body size	0.359 ± 0.063	.171	5.633	<.001	153
3.a Sexual size dimorphism (response variable)					
Group size	0.077 ± 0.015	.133	4.888	<.001	153
Mating system	0.137 ± 0.018	.343	7.345	<.001	102
3.b Mating system (response variable)					
Group size	0.784 ± 0.091	.418	8.637	<.001	94

TABLE 1 Relationships between ecology, body size and social organization in ungulates, analysed by bivariate phylogenetically corrected generalized linear squares models (PGLS)

Note: Feeding style, habitat type and mating system were binary variables. Body size is provided in kg. Sexual size dimorphism (SSD) was calculated as log_{10} (male body size / female body size). Group size refers to the mean number of individuals per group. Group size and body size were *log*-transformed prior to the analyses. We provide parameter estimates with standard error ($\beta \pm SE$), adjusted R^2, the corresponding t and p values and number of species (N). The diagnostic plots for the models are provided in Figure S5.

3.3 | Mating system and sexual size dimorphism

Consistent with Jarman's arguments, group size is associated with the extent of sexual size dimorphism, since species that live in larger groups exhibit more male-biased SSD (PGLS, $F_{148} = 23.90$, $p < .001$, $N = 150$ species; Table 1, Figure 4b). Furthermore, polygamous ungulates live in larger groups than monogamous ones (PGLS, $F_{92} = 76.61$, $p < .001$, $N = 94$ species; Table 1, Figure 5a). Consistently, SSD and mating system are also associated: in polygamous ungulates, the males are usually larger than females, whereas monogamous ungulates typically exhibit monomorphism or female-biased SSD (PGLS, $F_{100} = 53.95$, $p < .001$, $N = 102$ species; Table 1, Figure 5b). The diagnostic plots for the models are provided in Figure S5.

3.4 | Phylogenetic path analyses

Phylogenetic confirmatory path analysis supported most components of Jarman's (1974) scenario, although it also uncovered several additional relationships (Figure 1a,b). The best fitting path model has statistically acceptable fit to the data (Fisher's $C = 15.7$, $df = 12$, $p = .206$; Figure 1b). Consistent with Jarman's arguments, body size is associated with habitat type, and both habitat type and feeding style are associated with group size in the best supported model (Figure 1b). Furthermore, the proposed associations were confirmed between mating system, group size and SSD (Figure 1, Table S2), although not the one between body size and feeding style (Figure 1, Table S2). Importantly, the best model uncovered novel relationships that were not conjectured by Jarman that include association between body size and group size, and those between habitat type, feeding style and mating system (Figure 1, Table S2).

4 | DISCUSSION

Our study has revealed three major patterns. First, increased body size appears to trigger the evolution of different social systems and mating strategies among ungulates (Bell, 1971; Clutton-Brock, 2016; Davies et al., 2012; Geist, 1974; Pérez-Barbería et al., 2002). These results support Jarman's (1974) hypotheses and expose robust differences among different species. Body size is the main predictor of ecological variables, whereas ecological variables have significant effect on social organization. To satisfy their metabolic requirements, small-bodied species need lower amount of food but higher quality, compared to large-bodied species. Because of this trade-off between food quality and quantity, small-bodied ungulates have more time during the day to find appropriate food items compared to larger species (Bell, 1971; Jarman, 1974; Owen-Smith & Novellie, 1982). Since high-quality food items appear to occur in higher density in closed habitats (e.g. forest, shrublands), small-bodied ungulates tend to be closed-habitat dwelling species, whereas larger species forced to live in open fields where they can consume substantial amount of food (Bell, 1971; Jarman, 1974; Jarman & Sinclair, 1979; Kleiber, 1947).

Since open-habitat dwelling species seem more vulnerable to predators than species that live in closed habitats, group living and large body size are considered as adaptations to reduce predation risk via detecting and/or deterring predators (Capellini, 2006). Consistent with these expectations, our results confirm that large ungulates tend to live in groups, and group-living ungulates typically inhabit open habitats (e.g. savannah).

