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Social organization in ungulates: revisiting Jarman's hypotheses

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Professor Wolf Blanckenhorn
University of Zurich
Editor-in-Chief
Journal of Evolutionary Biology

25 February 2021

Dear Professor Blanckenhorn,

Please find attached our revised manuscript, "*Social organization in ungulates: revisiting Jarman's hypotheses*" for consideration as Research Paper in *Journal of Evolutionary Biology*.

We thank you, the Associate Editor for the thorough evaluation. We carefully checked all comments and suggestions, and carried out the revisions to address these issues. Please find attached the revised manuscript and our point-by-point responses to the Editor. We would also like to take this opportunity to express our thanks to the Editor for the positive feedback and helpful comments for correction or modification.

In addition, we carefully checked the whole text and cleared up ambiguities. We also changed the Discussion to highlight the scientific significance of re-analysing another textbook example of comparative sociobiology by Song, Liker, Yang & Székely, *American Naturalist*, in revision*. Given the significance of Jarman's analyses and the novel insights our work have produced, we believe these results will interest a broad range of evolutionary biologists.

We very much hope the revised manuscript is accepted for publication in *Journal of Evolutionary Biology*.

Sincerely yours,

A handwritten signature in blue ink, appearing to read 'Karola Szemán'.

Karola Szemán
PhD student, on behalf of all authors

*Song, Z., Liker, A., Liu, Y. & Székely, T. Evolution of social organization: phylogenetic analyses of ecology and sexual selection in weavers. *American Naturalist*, in revision.

Social organization in ungulates: revisiting Jarman's hypotheses

Responses to reviewers' comments

Text by the Editor and Reviewers are in Times New Roman font, whereas our responses in **bold Arial Black font**. Line numbers refer to the revised MS.

EDITOR'S COMMENTS TO THE AUTHORS

Editor: Dr Julia Schroeder
Comments to the author:

Dear Author,

Thank you for submitting your manuscript "Social organization in ungulates: revisiting Jarman's hypotheses" (JEB ms JEB-2020-00430.R1) to the Journal of Evolutionary Biology. I have found a number of points that preclude it from being acceptable for publication in its present form. I also liked your paper, and I am therefore willing to consider it further for acceptance provided that you revise it appropriately along the lines recommended below.

We appreciate the positive evaluation.

Minor comments:

Abstract - ten families (instead of 10 families)

Thank you, corrected (Line 8).

Introduction -third to last paragraph, last sentence: "a well-cited study as indicated by 1462 citations" Do you mean "by 1462"? And maybe update the numbers while you're at it

Thank you, corrected and updated (Lines 76-77).

Material and Methods - first sentence - "thammals" - is it "the mammals"?

Thank you, corrected (Line 104).

Statistical analysis, second paragraph:
"hypothesizes" - do you mean "hypotheses"?

Thank you, corrected (Line 139).

Can you clarify to me what you mean with "bivariate models" - you write you only have one response (body size), not two, as is usual in a bivariate model.

Bivariate models could be used in different contexts, although it seems we use it in the commonest sense (Wikipedia accessed 24 February 2021: "Bivariate analysis ... involves the analysis of two variables (often denoted as X , Y), for the purpose of determining the empirical relationship between them." We clarified the models' structure in the text (Line 139).

As to your "third set" of PGL analyses, this requires some clarification in the text. You say two included group size as explanatory variable - was that the only explanatory variable - please state that. The third model please also again confirm what is the response - I assume mating system? If so, how is this different from the previous model?

Thank you, we added explanation to this part (Lines 147-152).

Phylogenetic path analysis - you say you repeated this process for each variable - can you confirm in text which variables that are.

Thank you, we clarified the list of the used variables (Line 170).

Discussion

middle of third paragraph: "Giraffa camelopardalis) are taller than females" - missing space

Thank you, corrected (Line 267).

Second to last paragraph, first sentence: "Our study, however, have several" -> has

Thank you, corrected (Line 332).

1 Social organization in ungulates: revisiting Jarman's hypotheses

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10

11 Running title: Ungulate social evolution

12

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15

16 Data Accessibility Statement: Data and all scripts will be made publicly available

17

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22

23 **Acknowledgement**

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36 Competing interests: The authors have declared that no competing interests exist.

1 Social organization in ungulates: revisiting Jarman's hypotheses

2 **Abstract**

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

19

20 **Keywords:** Artiodactyla, social evolution, mating system, group size, habitat, feeding style,
21 phylogenetic path analysis, phylogenetic generalized least squares

22

23 **Introduction**

24 One of the core tenets in behavioral ecology and sociobiology is that spatial and temporal
25 distribution of resources influence social organization (Crook, 1964; Wilson, 1975; Alcock,
26 2013; Davies et al., 2012). Thus, the availability of food resources, breeding sites along with
27 predators and parasites are expected to influence territoriality, group formation and colonial
28 breeding (Estes, 1974; Krause & Ruxton, 2002; Clutton-Brock, 2016). Specifically, group
29 formation and group size are thought to be influenced by various costs and benefits of group
30 living in a particular environment. Benefits of group formation, for instance enhanced feeding
31 efficiency, defense against predators, access to potential mates, may be negated by the cost of
32 group living such as increased competition for food and mates, increased detectability by
33 predators, and a higher chance of infections by diseases and parasites (Krause & Ruxton,
34 2002; Davies et al., 2012; Clutton-Brock, 2016).

35
36 Artiodactyla (antelopes, deer, bovids and relatives, approx. 250 species; ungulates henceforth)
37 is one of the most diverse mammalian order, since body size vary several magnitudes between
38 species, they inhabit six continents and they live in diverse habitats that include deserts,
39 grasslands and forests. In addition, their social behaviour, breeding system and associated
40 traits such as sexual size dimorphism (SSD) are also highly variable (Jarman, 1974; Pérez-
41 Barbería et al., 2002; Wilson & Mittermeier, 2011; Clutton- Brock, 2016). In a seminal study,
42 Jarman (1974) conjectured that interspecific variation in ecology and social organization of
43 ungulates are associated. Following Crook's (1964) pioneering work on social organization in
44 weaverbirds (*Ploceidae*), Jarman (1974) laid the foundations of behavioral ecology and
45 sociobiology by adopting an ecological cross-species thinking that has become known as the
46 comparative approach (Felsenstein, 1985; Harvey & Pagel, 1991).

47

48 Jarman (1974) focused on African antelopes, and he recognized five groups based on their
49 ecology, primarily habitat and feeding style. He noticed that body size, mating systems,
50 sexual size dimorphism and anti-predator behaviour tend to match the ecological conditions.
51 He argued that body size should be associated with metabolic rate since metabolic
52 requirement per unit weight is higher in small-bodied species. Therefore, small-bodied
53 ungulates are expected to select more nutritious and higher calorie content food items such as
54 fresh leaves and berries. Since these items are often scarce and dispersed, small-bodied
55 ungulates are expected to hold territories alone or in pairs to monopolize food-resources. In
56 contrast, large-bodied species can feed on lower quality food in bulk such as grasses, and
57 since this type of food is less defensible economically the large-bodied ungulates roam in
58 herds. Jarman (1974) synthesized these relationships into an evolutionary scenario whereby
59 polygamy and sexual size dimorphism was a consequence of habitats (i.e., closed forests
60 versus open savannah) and feeding styles (i.e., browsers versus grazers) via metabolic
61 demands of having a small or large body size (Fig. 1a). Jarman's arguments were based on the
62 idea that habitat types and feeding styles may influence the spatial distribution of females, that
63 in turn have knock-on effect on males' strategy to secure mating rights. Females' tendency to
64 aggregate seasonally or all-year-round create an opportunity for males to monopolize mating
65 rights and thus facilitate the evolution of polygamous matings. Given the high mating stakes
66 in polygamous systems, male-male conflicts are expected to intensify leading to increased
67 male body size, and ultimately, to extensive sexual size dimorphism and elaboration of
68 different weaponry including horns and antlers (Geist, 1966; Jarman, 1974).

69

70 Jarman (1974) stimulated much follow up studies and it became one of the best-cited
71 examples of the impact of resource distribution on social organization (Emlen & Oring, 1977;
72 Greenwood, 1980; Wittenberger, 1981; Clutton-Brock, 1989; Shultz et al., 2011; Clutton-

73 Brock, 2016; Bravo et al., 2019; Jaeggi et al., 2020; Lukas & Clutton-Brock, 2020; Winterton
74 et al., 2020). As a result, the ungulates became a prime example of comparative approach
75 (Wittenberger, 1981; Harvey & Pagel, 1991; Davies et al., 2012; Clutton-Brock, 2016).
76 Consistently, it is a well-cited study as indicated by 1484 citations in Web of Science and
77 2359 citations in Google Scholar (accessed on 24.02.2021).

78

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

92

93 Here we revisit Jarman's (1974) hypotheses using phylogenetically controlled analyses.
94 Using data from 230 ungulate species worldwide from 10 families, recent phylogenetic
95 hypotheses and modern phylogenetic methods, we investigate (1) whether habitat type and
96 feeding style predict body size, (2) whether habitat and feeding style predict group size, and
97 (3) the associations between group size, mating system and sexual size dimorphism. By using

98 phylogenetic confirmatory path analyses (Santos and Cantanella, 2011; Santos, 2012;
99 Gonzalez-Voyer & von Hardenberg, 2014), (4) we also test the fits of several evolutionary
100 hypotheses – including Jarman’s scenario – to the data.

101

102 **Material and Methods**

103 Data Collection

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

113

114 We used group size as one of the indicators of social organization defined as the mean
115 number of individuals in a group. For species where there were no available data for mean
116 number of individuals, we calculated it as the mean value of minimum and maximum group
117 size. We used mating system as a further proxy of social organization, defined as a binary
118 variable: we considered a species polygamous if the individuals typically have more than one
119 mate per breeding season and monogamous if individuals of both sexes have only one mate
120 per breeding season. Habitat types were classified as open or closed: open-habitat dwelling
121 species were those that spend most of the year in habitats with low vegetation like grasses
122 whereas closed-habitat dwelling species were those that live in dense habitats such as forests.

123 Feeding style was scored as a binary trait: grazer or not-grazer. Grazers were those species
124 that predominantly feed on grasses, whereas non-grazers feed on the leaves and branches of
125 trees and shrubs and may also consume fruits, mushrooms or even some animals. Male and
126 female body size were expressed in kg, and we calculated average body size as the average of
127 female and male mass. We calculated sexual size dimorphism (SSD) as $\log_{10}(\text{male body size} /$
128 $\text{female body size})$ following Fairbairn et al. (2007).

129

130 Statistical Analyses

131 *Phylogenetic Generalized Least Squares Models*

132 We analyzed the relationships between the variables using Phylogenetic Generalized Least
133 Squares (PGLS, Freckleton et al., 2002), that controls for the phylogenetic non-independence
134 among species. The analyses were conducted in the R software (version 3.5.3.; R Core Team,
135 2016), with package ‘caper’ (Orme & Freckleton, 2013). We used the phylogenetic tree
136 published by Bininda-Emonds et al. (2007) to represent phylogenetic relationships between
137 species, because this is the most complete phylogenetic tree for mammals.

138

139 To test specific hypotheses, we conducted eight bivariate (with one response variable and one
140 explanatory variable in each model) PGLS models. We grouped the models into three sets,
141 according to the structure of relationships proposed by Jarman (Fig. 1a). The first set of
142 analyses investigated the putative factors related to body size. The bivariate models included
143 habitat type and feeding style as explanatory variables (one predictor in each model) and body
144 size as response variable. The second set of models focused on group size: here we had three
145 bivariate models in which group size was the response variable and body size, feeding style
146 and habitat type were the explanatory variables. The third set of PGLS analyses comprised of
147 three bivariate models. The first model included group size as response variable and SSD as

148 explanatory variable. In the second model group size was the response variable and mating
149 system appeared as explanatory variable. The third model investigated the association
150 between mating system and SSD where SSD was included as response variable and mating
151 system as explanatory variable. Group size and body size were log-transformed prior to the
152 analysis.

153

154 *Phylogenetic Path Analysis*

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

159

160 To find the best fitting path model to the data, we followed the method proposed by Santos
161 and Canatella (2011) and Santos (2012), using the R package ‘piecewiseSEM’ (Lefcheck,
162 2016). Before the path analysis we transformed the data phylogenetically, so we were able to
163 control for phylogenetic relatedness among species (Santos, 2012). For the latter purpose, we
164 (1) determined Pagel’s λ (a measure of the strength of phylogenetic signal in the data)
165 separately for each variable by PGLS models using maximum likelihood, (2) used this
166 variable-specific λ value to re-scale the phylogenetic tree to a unit tree, and (3) used the
167 transformed tree to calculate phylogenetically independent contrasts for the variable by the
168 ‘pic’ function of the ‘ape’ R package (Paradis, 2012). We repeated this process for each
169 variable (body size, feeding style, habitat type, group size, mating system and SSD), and the
170 resulting phylogenetically transformed values were used for fitting path models (see Santos
171 (2012) for a similar approach).

172

173 Our approach for finding the best fitting model was based on a model selection procedure
174 proposed by Santos and Canatella (2011) and Santos (2012). We used Jarman's (1974)
175 hypothesis as a starting model (Fig. 1a). According to this model, we created a full initial (i.e.
176 just-identified) model which included all the pathways between the variables (Supplementary
177 material 2 Fig. S1). After fitting the full initial model, we excluded the non-significant
178 pathways from the model one-by-one. In each step, we eliminated the path which had the path
179 coefficient with the highest p value, then re-fitted the new, reduced model to the data. We had
180 seven steps until a model with the acceptable fit was reached. Model fit was evaluated by
181 Fisher C statistics. The C statistic tests the goodness of fit of the whole path model, and the
182 model is rejected, i.e. it does not provide a good fit to the data, if the result of this C statistic is
183 statistically significant (and conversely a statistically non-significant result means acceptable
184 fit; Lefcheck 2016). In the accepted model all the pathways had path coefficient with less than
185 0.05 p value (Supplementary material 2 Table S2).

186

187 **Results**

188 Diversity in Ecology and Social Organisation of Ungulates

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

198

199 Ecology, Body Size and Group Size

200 Both feeding style and habitat correlate with body size, since grazers are larger than not-
201 grazers (PGLS, $F_{159} = 6.059$, $p = 0.014$, $N = 148$ species; Table 1, Fig. 3a), and ungulates that
202 live in open habitats are larger than those that live in closed habitats (PGLS, $F_{147} = 23.81$, $p <$
203 0.01 , $N = 148$ species; Table 1, Fig. 3b). These differences are consistent with sex specific
204 data (Supplementary material 2 Fig. S4).

205

206 Feeding style and habitat also associate with group size, since grazers live in larger groups
207 than browsers (PGLS, $F_{175} = 26.14$, $p < 0.001$, $N = 177$ species; Table 1, Fig. 3c), and open-
208 habitat dwelling species live in larger groups than those in closed habitats (PGLS, $F_{157} =$
209 22.40 , $p < 0.001$, $N = 159$ species; Table 1, Fig. 3d). Consistently, body size and group size
210 are associated since large-bodied species live in groups whereas small ones usually live alone
211 or in pairs (PGLS, $F_{148} = 31.73$, $p < 0.01$, $N = 148$ species; Table 1, Fig. 4a).

212

213 Mating System and Sexual Size Dimorphism (SSD)

214 Consistently with Jarman's arguments, group size is associated with the extent of sexual size
215 dimorphism, since species that live in larger groups exhibit more male-biased SSD (PGLS,
216 $F_{148} = 23.90$, $p < 0.001$, $N = 150$ species; Table 1, Fig. 4b). Furthermore, polygamous
217 ungulates live in larger groups than monogamous ones (PGLS, $F_{92} = 76.61$, $p < 0.001$, $N = 94$
218 species; Table 1, Fig. 5a). Consistently, SSD and mating system are also associated: in
219 polygamous ungulates the males are usually larger than females, whereas monogamous
220 ungulates typically exhibit monomorphism or female-biased SSD (PGLS, $F_{100} = 53.95$, $p <$
221 0.001 , $N = 102$ species; Table 1, Fig. 5b). The diagnostic plots for the models are provided in
222 Supplementary Material Fig. S5.

223

224 Phylogenetic Path Analyses

225 Phylogenetic confirmatory path analysis supported most components of Jarman's (1974)
226 scenario, although it also uncovered several additional relationships (Fig. 1a, b). The best
227 fitting path model has statistically acceptable fit to the data (Fisher's $C = 15.7$, $df = 12$, $p =$
228 0.206 ; Fig. 1b). Consistently with Jarman's arguments, body size is associated with habitat
229 type, and both habitat type and feeding style are associated with group size in the best
230 supported model (Fig 1b). Furthermore, the proposed associations were confirmed between
231 mating system, group size and SSD (Fig. 1., Supplementary material 2 Table S2), although
232 not the one between body size and feeding style (Fig. 1., Supplementary material 2 Table S2).
233 Importantly, the best model uncovered novel relationships that were not conjectured by
234 Jarman that include association between body size and group size, and those between habitat
235 type, feeding style and mating system (Fig. 1., Supplementary material 2 Table S2).

236

237 **Discussion**

238 Our study has revealed three major patterns. First, increased body size appears to trigger the
239 evolution of different social systems and mating strategies among ungulates (Geist, 1974;
240 Bell, 1971; Perez-Barbería et al., 2002, Davies et al. 2012; Clutton-Brock, 2016). These
241 results support Jarman's (1974) hypotheses and expose robust differences among different
242 species. Body size is the main predictor of ecological variables, whereas ecological variables
243 have significant effect on social organization. To satisfy their metabolic requirements, small-
244 bodied species need lower amount of food but higher quality, compared to large-bodied
245 species. Because of this trade-off between food quality and quantity, small-bodied ungulates
246 have more time during the day to find appropriate food items compared to larger species
247 (Bell, 1971; Jarman, 1974; Owen-Smith & Novellie, 1982). Since high-quality food items

248 appear to occur in higher density in closed habitats (e.g. forest, shrublands), small-bodied
249 ungulates tend to be closed-habitat dwelling species, whereas larger species forced to live in
250 open fields where they can consume substantial amount of food (Kleiber, 1947; Bell, 1971;
251 Jarman, 1974; Jarman & Sinclair, 1979).

252

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

258

259 Second, our study show that group size was associated with different mating strategies among
260 Artiodactyls. Living in groups increases the probability of polygamy and may amplify sexual
261 selection (Jarman, 1974; Pérez-Barbería et al., 2002; Gordon & Pagel, 2002). More intense
262 sexual selection could be responsible for larger SSD in polygamous species than in
263 monogamous ones (Pérez-Barbería & Grodon, 2000; Pérez-Barbería et al., 2002). Sexual size
264 dimorphism may also be advantageous for dividing the resources between males and females
265 that can reduce intersexual competition (Fairbairn et al. 2007). For example, male kudu
266 (*Tragelaphus strepsiceros*) and giraffes (*Giraffa camelopardalis*) are taller than females and
267 capable of feeding on tall bushes and trees (Ginnet & Demmet, 1997; Mysterud, 2000; du
268 Toit, 2005; Main and du Toit, 2005). In red deer (*Cervus elaphus*) and some African
269 antelopes males and females live separately during the year and exhibit different habitats,
270 feeding strategies and time-budgets (Staines & Crisp, 1978; Clutton-Brock et al., 1982;
271 Conrad et al., 2000; du Toit, 2005; Main & du Toit, 2005; Lindsay, 2011). The latter patterns
272 occur in other mammals as well: in arboreal primates males are heavier and unable to climb as

273 high as females in the canopy, thus their foraging behaviour differs from the females'
274 foraging strategies (Clutton-Brock, 1977; Grassi, 2002). These ecological differences between
275 sexes may imply different energy intake rates and energy requirement of males and females in
276 sexually dimorphic species (Clutton-Brock et al., 1987; Pérez-Barbería & Gordon, 1998).
277 This in turn would suggest that some males in strongly dimorphic species may be forced into
278 secondary habitats due the strong intersexual competition for females and this may increase
279 mortality among males (Bowyer 2004; du Toit 2015, Clutton-Brock 2016). Due to the variety
280 of ecological and sexual selective processes between males and females that have
281 implications for body sizes, the jury is still out there how these different processes shape body
282 sizes of males, females and/or of both sexes (reviewed by De Lisle 2019).

283

284 Third, using phylogenetic path analysis we confirmed several elements of Jarman's scenario,
285 and also highlighted additional associations. As proposed by Jarman (1974), our best model
286 supports that body size is related to habitat type, whereas a species' ecology predict group
287 size, group size presages the type of mating system and mating system predicts the degree of
288 SSD. It appears that the available forest habitats have decreased in the Miocene (Janis, 1982),
289 and forest fragmentation may have forced ancestral ungulates into open habitats. Increased
290 group size possibly evolved to reduce predation risk in the new habitat. With large social
291 groups possibly came the opportunity for males to monopolize mating opportunities and this
292 favored the evolution of polygamy. With polygamy male-male conflicts also escalated, which
293 possibly led to extensive sexual dimorphism and the appearance of weaponry (Geist, 1974;
294 Pérez-Barbería et al., 2002).

295

296 Our path analysis – consistently with a recent re-analysis of Crook (1964) hypotheses of
297 weavers social organization (Song et al. unpublished data) – suggest that field based intuition

298 can identify evolutionary scenarios that are supported by modern phylogenetic analyses.
299 However, both our work on ungulates and Song et al. (unpublished data) on weavers suggest
300 novel relationships not envisaged by Jarman and Crook, respectively. For example,
301 phylogenetic confirmatory path analysis has uncovered a direct effect of body size on group
302 size in ungulates. A possible explanation is that parallel with increased body size predation
303 risk also increased which may have favoured the evolution of different anti-predator
304 strategies, like group living (Krause & Ruxton, 2002). The direct effect of species' ecology on
305 mating system was also a new relationship uncovered by the phylogenetic path analysis.
306 Jarman seems to have considered only the social route to polygamy, although polygamy may
307 have a direct ecological route as well: structure of the habitat and feeding style, due resource
308 distribution, should promote the opportunity to defend key resources and/or mates. Without
309 favourable ecological conditions, maintaining polygamy can be too costly, therefore animals
310 may adopt alternative strategies (Emlen & Oring, 1977).