Second, our study shows that group size was associated with different mating strategies among Artiodactyls. Living in groups increases the probability of polygamy and may amplify sexual selection (Jarman, 1974; Pérez-Barbería et al., 2002). More intense

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FIGURE 3 Ecology (habitat type, feeding style) of ungulates in relation to (a,b) body size and (c,d) social organization. *** indicates significant differences (p < .001). See statistics in Table 1
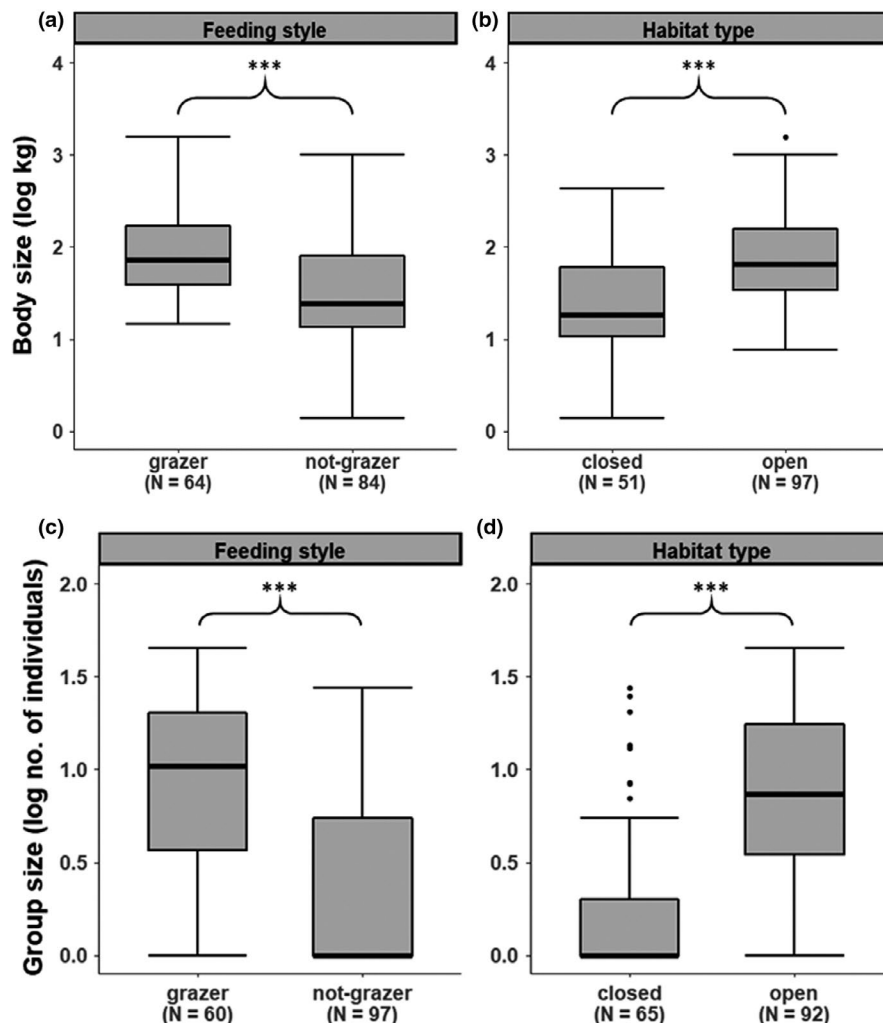

sexual selection could be responsible for larger SSD in polygamous species than in monogamous ones (Pérez-Barbería & Grodon, 2000; Pérez-Barbería et al., 2002). Sexual size dimorphism may also be advantageous for dividing the resources between males and females that can reduce intersexual competition (Fairbairn et al., 2007). For example, male kudus (*Tragelaphus strepsiceros*) and giraffes (*Giraffa camelopardalis*) are taller than females and capable of feeding on tall bushes and trees (Ginnet & Demmet, 1997; Main & du Toit, 2005; Mysterud, 2000; du Toit, 2005). In red deer (*Cervus elaphus*) and some African antelopes, males and females live separately during the year and exhibit different habitats, feeding strategies and time budgets (Clutton-Brock et al., 1982; Conrad et al., 2000; Lindsay, 2011; Main & du Toit, 2005; Staines & Crisp, 1978; du Toit, 2005). The latter patterns occur in other mammals as well: in arboreal primates, males are heavier and unable to climb as high as females in the canopy; thus, their foraging behaviour differs from the females' foraging strategies (Clutton-Brock, 1977; Grassi, 2002). These ecological differences between sexes may imply different energy intake rates and energy requirement of males and females in sexually dimorphic species (Clutton-Brock et al., 1987; Pérez-Barbería & Gordon, 1998). This in turn would suggest that some males in strongly dimorphic species may

be forced into secondary habitats due to the strong intersexual competition for females and this may increase mortality among males (Bowyer, 2004; Clutton-Brock, 2016; du Toit, 2005). Due to the variety of ecological and sexual selective processes between males and females that have implications for body sizes, the jury is still out there how these different processes shape body sizes of males, females and/or of both sexes (reviewed by De Lisle, 2019).