311

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

318

319 Recent studies, however, suggest additional ecological and social factors in the evolution of
320 mating systems that have not been envisaged in Jarman's time. First, population density
321 seems to have a major impact on mating system variation in mammals (Lukas & Clutton-
322 Brock, 2013). Specifically, when densities are low, males cannot monopolise several females,

323 so that monogamy more likely occur than polygamy (Lukas & Clutton-Brock, 2013). Second,
324 harsh and/or extreme climate has been shown to facilitate cooperation between group
325 members and also, may induce male and female permanent association and males'
326 involvement in care (West & Capellini, 2016; Shen et al., 2017). Such effects of extreme
327 climatic events have been shown in birds and in rodents, although their influence may be
328 more general (Rubenstein & Lovette, 2007; Firman et al., 2020). Third, recent studies suggest
329 that the social environment – as characterised by adult sex ratio (ASR) – can facilitate certain
330 mating systems and parenting in humans and birds since when one sex is more abundant in
331 the population than the other, this would increase the mating opportunities of the rarer sex,
332 and thus facilitate polygamy by the rarer sex (Liker et al., 2013; Székely et al. 2014; Schacht
333 et al., 2015, 2017). Phylogenetic comparative analyses will be useful to explore these
334 processes that go beyond Jarman's conjectures.

335
336 Our study, however, has five main limitations. First, here we focus on Jarman's scenario, and
337 we did not explicitly investigate additional variables that may influence social organization,
338 for example timing of breeding and/or spatial and temporal variation in resources (Clutton-
339 Brock, 1989; Davies et al., 2012; Clutton-Brock 2016). Further analyses are needed to address
340 these aspects of ungulate social organization. Second, we assume a single data point for each
341 variable for a given species. This may not be the case, since body size, group size and mating
342 systems may all be variable within a species. This variation could be due to age differences,
343 or to geographic variation that produces differences between distant populations. Jaeggi et al.
344 (2020) recently argued that majority of ancestral and extant ungulates exhibit variation in their
345 social behavior and comparative studies should consider intraspecific variations in the
346 analyses of social organization. Whilst we fully agree with the spirit of Jaeggi et al. (2020),
347 we note that lack of data from different breeding populations could limit the power of such

348 analyses especially if the objective is to explore broad-scale patterns for hundreds of species.
349 Third, we used a single phylogenetic hypothesis, and this can be erroneous. With increasing
350 availability of genomic data, this limitation can be overcome by using hundreds of
351 phylogenetic hypotheses simultaneously. Fourth, here we used bivariate PGLS models to
352 obviate interdependence between explanatory variables and therefore some association
353 between variables may stay uncovered. To resolve interdependence among ecological,
354 social and life-history data, we need further analysis with higher resolution data. Finally,
355 phylogenetic comparative analyses are designed to investigate associations but not causation.
356 Even in phylogenetic path analyses, the directionality of associations are confirmatory rather
357 than causative such as in an experimental work.

358

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

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547 **Figure legends**

548 **Figure 1.** Social evolution in ungulates. (A) An ecological scenario proposed by Jarman
549 (1974), and (B) best-fit model in phylogenetic confirmatory analyses (Fisher's $C = 15.689$, df
550 $= 12$, $p = 0.206$). We provide path coefficients for each pathway. Width of the arrows indicate
551 the robustness of a particular pathway.

552

553 **Figure 2.** Phylogenetic distribution of ecological and social variables in ungulates. For
554 illustrative purpose, continuous variables were split into binary variables as follows. For body
555 size and group size, we calculated the mean value of these variables, and species were split
556 whether below or above the mean for a given variable. Sexual size dimorphism (SSD) was
557 termed monomorphic if SSD was zero, whereas species with SSD larger than zero were
558 termed male-biased SSD, and species with SSD less than zero were termed female-biased
559 SSD. Note that Tayassuidae represented only on A, since we have no data on any species'
560 mating system from this family (See distribution of variables in S2 supplementary material
561 Table S1 and Fig. S2).

562

563 **Figure 3.** Ecology (habitat type, feeding style) of ungulates in relation to (A, B) body size and
564 (C, D) social organization. See statistics in Table 1.

565

566 **Figure 4.** Group size is related to (A) body size and (B) sexual size dimorphism in ungulates.
567 See statistics in Table 1.

568

569 **Figure 5.** Mating system in relation to (A) group size and (B) sexual size dimorphism in
570 ungulates. See statistics in Table 1.

571 Table 1: Ecology, body size and social organisation in ungulates using bivariate
 572 phylogenetically corrected generalized linear squares models (PGLS). Feeding style, habitat
 573 type and mating system were binary variables. Body size provided in kg. Sexual size
 574 dimorphism (SSD) was calculated as \log_{10} (male body size / female body size). Group size
 575 refers to the mean number of individuals per group. Group size and body size were *log*-
 576 transformed prior to the analyses. We provide parameter estimates with standard error ($\beta \pm$
 577 *SE*), adjusted R^2 , the corresponding *t* and *p* values and number of species (*N*). The diagnostic
 578 plots for the models are provided in Supplementary Material Fig. S5.

1. *Body size (response variable)*

	$\beta \pm SE$	adjusted R^2	<i>t</i>	<i>p</i> -value	<i>N</i>
Feeding style	-0.152 ± 0.061	0.031	-2.4636	0.014	161
Habitat type	0.371 ± 0.076	0.133	4.879	< 0.001	149

2. *Group size (response variable)*

	$\beta \pm SE$	adjusted R^2	<i>T</i>	<i>p</i> -value	<i>N</i>
Feeding style	-0.385 ± 0.075	0.125	-5.113	< 0.001	176
Habitat type	0.391 ± 0.082	0.119	4.732	< 0.001	159
Body size	0.359 ± 0.063	0.171	5.633	< 0.001	153

3.a *Sexual size dimorphism (response variable)*

	$\beta \pm SE$	adjusted R^2	<i>t</i>	<i>p</i> -value	<i>N</i>
Group size	0.077 ± 0.015	0.133	4.888	< 0.001	153
Mating system	0.137 ± 0.018	0.343	7.345	< 0.001	102

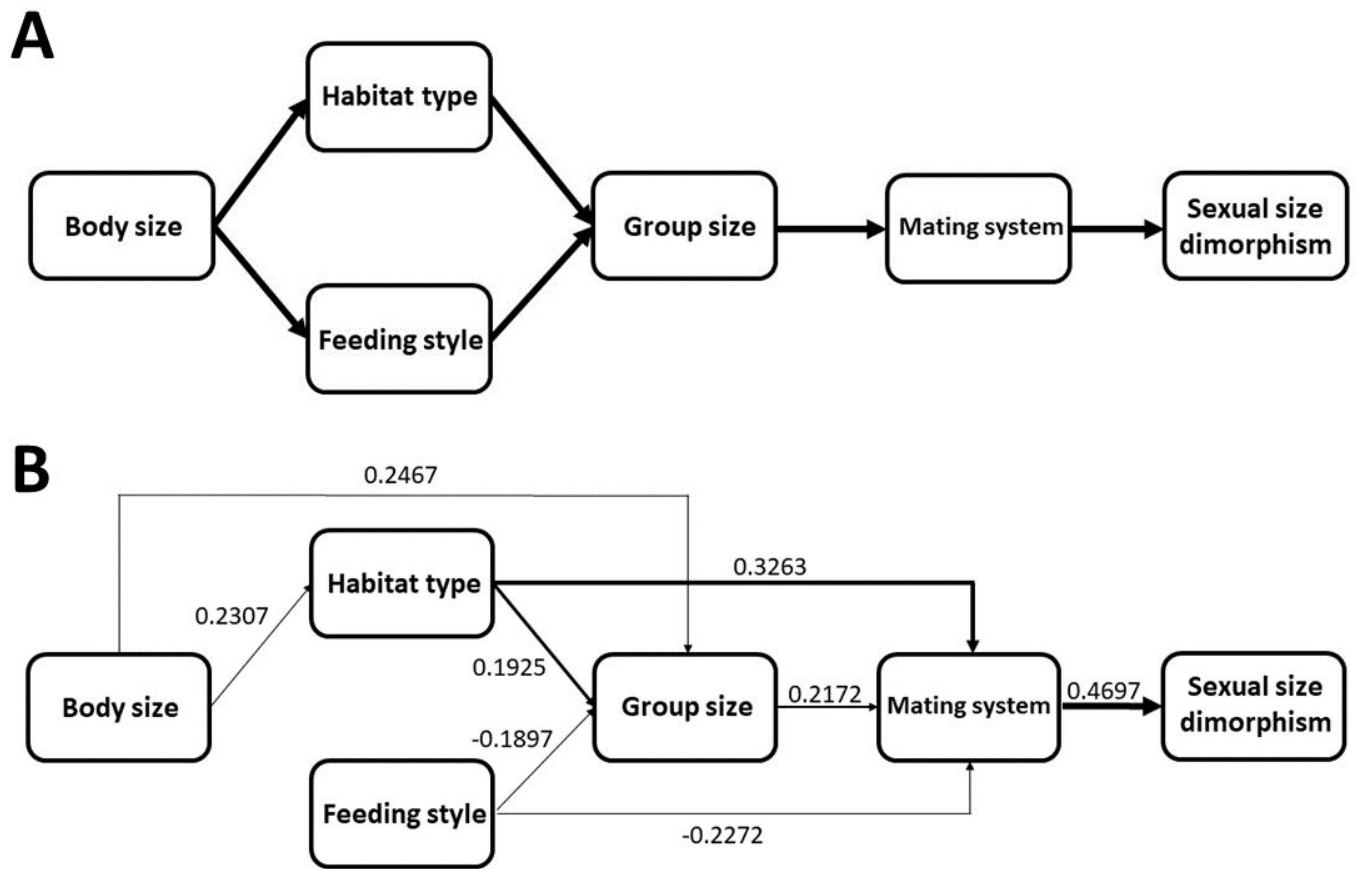
3.b Mating system (response variable)

	$\beta \pm \text{SE}$	adjusted R²	t	p- value	N
Group size	0.784 ± 0.091	0.418	8.637	< 0.001	94

579

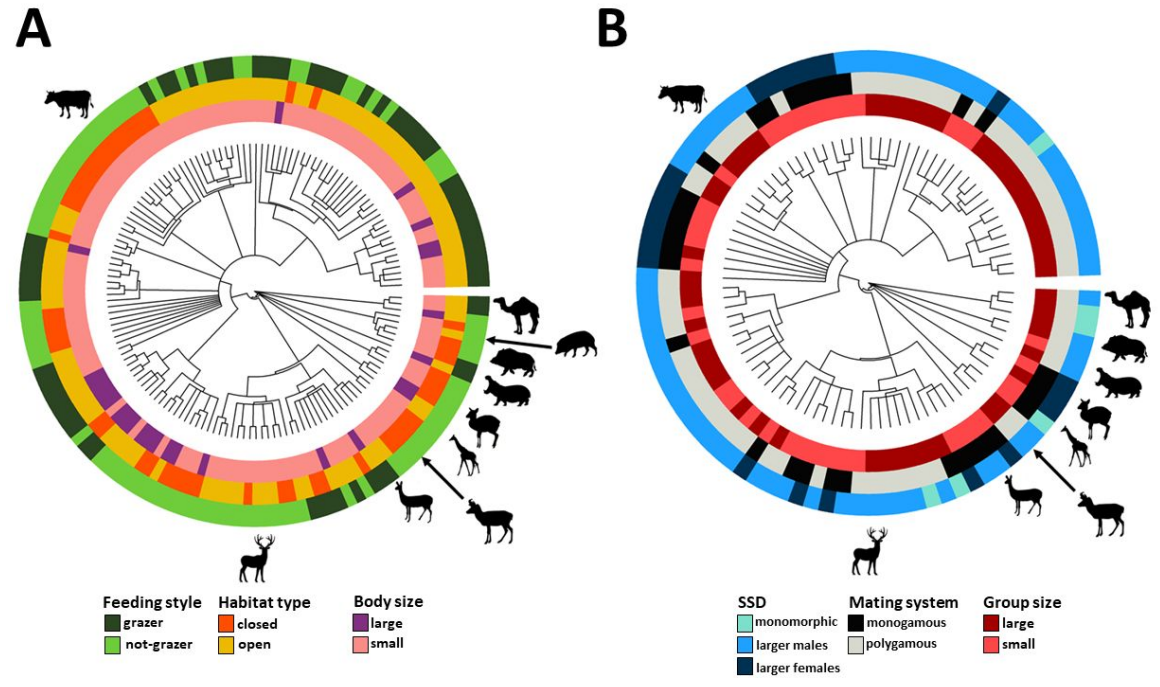
580

581 Figure 1

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583

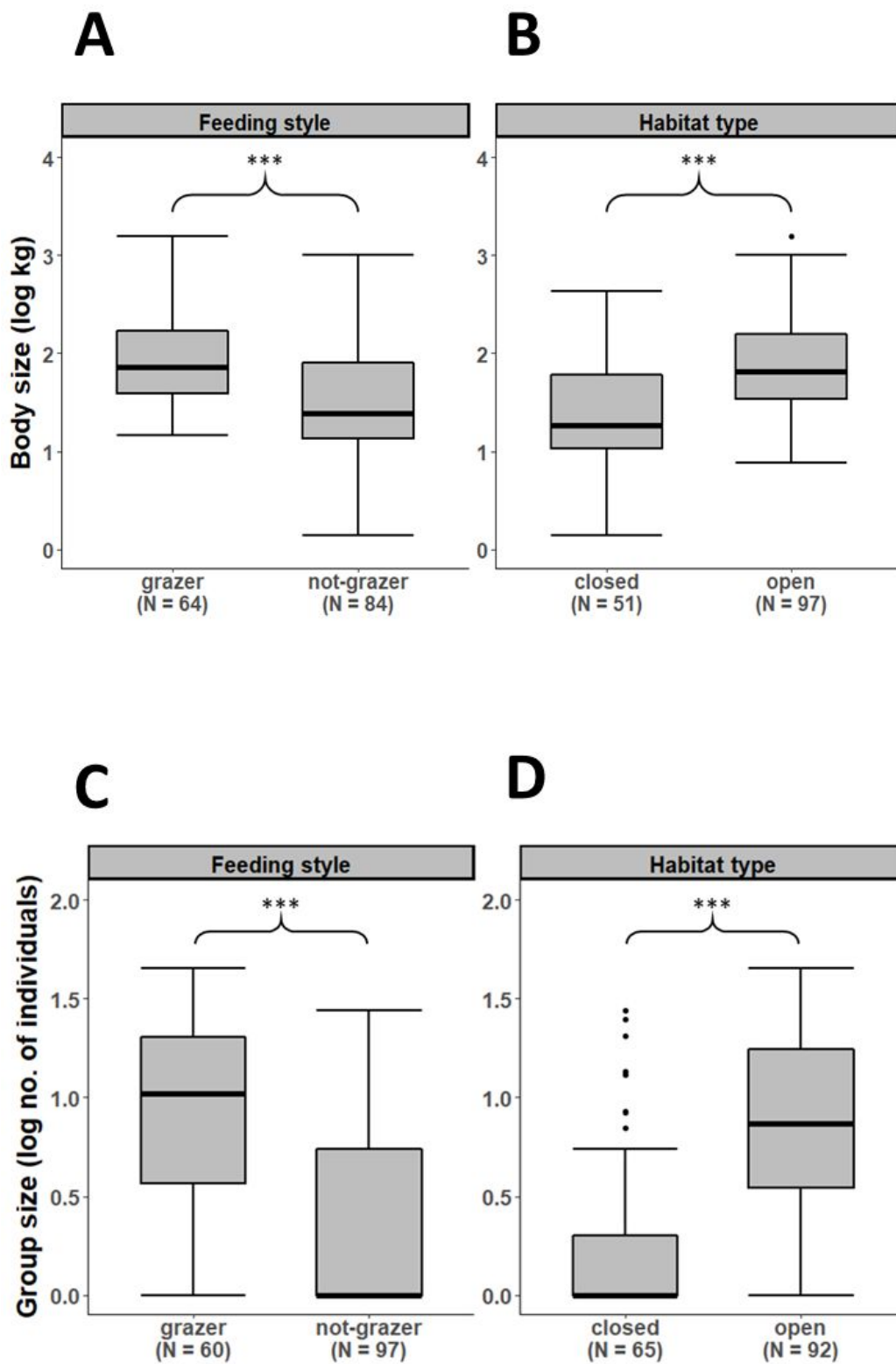
584 Figure 2

585



586

587 Figure 3

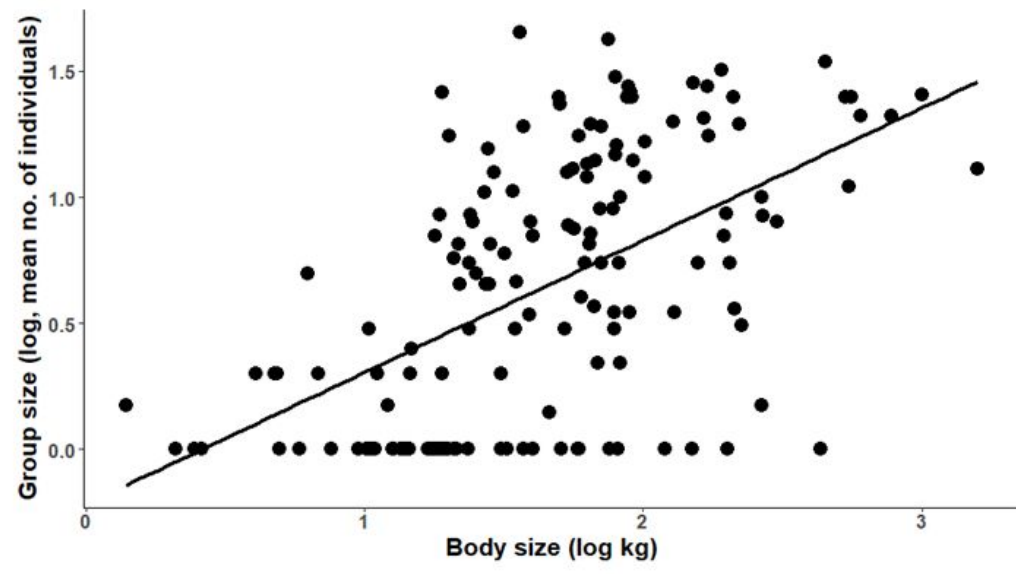


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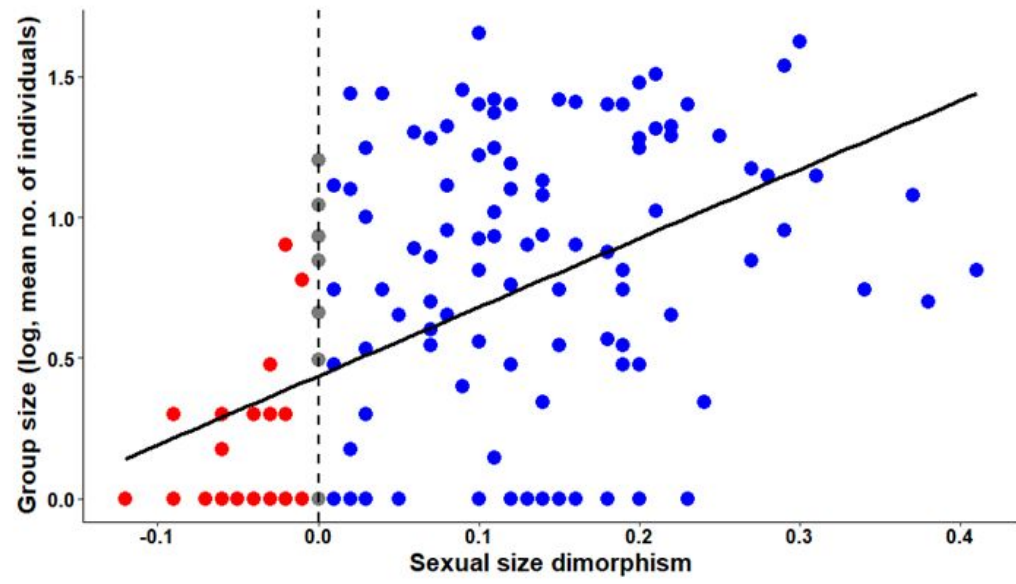
589