Third, using phylogenetic path analysis we confirmed several elements of Jarman's scenario and also highlighted additional associations. As proposed by Jarman (1974), our best model supports that body size is related to habitat type, whereas a species' ecology predicts group size, group size presages the type of mating system, and mating system predicts the degree of SSD. It appears that the available forest habitats have decreased in the Miocene (Janis, 1982), and forest fragmentation may have forced ancestral ungulates into open habitats. Increased group size possibly evolved to reduce predation risk in the new habitat. With large social groups possibly came the opportunity for males to monopolize mating opportunities and this favoured the evolution of polygamy. With polygamy male–male conflicts also escalated, which possibly led to extensive sexual dimorphism and the appearance of weaponry (Geist, 1974; Pérez-Barbería et al., 2002).
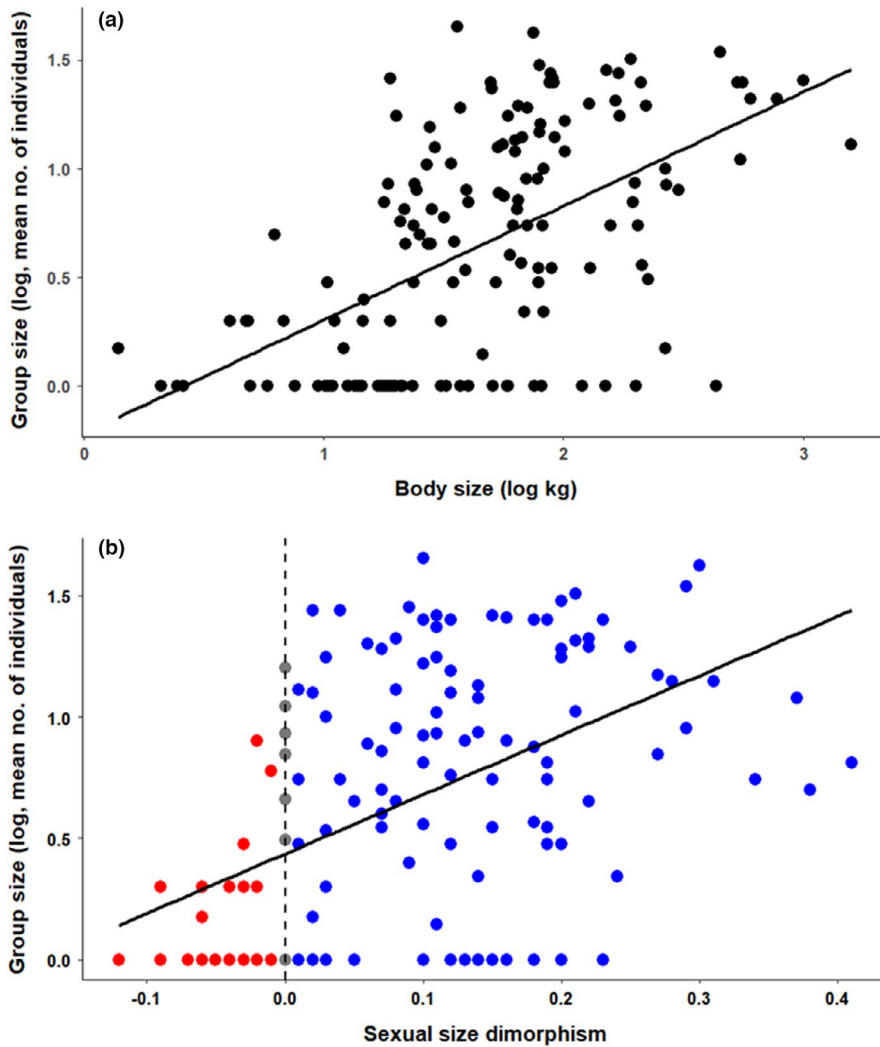
FIGURE 4 Group size in relation to (a) body size and (b) sexual size dimorphism in ungulates. See statistics in Table 1
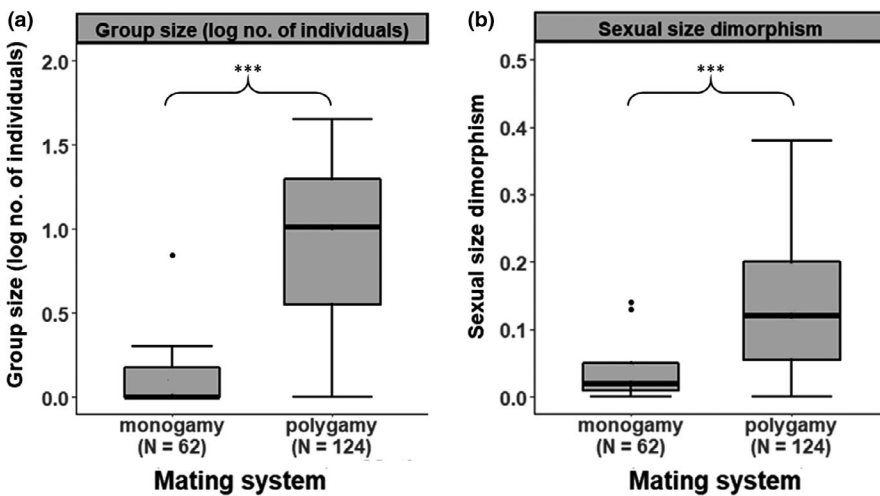
FIGURE 5 Mating system in relation to (a) group size and (b) sexual size dimorphism in ungulates. *** indicates significant differences (p < .001). See statistics in Table 1

Our path analysis—consistent with a recent re-analysis of Crook (1964) hypotheses of weavers social organization (Song et al., 2021)—suggests that field-based intuition can identify evolutionary scenarios that are supported by modern phylogenetic analyses. However, both our work on ungulates and Song et al.

(2021) on weavers suggest novel relationships not envisaged by Jarman and Crook, respectively. For example, phylogenetic confirmatory path analysis has uncovered a direct effect of body size on group size in ungulates. A possible explanation is that parallel with increased body size predation risk also increased which may

have favoured the evolution of different anti-predator strategies, like group living (Krause & Ruxton, 2002). The direct effect of species' ecology on mating system was also a new relationship uncovered by the phylogenetic path analysis. Jarman seems to have considered only the social route to polygamy, although polygamy may have a direct ecological route as well: structure of the habitat and feeding style, due resource distribution, should promote the opportunity to defend key resources and/or mates. Without favourable ecological conditions, maintaining polygamy can be too costly; therefore, animals may adopt alternative strategies (Emlen & Oring, 1977).