590 Figure 4

A

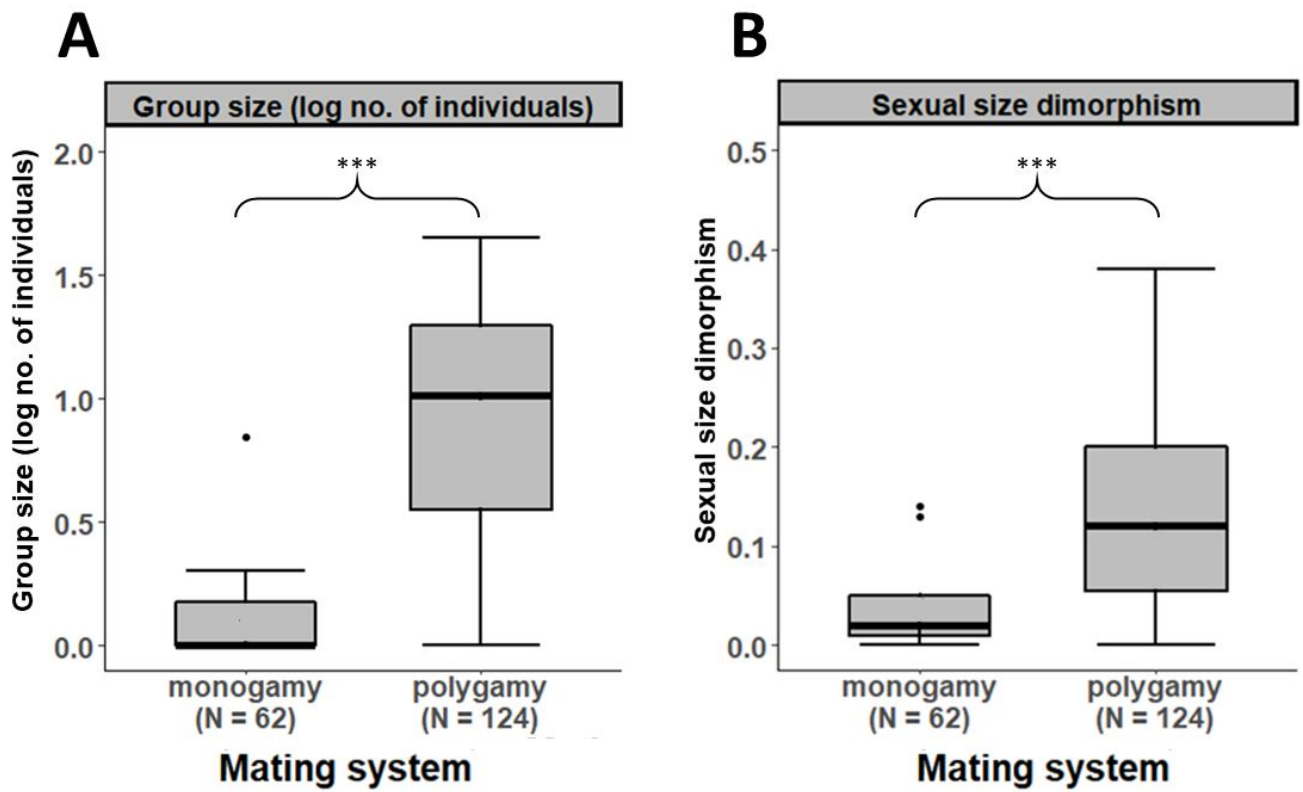


B



591

592 Figure 5



593

Species	Family	Feeding style_reference
Addax_nasomaculatus	Bovidae	Wilson and Mittermeier 20
Aepyceros_melampus	Bovidae	Wilson and Mittermeier 20
Alcelaphus_buselaphus	Bovidae	Wilson and Mittermeier 20
Alcelaphus_caama	Bovidae	Wilson and Mittermeier 20
Alcelaphus_lichtensteini	Bovidae	Wilson and Mittermeier 20
Alces_alces	Cervidae	Wilson and Mittermeier 20
Alces_americanus	Cervidae	
Ammodorcas_clarkei	Bovidae	Wilson and Mittermeier 20
Ammotragus_lervia	Bovidae	Wilson and Mittermeier 20
Antidorcas_marsupialis	Bovidae	Wilson and Mittermeier 20
Antilocapra_americana	Antilocapridae	Wilson and Mittermeier 20
Antilope_cervicapra	Bovidae	Wilson and Mittermeier 20
Axis_axis	Cervidae	Wilson and Mittermeier 20
Axis_calamianensis	Cervidae	Wilson and Mittermeier 20
Axis_kuhlii	Cervidae	Wilson and Mittermeier 20
Axis_porcinus	Cervidae	Wilson and Mittermeier 20
Babyrousa_babyrussa	Suidae	Wilson and Mittermeier 20
Babyrousa_bolabatuensis	Suidae	
Babyrousa_celebensis	Suidae	Wilson and Mittermeier 20
Babyrousa_togeanensis	Suidae	Wilson and Mittermeier 20
Damaliscus_hunteri	Bovidae	Wilson and Mittermeier 20
Bison_bison	Bovidae	Wilson and Mittermeier 20
Blastocerus_dichotomus	Cervidae	Wilson and Mittermeier 20
Bos_frontalis	Bovidae	Wilson and Mittermeier 20
Bos_grunniens	Bovidae	Wilson and Mittermeier 20
Bos_javanicus	Bovidae	Wilson and Mittermeier 20
Bos_sauveli	Bovidae	Wilson and Mittermeier 20
Boselaphus_tragocamelus	Bovidae	Wilson and Mittermeier 20
Bubalus_bubalis	Bovidae	Wilson and Mittermeier 20
Bubalus_depressicornis	Bovidae	Wilson and Mittermeier 20
Bubalus_mindorensis	Bovidae	Wilson and Mittermeier 20
Bubalus_quarlesi	Bovidae	Wilson and Mittermeier 20
Budorcas_taxicolor	Bovidae	Wilson and Mittermeier 20
Camelus_bactrianus	Camelidae	Wilson and Mittermeier 20
Camelus_dromedarius	Camelidae	Wilson and Mittermeier 20
Capra_aegagrus	Bovidae	Wilson and Mittermeier 20
Capra_caucasica	Bovidae	Wilson and Mittermeier 20
Capra_falconeri	Bovidae	Wilson and Mittermeier 20
Capra_ibex	Bovidae	Wilson and Mittermeier 20
Capra_nubiana	Bovidae	Wilson and Mittermeier 20
Capra_pyrenaica	Bovidae	Wilson and Mittermeier 20
Capra_sibirica	Bovidae	Wilson and Mittermeier 20
Capra_walie	Bovidae	Wilson and Mittermeier 20
Capreolus_capreolus	Cervidae	Wilson and Mittermeier 20
Capreolus_pygargus	Cervidae	Wilson and Mittermeier 20
Naemorhedus_crispus	Bovidae	Wilson and Mittermeier 20
Capricornis_milneedwardsii	Bovidae	Wilson and Mittermeier 20
Capricornis_rubidus	Bovidae	Wilson and Mittermeier 20
Naemorhedus_sumatraensis	Bovidae	Wilson and Mittermeier 20
Naemorhedus_swinhoei	Bovidae	Wilson and Mittermeier 20
Capricornis_thar	Bovidae	Wilson and Mittermeier 20
Catagonus_wagneri	Tayassuidae	Wilson and Mittermeier 20

<i>Cephalophus_adersi</i>	Bovidae	Wilson and Mittermeier 20
<i>Cephalophus_brookei</i>	Bovidae	Wilson and Mittermeier 20
<i>Cephalophus_callipygus</i>	Bovidae	Wilson and Mittermeier 20
<i>Cephalophus_dorsalis</i>	Bovidae	Wilson and Mittermeier 20
<i>Cephalophus_jentinki</i>	Bovidae	Wilson and Mittermeier 20
<i>Cephalophus_leucogaster</i>	Bovidae	Wilson and Mittermeier 20
<i>Cephalophus_natalensis</i>	Bovidae	Wilson and Mittermeier 20
<i>Cephalophus_niger</i>	Bovidae	Wilson and Mittermeier 20
<i>Cephalophus_nigrifrons</i>	Bovidae	Wilson and Mittermeier 20
<i>Cephalophus_ogilbyi</i>	Bovidae	Wilson and Mittermeier 20
<i>Cephalophus_rufilatus</i>	Bovidae	Wilson and Mittermeier 20
<i>Cephalophus_silvicultor</i>	Bovidae	Wilson and Mittermeier 20
<i>Cephalophus_spadix</i>	Bovidae	Wilson and Mittermeier 20
<i>Cephalophus_zebra</i>	Bovidae	Wilson and Mittermeier 20
<i>Cervus_canadensis</i>	Cervidae	Wilson and Mittermeier 20
<i>Cervus_elaphus</i>	Cervidae	Wilson and Mittermeier 20
<i>Cervus_nippon</i>	Cervidae	Wilson and Mittermeier 20
<i>Cervus timorensis</i>	Cervidae	Wilson and Mittermeier 20
<i>Connochaetes_gnou</i>	Bovidae	Wilson and Mittermeier 20
<i>Connochaetes_taurinus</i>	Bovidae	Wilson and Mittermeier 20
<i>Dama_dama</i>	Cervidae	Wilson and Mittermeier 20
<i>Damaliscus_korrigum</i>	Bovidae	Wilson and Mittermeier 20
<i>Damaliscus_lunatus</i>	Bovidae	Wilson and Mittermeier 20
<i>Damaliscus_pygargus</i>	Bovidae	Wilson and Mittermeier 20
<i>Dorcatragus_megalotis</i>	Bovidae	Wilson and Mittermeier 20
<i>Elaphodus_cephalophus</i>	Cervidae	Wilson and Mittermeier 20
<i>Gazella_rufifrons</i>	Bovidae	Wilson and Mittermeier 20
<i>Gazella_thomsonii</i>	Bovidae	Wilson and Mittermeier 20
<i>Gazella_arabica</i>	Bovidae	
<i>Gazella_bennettii</i>	Bovidae	Wilson and Mittermeier 20
<i>Gazella_cuvieri</i>	Bovidae	Wilson and Mittermeier 20
<i>Gazella_dorcas</i>	Bovidae	Wilson and Mittermeier 20
<i>Gazella_erlangeri</i>	Bovidae	Wilson and Mittermeier 20
<i>Gazella_gazella</i>	Bovidae	Wilson and Mittermeier 20
<i>Gazella_leptoceros</i>	Bovidae	Wilson and Mittermeier 20
<i>Gazella_spekei</i>	Bovidae	Wilson and Mittermeier 20
<i>Gazella_subgutturosa</i>	Bovidae	Wilson and Mittermeier 20
<i>Giraffa_camelopardalis</i>	Giraffidae	Wilson and Mittermeier 20
<i>Hemitragus_hylocrius</i>	Bovidae	Wilson and Mittermeier 20
<i>Hemitragus_jayakari</i>	Bovidae	Wilson and Mittermeier 20
<i>Hemitragus_jemlahicus</i>	Bovidae	Wilson and Mittermeier 20
<i>Hexaprotodon_liberiensis</i>	Hippopotamidae	Wilson and Mittermeier 20
<i>Hippocamelus_antisensis</i>	Cervidae	Wilson and Mittermeier 20
<i>Hippocamelus_bisulcus</i>	Cervidae	Wilson and Mittermeier 20
<i>Hippopotamus_amphibius</i>	Hippopotamidae	Wilson and Mittermeier 20
<i>Hippotragus_equinus</i>	Bovidae	Wilson and Mittermeier 20
<i>Hippotragus_niger</i>	Bovidae	Wilson and Mittermeier 20
<i>Hydropotes_inermis</i>	Cervidae	Wilson and Mittermeier 20
<i>Hyemoschus_aquaticus</i>	Tragulidae	Wilson and Mittermeier 20
<i>Hylochoerus_meinertzhageni</i>	Suidae	Wilson and Mittermeier 20
<i>Kobus_ellipsiprymnus</i>	Bovidae	Wilson and Mittermeier 20
<i>Kobus_kob</i>	Bovidae	Wilson and Mittermeier 20
<i>Kobus_leche</i>	Bovidae	Wilson and Mittermeier 20