The best path model does not support one element of Jarman's hypothesis: the effect of body size on feeding style. This can be a consequence of that other variables—not included in our study—influenced feeding style (e.g. anatomical changes) and/or methodological limitations; for example, the high ratio of binary variables and multi-collinearity between some predictors can affect the results of phylogenetic path analysis. Future comparative analyses with refined data could shed light on these alternatives.

Recent studies, however, suggest additional ecological and social factors in the evolution of mating systems that have not been envisaged in Jarman's time. First, population density seems to have a major impact on mating system variation in mammals (Lukas & Clutton-Brock, 2013). Specifically, when densities are low, males cannot monopolize several females, so that monogamy more likely occurs than polygamy (Lukas & Clutton-Brock, 2013). Second, harsh and/or extreme climate has been shown to facilitate cooperation between group members and also may induce male and female permanent association and males' involvement in care (Shen et al., 2017; West & Capellini, 2016). Such effects of extreme climatic events have been shown in birds and in rodents, although their influence may be more general (Firman et al., 2020; Rubenstein & Lovette, 2007). Third, recent studies suggest that the social environment—as characterized by adult sex ratio (ASR)—can facilitate certain mating systems and parenting in humans and birds since when one sex is more abundant in the population than the other, this would increase the mating opportunities of the rarer sex and thus facilitate polygamy by the rarer sex (Liker et al., 2013; Schacht & Borgerhoff Mulder, 2015; Schacht et al., 2017; Székely et al., 2014). Phylogenetic comparative analyses will be useful to explore these processes that go beyond Jarman's conjectures.

Our study, however, has five main limitations. First, here we focus on Jarman's scenario, and we did not explicitly investigate additional variables that may influence social organization, for example timing of breeding and/or spatial and temporal variation in resources (Clutton-Brock, 1989, 2016; Davies et al., 2012). Further analyses are needed to address these aspects of ungulate social organization. Second, we assume a single data point for each variable for a given species. This may not be the case, since body size, group size and mating systems may all be variable within a species. This variation could be due to age differences or to geographic variation that produces differences between distant populations. Jaeggi

et al. (2020) recently argued that majority of ancestral and extant ungulates exhibit variation in their social behaviour and comparative studies should consider intraspecific variations in the analyses of social organization. Although we fully agree with the spirit of Jaeggi et al. (2020), we note that lack of data from different breeding populations could limit the power of such analyses especially if the objective is to explore broad-scale patterns for hundreds of species. Third, we used a single phylogenetic hypothesis, and this can be erroneous. With increasing availability of genomic data, this limitation can be overcome by using hundreds of phylogenetic hypotheses simultaneously. Fourth, here we used bivariate PGLS models to obviate interdependence between explanatory variables and therefore some association between variables may stay uncovered. To resolve interdependence among ecological, social and life-history data, we need further analysis with higher resolution data. Finally, phylogenetic comparative analyses are designed to investigate associations but not causation. Even in phylogenetic path analyses, the directionality of associations is confirmatory rather than causative unlike as in an experimental work.

In conclusion, our study supports Jarman's scenario by suggesting that body size is an important trait in social evolution of ungulates. To satisfy their metabolic needs, different species live in several different habitats across the globe; hence, it demands different strategies in different species to thrive. Thus, wide range of social organization evolved in ungulates, together with various reproductive strategies. To further advance studies of social organization, it will be important to quantify the ecology, behaviour and natural history of yet unstudied species. A more detailed understanding on ungulates' social organization will provide important contribution to understanding of evolution of Artiodactyla and move forward evolutionary understanding and the conservation of threatened species and their habitats.

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CONFLICT OF INTEREST

The authors have declared that no competing interests exist.

PEER REVIEW

The peer review history for this article is available at https://publo ns.com/publon/10.1111/jeb.13782.

DATA AVAILABILITY STATEMENT

Data and all scripts will be made publicly available. All relevant data are within the paper and its electronic supplementary material and are available from the Dryad Digital Repository: https://doi. org/10.5061/dryad.000000033

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