Kobus_megaceros	Bovidae	Wilson and Mittermeier 20
Kobus_vardonii	Bovidae	Wilson and Mittermeier 20
Lama_guanicoe	Camelidae	Wilson and Mittermeier 20
Litocranius_walleri	Bovidae	Wilson and Mittermeier 20
Madoqua_guentheri	Bovidae	Wilson and Mittermeier 20
Madoqua_kirkii	Bovidae	Wilson and Mittermeier 20
Madoqua_piacentinii	Bovidae	
Madoqua_saltiana	Bovidae	Wilson and Mittermeier 20
Mazama_americana	Cervidae	Wilson and Mittermeier 20
Mazama_bororo	Cervidae	Wilson and Mittermeier 20
Mazama_bricenii	Cervidae	
Mazama_chunyi	Cervidae	Wilson and Mittermeier 20
Mazama_gouazoupira	Cervidae	Wilson and Mittermeier 20
Mazama_nana	Cervidae	Wilson and Mittermeier 20
Mazama_pandora	Cervidae	Wilson and Mittermeier 20
Mazama_rufina	Cervidae	Wilson and Mittermeier 20
Mazama_temama	Cervidae	Wilson and Mittermeier 20
Moschiola_meminna	Tragulidae	
Moschus_anhuiensis	Moschidae	
Moschus_berezovskii	Moschidae	Wilson and Mittermeier 20
Moschus_chrysogaster	Moschidae	Wilson and Mittermeier 20
Moschus_cupreus	Moschidae	Wilson and Mittermeier 20
Moschus_fuscus	Moschidae	Wilson and Mittermeier 20
Moschus_leucogaster	Moschidae	Wilson and Mittermeier 20
Moschus_moschiferus	Moschidae	Wilson and Mittermeier 20
Muntiacus_atherodes	Cervidae	Wilson and Mittermeier 20
Muntiacus_crinifrons	Cervidae	Wilson and Mittermeier 20
Muntiacus_feae	Cervidae	Wilson and Mittermeier 20
Muntiacus_gongshanensis	Cervidae	Wilson and Mittermeier 20
Muntiacus_muntjak	Cervidae	Wilson and Mittermeier 20
Muntiacus_puhoatensis	Cervidae	
Muntiacus_putaoensis	Cervidae	Wilson and Mittermeier 20
Muntiacus_reevesi	Cervidae	Wilson and Mittermeier 20
Muntiacus_rooseveltorum	Cervidae	Wilson and Mittermeier 20
Muntiacus_truongsonensis	Cervidae	Wilson and Mittermeier 20
Muntiacus_vuquangensis	Cervidae	Wilson and Mittermeier 20
Naemorhedus_baileyi	Bovidae	Wilson and Mittermeier 20
Naemorhedus_caudatus	Bovidae	Wilson and Mittermeier 20
Naemorhedus_goral	Bovidae	Wilson and Mittermeier 20
Naemorhedus_griseus	Bovidae	Wilson and Mittermeier 20
Gazella_dama	Bovidae	Wilson and Mittermeier 20
Gazella_granti	Bovidae	Wilson and Mittermeier 20
Gazella_soemmerringii	Bovidae	Wilson and Mittermeier 20
Neotragus_batesi	Bovidae	Wilson and Mittermeier 20
Neotragus_moschatus	Bovidae	Wilson and Mittermeier 20
Neotragus_pygmaeus	Bovidae	Wilson and Mittermeier 20
Odocoileus_hemionus	Cervidae	Wilson and Mittermeier 20
Odocoileus_virginianus	Cervidae	Wilson and Mittermeier 20
Okapia_johnstoni	Giraffidae	Wilson and Mittermeier 20
Oreamnos_americanus	Bovidae	Wilson and Mittermeier 20
Oreotragus_oreotragus	Bovidae	Wilson and Mittermeier 20
Oryx_dammah	Bovidae	Wilson and Mittermeier 20
Oryx_gazella	Bovidae	Wilson and Mittermeier 20

<i>Oryx_leucoryx</i>	Bovidae	Wilson and Mittermeier 20
<i>Ourebia_ourebi</i>	Bovidae	Wilson and Mittermeier 20
<i>Ovibos_moschatus</i>	Bovidae	Wilson and Mittermeier 20
<i>Ovis_ammon</i>	Bovidae	Wilson and Mittermeier 20
<i>Ovis_canadensis</i>	Bovidae	Wilson and Mittermeier 20
<i>Ovis_dalli</i>	Bovidae	Wilson and Mittermeier 20
<i>Ovis_nivicola</i>	Bovidae	Wilson and Mittermeier 20
<i>Ozotoceros_bezoarticus</i>	Cervidae	Wilson and Mittermeier 20
<i>Pantholops_hodgsonii</i>	Bovidae	Wilson and Mittermeier 20
<i>Pecari_tajacu</i>	Tayassuidae	Wilson and Mittermeier 20
<i>Pelea_capreolus</i>	Bovidae	Wilson and Mittermeier 20
<i>Phacochoerus_aethiopicus</i>	Suidae	
<i>Phacochoerus_africanus</i>	Suidae	Wilson and Mittermeier 20
<i>Cephalophus_maxwellii</i>	Bovidae	Wilson and Mittermeier 20
<i>Cephalophus_monticola</i>	Bovidae	Wilson and Mittermeier 20
<i>Potamochoerus_larvatus</i>	Suidae	Wilson and Mittermeier 20
<i>Potamochoerus_porcus</i>	Suidae	Wilson and Mittermeier 20
<i>Procapra_gutturosa</i>	Bovidae	Wilson and Mittermeier 20
<i>Procapra_picticaudata</i>	Bovidae	Wilson and Mittermeier 20
<i>Procapra_przewalskii</i>	Bovidae	Wilson and Mittermeier 20
<i>Cervus_albirostris</i>	Cervidae	Wilson and Mittermeier 20
<i>Pseudois_nayaur</i>	Bovidae	Wilson and Mittermeier 20
<i>Pseudois_schaeferi</i>	Bovidae	Wilson and Mittermeier 20
<i>Pseudoryx_nghetinhensis</i>	Bovidae	Wilson and Mittermeier 20
<i>Pudu_mephistophiles</i>	Cervidae	Wilson and Mittermeier 20
<i>Pudu_puda</i>	Cervidae	Wilson and Mittermeier 20
<i>Rangifer_tarandus</i>	Cervidae	Wilson and Mittermeier 20
<i>Raphicerus_campestris</i>	Bovidae	Wilson and Mittermeier 20
<i>Raphicerus_melanotis</i>	Bovidae	Wilson and Mittermeier 20
<i>Raphicerus_sharpei</i>	Bovidae	Wilson and Mittermeier 20
<i>Redunca_arundinum</i>	Bovidae	Wilson and Mittermeier 20
<i>Redunca_fulvorufula</i>	Bovidae	Wilson and Mittermeier 20
<i>Redunca_redunda</i>	Bovidae	Wilson and Mittermeier 20
<i>Cervus_duvaucelii</i>	Cervidae	Wilson and Mittermeier 20
<i>Cervus_eldii</i>	Cervidae	Wilson and Mittermeier 20
<i>Rupicapra_pyrenaica</i>	Bovidae	Wilson and Mittermeier 20
<i>Rupicapra_rupicapra</i>	Bovidae	Wilson and Mittermeier 20
<i>Cervus_alfredi</i>	Cervidae	Wilson and Mittermeier 20
<i>Cervus_mariannus</i>	Cervidae	Wilson and Mittermeier 20
<i>Cervus_timorensis</i>	Cervidae	Wilson and Mittermeier 20
<i>Cervus_unicolor</i>	Cervidae	Wilson and Mittermeier 20
<i>Saiga_borealis</i>	Bovidae	Wilson and Mittermeier 20
<i>Saiga_tatarica</i>	Bovidae	Wilson and Mittermeier 20
<i>Sus_ahoenobarbus</i>	Suidae	Wilson and Mittermeier 20
<i>Sus_barbatus</i>	Suidae	Wilson and Mittermeier 20
<i>Sus_cebifrons</i>	Suidae	Wilson and Mittermeier 20
<i>Sus_celebensis</i>	Suidae	Wilson and Mittermeier 20
<i>Sus_oliveri</i>	Suidae	
<i>Sus_philippensis</i>	Suidae	Wilson and Mittermeier 20
<i>Sus_salvanus</i>	Suidae	Wilson and Mittermeier 20
<i>Sus_scrofa</i>	Suidae	Wilson and Mittermeier 20
<i>Sus_verrucosus</i>	Suidae	Wilson and Mittermeier 20
<i>Sylvicapra_grimmia</i>	Bovidae	Wilson and Mittermeier 20

<i>Syncerus_caffer</i>	Bovidae	Wilson and Mittermeier 20
<i>Taurotragus_derbianus</i>	Bovidae	Wilson and Mittermeier 20
<i>Taurotragus_oryx</i>	Bovidae	Wilson and Mittermeier 20
<i>Tayassu_pecari</i>	Tayassuidae	Wilson and Mittermeier 20
<i>Tetracerus_quadricornis</i>	Bovidae	Wilson and Mittermeier 20
<i>Tragelaphus_angasii</i>	Bovidae	Wilson and Mittermeier 20
<i>Tragelaphus_buxtoni</i>	Bovidae	Wilson and Mittermeier 20
<i>Tragelaphus_eurycerus</i>	Bovidae	Wilson and Mittermeier 20
<i>Tragelaphus_imberbis</i>	Bovidae	Wilson and Mittermeier 20
<i>Tragelaphus_scriptus</i>	Bovidae	Wilson and Mittermeier 20
<i>Tragelaphus_spekii</i>	Bovidae	Wilson and Mittermeier 20
<i>Tragelaphus_strepsiceros</i>	Bovidae	Wilson and Mittermeier 20
<i>Tragulus_javanicus</i>	Tragulidae	Wilson and Mittermeier 20
<i>Tragulus_kanchil</i>	Tragulidae	Wilson and Mittermeier 20
<i>Tragulus_napu</i>	Tragulidae	Wilson and Mittermeier 20
<i>Tragulus_nigricans</i>	Tragulidae	Wilson and Mittermeier 20
<i>Tragulus_versicolor</i>	Tragulidae	
<i>Tragulus_williamsoni</i>	Tragulidae	Wilson and Mittermeier 20
<i>Vicugna_vicugna</i>	Camelidae	Wilson and Mittermeier 20

Habitat type_reference	Mating system_reference	Group size_reference
Wilson and Mittermeier 2011		East 1990
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Skinner and Chimimba 2005
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011		
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Skinner and Chimimba 2005
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011		Chubbs and Shafer 1997
Wilson and Mittermeier 2011		East 1988
Wilson and Mittermeier 2011		Cassinello 2000
Wilson and Mittermeier 2011		
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Nowak and Paradiso 1983
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Mallon 2001
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	
Wilson and Mittermeier 2011		Wemmer 1998
Wilson and Mittermeier 2011		Semiadi et al. 2005
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011		Macdonald et al. 2008
Wilson and Mittermeier 2011		
Wilson and Mittermeier 2011		Leus et al. 2016
Wilson and Mittermeier 2011		Macdonald et al. 2016
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Kingdon 2015
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Nowak and Paradiso 1983
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Leslie and Shaller 2009
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Nowak and Paradiso 1983
Wilson and Mittermeier 2011		Nowak and Paradiso 1983
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Mallon 2001
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Burton et al. 2016a
Wilson and Mittermeier 2011		Custodio et al. 1996
Wilson and Mittermeier 2011		Burton et al. 2016b
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Neas and Hoffmann 1987, S
Wilson and Mittermeier 2011		Reading et al. 1999
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011		Nickolson and Husband 199
Wilson and Mittermeier 2011		Baskin and Danell 2003
Wilson and Mittermeier 2011		Baskin and Danell 2003
Wilson and Mittermeier 2011		Aulagnier et al. 2008
Wilson and Mittermeier 2011		Aulagnier et al. 2008
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Habibi 1996
Wilson and Mittermeier 2011		Perez et al. 1994
Wilson and Mittermeier 2011		Fedosenko and Blank 2001
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Ejigu et al. 2015
Wilson and Mittermeier 2011		Hutchins et al. 2003
Wilson and Mittermeier 2011	Tokida 2008 IUCn report	Hutchins et al. 2003
Wilson and Mittermeier 2011		Vongkhamheng et al. 2013
Wilson and Mittermeier 2011		
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Nowak and Paradiso 1983, I
Wilson and Mittermeier 2011		Chiang 2008
Wilson and Mittermeier 2011		Bhattacharya et al. 2012, Gi
Wilson and Mittermeier 2011		Hutchins et al. 2003

Wilson and Mittermeier 2011	East 1988
Wilson and Mittermeier 2011	Kingdon and Hoffmann 201
Wilson and Mittermeier 2011	Kingdon 2015
Wilson and Mittermeier 2011	Kingdon and Hoffmann 201
Wilson and Mittermeier 2011	Kingdon and Hoffmann 201
Wilson and Mittermeier 2011	Skinner and Chimimba 2005
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	Skinner and Chimimba 2005
Wilson and Mittermeier 2011	Kingdon and Hoffmann 201
Wilson and Mittermeier 2011	Kingdon and Hoffmann 201
Wilson and Mittermeier 2011	Kingdon and Hoffmann 201
Wilson and Mittermeier 2011	East 1990
Wilson and Mittermeier 2011	East 1988
Wilson and Mittermeier 2011	Kingdon and Hoffmann 201
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	Kingdon 2015
Wilson and Mittermeier 2011	Strushaker 1967
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011	
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	Vrahimis 1994
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	Skinner and Chimimba 2005
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	Feldhamer et al. 1988
)11	Jewell 1972, Grant et al. 19!
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011	Kingdon 2015
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	East 1988, Kingdon 2015
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	Hutchins et al. 2003
)11	East 1990
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	East 1988
)11	Wronski 2013
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	Dookia and Jakher 2013
Wilson and Mittermeier 2011	Kingdon 2015
)11	East 1990
Wilson and Mittermeier 2011	Wilson and Mittermeier 20:
)11	Mallon 2001
)11	East 1990, Mallon 2001
Wilson and Mittermeier 2011	Kingdon 2015
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	Kingswood and Blank 1996
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	Kingdon 2015
Wilson and Mittermeier 2011	Wilson and Mittermeier 20:
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	Wilson and Mittermeier 20:
Wilson and Mittermeier 2011	Green 1978
Wilson and Mittermeier 2011	Oliver 1993
Wilson and Mittermeier 2011	Mertk 1985
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	Karstad and Hudson 1986
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	Kingdon 2015
Wilson and Mittermeier 2011	
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	East 1988, 1990
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002	Kingdon 2015

- Wilson and Mittermeier 2011 Pérez-Barbería et al.. 2002
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Pérez-Barbería and Gordon 2000	Pérez-Barbería and Gordon 2000
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
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O’Gara1990	O’Gara1990
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
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- Feeding style** = type of the foraging strategy; grazer = predominately feed on grasses, not-grazer :
- Habitat type** = type of habitat where te given species lives, open = open fields and plains, closec
- Mating system** = type of the mating system, monogamous = species where individuals have only c
- Group size_mean** = mean number of individuals per group
- Male body size** = size of the males in kg
- Female body size** = size of the females in kg

SSD values were calculated from sex specific body size data: $\log_{10}(\text{Male body size (kg)}/\text{Female body size (kg)})$

Average body size values for each species were calculated from sex specific body size data for the anal

Group size_mean and avarge body size were log transformed before PGLS analyses.

= predominantly feed on shrubs, leaves, berries, flowers and even some animal

d = closed habitats, like forest or shrublands

one mating partner per breeding season, polygamous = species where individuals have more than one m

ize (kg)

lyses: $(\text{Male body size (kg)} + \text{Female body size (kg)})/2$

rate per breeding season

1 Social organization in ungulates: revisiting Jarman's hypotheses

2 **Supplementary material 2**

3

4 Table S1: The table represent the distribution of our variables among the Artiodactyla

5 families. Numbers represents the number of species.

Families	No. of species	Group living			Group size	Habitat			Feeding style			Mating system		
		<i>yes</i>	<i>no</i>	<i>no data</i>		<i>open</i>	<i>closed</i>	<i>no data</i>	<i>grazer</i>	<i>non-grazer</i>	<i>no data</i>	<i>poly-gamy</i>	<i>mono-gamy</i>	<i>no data</i>
Antilocapridae	1	1	0	0	2-23	1	0	0	0	1	0	1	0	0
Bovidae	134	89	45	11	1-45	78	38	18	68	64	2	49	17	68
Camelidae	4	4	0	0	1-16	4	0	0	2	2	0	3	1	1
Cervidae	51	16	30	5	1-35	22	21	8	14	36	3	15	9	27
Giraffidae	2	1	1	0	1-50	1	1	0	0	2	0	1	1	0
Hippopotamidae	2	1	1	0	1-100	2	0	0	1	1	0	1	0	1
Moschidae	7	0	7	0	1	1	5	1	0	6	1	0	1	6
Suidae	18	14	0	4	1-300	3	9	6	0	15	3	3	0	15
Tayassuidae	3	2	0	1	2-15	0	2	1	0	3	0	0	0	3
Tragulidae	8	0	8	0	1	0	8	0	0	6	2	0	3	5

6

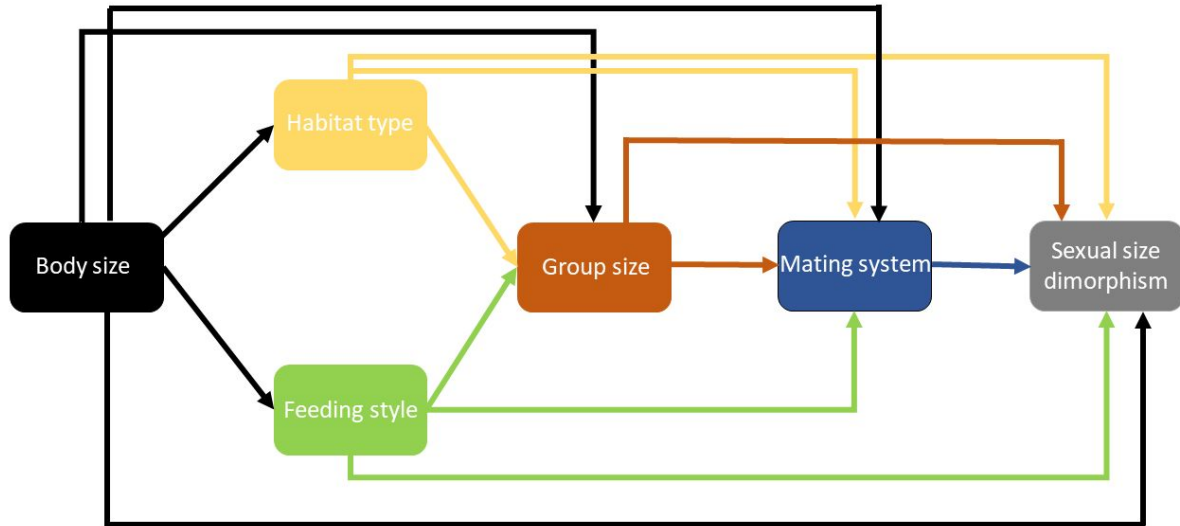
7 **Table S2:** Summary of path models (Fisher's $C = 15.689$, $df = 12$, $p = 0.206$).

Response	Predictor	Estimate	Standardized Estimate	Standard Error	df	Crit. Value	P value
SSD	Mating system	0.1017	0.4697	0.0187	104	5.4263	0
Mating system	Habitat type	0.3214	0.3263	0.0858	102	3.7447	0.00003
Mating system	Feeding style	-0.1588	-0.2272	0.0603	102	-2.6315	0.0098
Mating system	Group size	0.0112	0.2172	0.0046	102	2.448	0.0161
Group size	Habitat type	3.6877	0.1925	1.7862	102	2.0645	0.0415
Group size	Feeding style	-2.5788	-0.1897	1.2404	102	-2.079	0.0401
Group size	Body size	0.01	0.2467	0.0037	102	2.6665	0.0089
Habitat type	Body size	0.00005	0.2307	0.00002	104	2.4183	0.0173

8

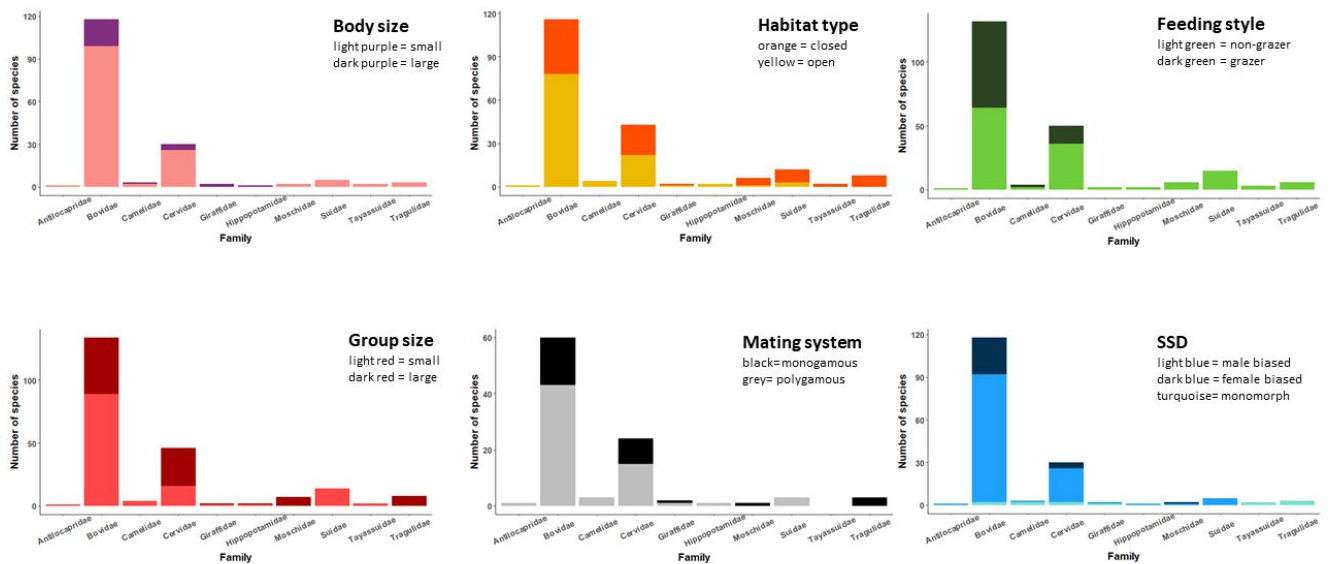
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10 Figure S1: Full initial model of the phylogenetically controlled path analysis. The model
11 based on Jarman's (1974) hypothesis. We represent each variable and the connected pathways
12 with different colors.



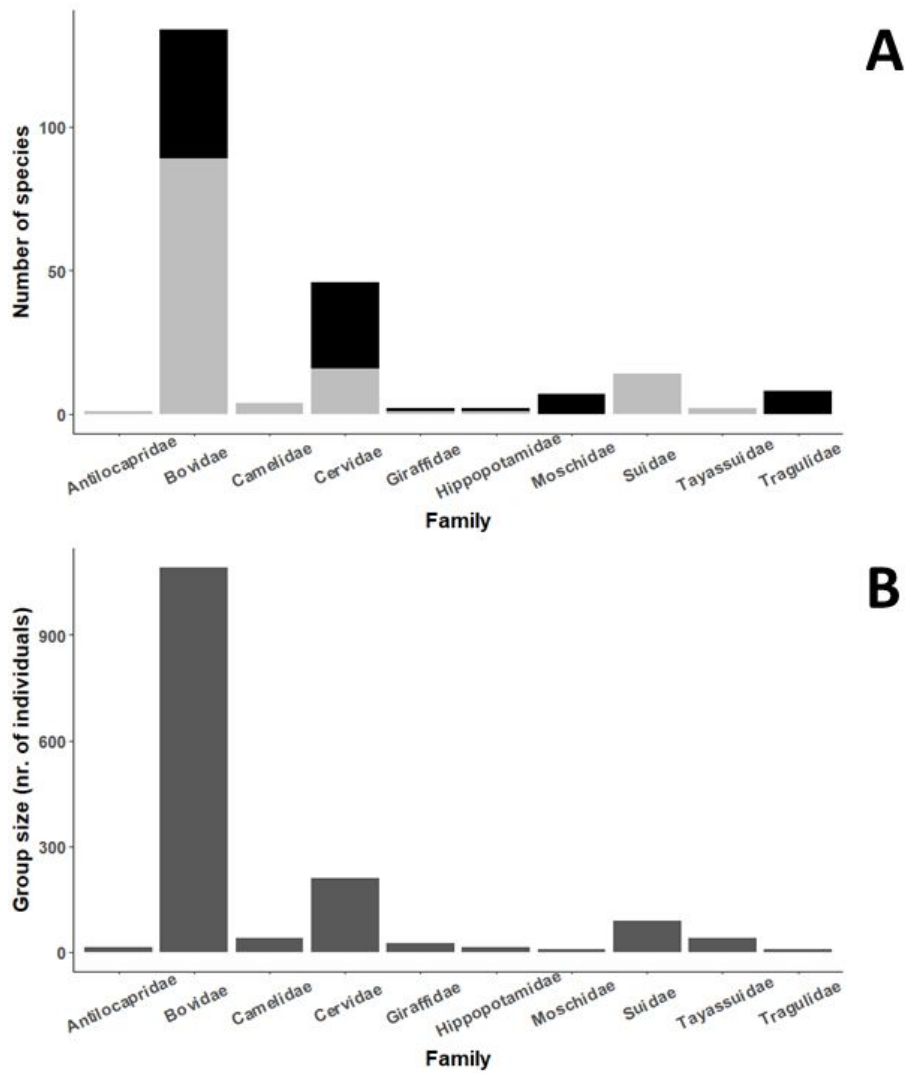
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14 Figure S2: Phylogenetic distribution of ecological and social variables in ungulates. Here we
 15 collapsed the continuous variables, group size, body size and sexual size dimorphism (SSD),
 16 into binary traits as follows. In case of body size and group size we calculated the mean value
 17 of the variables: small bodied species were those which were lighter than the mean value, large
 18 bodied species were heavier than the mean value. Small groups were those which have less
 19 member than the mean value, in large groups there are more individuals than the mean value.
 20 In case of SSD, if the degree of dimorphism was 0 the species was categorized as
 21 monomorphic, if the value was less than 0 we defined as female biased SSD, if the value was
 22 more than 0 we defined as male biased SSD.



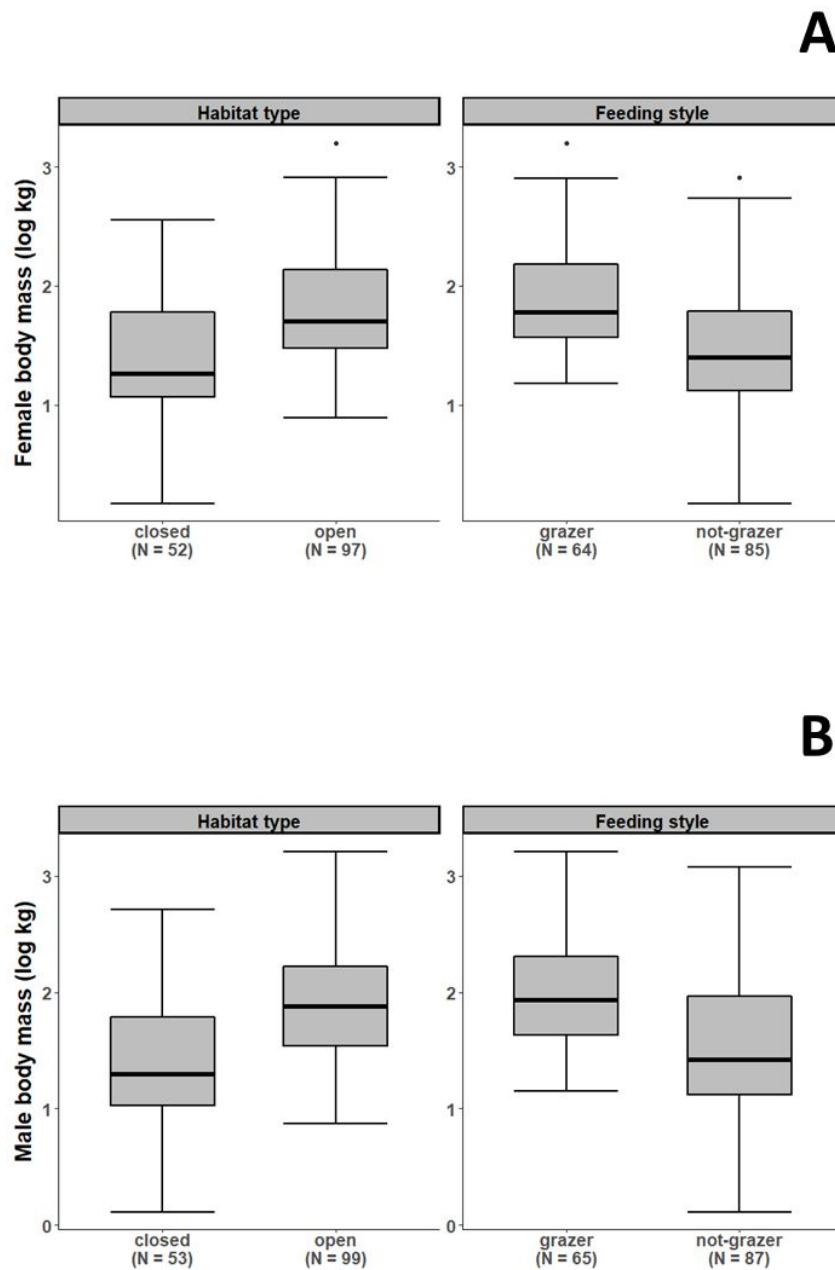
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24 Figure S3: Group living and its distribution among ungulate families. (A) present the number
 25 of group- living species in each family (black = solitary, grey = group living). (B) represent
 26 mean group size among the ten odd- toed ungulates family.



27

28 Figure S4: Species' ecology predicts (A) female (feeding style: $F = 4.42$, $df = 160$, $p = 0.037$,
 29 $n = 162$ species; habitat type: $F = 21.17$, $df = 148$, $p < 0.001$, $n = 150$ species) and (B) male
 30 (feeding style: $F = 7.31$, $df = 163$, $p < 0.001$, $n = 165$ species; habitat type: $F = 25.11$, $df = 151$,
 31 $p < 0.001$, $n = 153$ species) body mass in Artiodactyla.



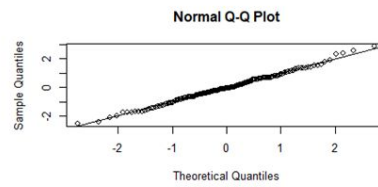
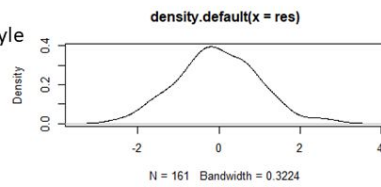
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34 **Figure S5:** Distribution of the eight bivariate PGLS models' (described in Table 1) residues.

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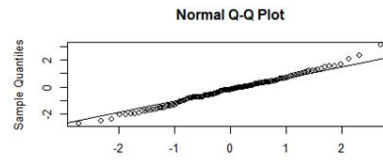
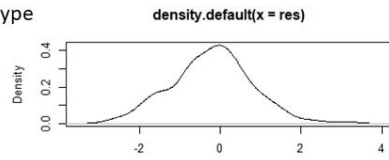
Model 1

Body size ~ Feeding style



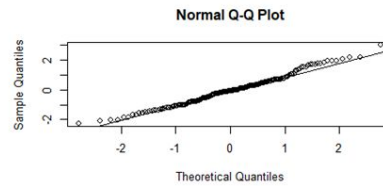
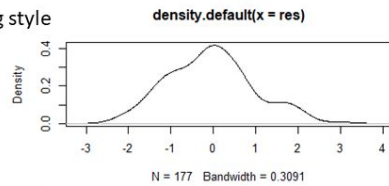
Model 2

Body size ~ Habitat type



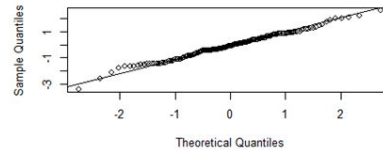
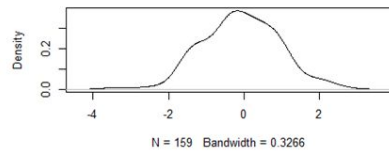
Model 3

Group size ~ Feeding style



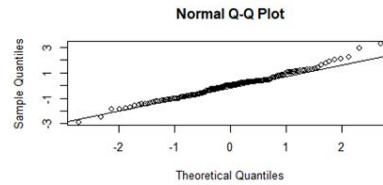
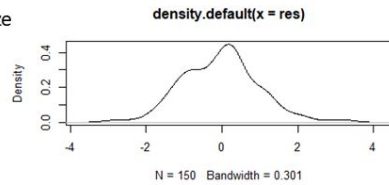
Model 4

Group size ~ Habitat type



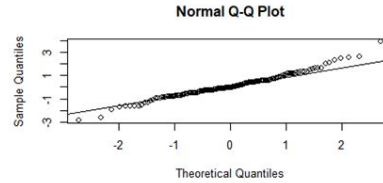
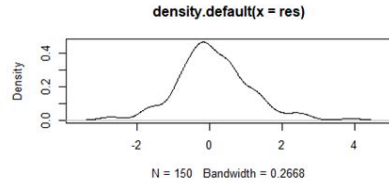
Model 5

Group size ~ Body size



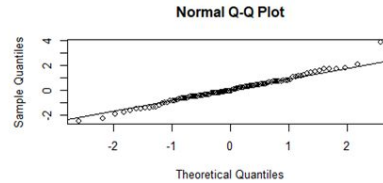
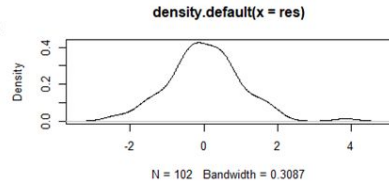
Model 6

SSD ~ Group size



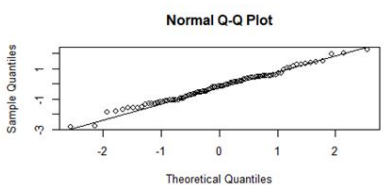
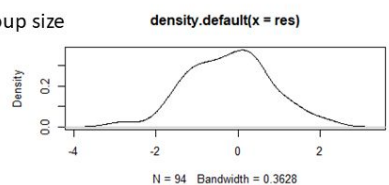
Model 7

SSD ~ Mating system



Model 8

Mating system ~ Group size



36

Ecology of social organisation in ungulates (antelopes, deer, bovids and relatives)

