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1 Variable social organisation is ubiquitous in Artiodactyla and probably evolved from pair-
living ancestors

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19 **Abstract**

20

21 Previous studies to understand the evolution of *inter*-specific variation in mammalian social
22 organisation (SO; composition of social units) produced inconsistent results, possibly by
23 ignoring *intra*-specific variation. Here we present systematic data on SO in artiodactyl
24 populations, coding SO as solitary, pair-living, group-living, sex-specific, or variable (different
25 kinds of SOs in the same population). We found that 62% of 245 populations and 83% of species
26 (83/100) exhibited variable SO. Using Bayesian phylogenetic mixed-effects models, we
27 simultaneously tested whether research effort, habitat, sexual dimorphism, breeding seasonality,
28 or body size predicted the likelihood of different SOs and inferred the ancestral SO. Body size
29 and sexual dimorphism were strongly associated with different SOs. Contingent on the small
30 body size (737g) and putative sexual monomorphism of the earliest fossil artiodactyl, the
31 ancestral SO was most likely pair-living (probability=0.76, 95%CI=0-1), followed by variable
32 (p=0.19, 95%CI=0-0.99). However, at body size values typical of extant species, variable SO
33 becomes the dominant form (p=0.74, 95% CI = 0.18-1.00). Distinguishing different kinds of
34 “variable” highlights transitions from SOs involving pair-living to SOs involving solitary and/or
35 group-living with increasing body size and dimorphism. Our results support the assumption that
36 ancestral artiodactyl was pair-living and highlight the ubiquity of intra-specific variation in SO.

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38 Key words: Intraspecific variation, Social organisation, Artiodactyla, phylogenetic mixed-effects
39 model

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50 **1. Introduction**

51

52 A fundamental goal of behavioural ecology is to understand the remarkable diversity in animal
53 social systems (used synonymously with ‘society’ and ‘social unit’ [1])[2-6]. When studying the
54 social system of a species it is useful to distinguish between four components (each referring to
55 adult males and adult females only), as they are not necessarily congruent [1, 6] (Figure 1) – (i)
56 social organisation (SO, i.e. size, sexual composition and spatiotemporal cohesion of a social
57 system), (ii) social structure (patterns of social interactions, including dominance hierarchies and
58 territoriality), (iii) mating system (who mates with whom) and (iv) care system (who takes care
59 of offspring). As each component has many possible states, more than 600 forms of social
60 systems are possible, indicating why one has to focus on one component to avoid confusion
61 about targets of selection [1]. Here, we focus on adult male-female SO, i.e. the composition of
62 social units within a population. By constraining who lives with whom, SO can impact social
63 relationships and mating strategies, influencing the entire social system [1, 6, 7].

64

65 Comparative analyses of mammalian SO have aimed to estimate the SO of ancestral species and
66 how different forms of SO (e.g., pair-living) evolved [8-10]. Inconsistent results have emerged
67 from these studies for several taxa, including primates and carnivorans [8-12]. This likely
68 occurred for several reasons. First, studies relied on different datasets, methods of analysis, and
69 conceptual frameworks [6]. In an effort to account for as many species as possible, some authors
70 used information from secondary sources and taxonomic inference, i.e. the untested assumption
71 that members of the same genus share the same SO [13]. Other studies used confusing
72 terminology or did not distinguish between SO and mating system [6]. For example, some
73 inferred monogamy (mating system) from the observation of male-female pairs (SO) [10, 14]. To
74 resolve these inconsistent results, comparative studies should rely on data from primary sources
75 whenever possible, and distinguish SO from other social system components. Furthermore,
76 inferring ancestral SO from observations of extant species can be unreliable if SO is strongly
77 associated with factors, such as body size, that have evolved away from ancestral values [15].

78

79 Most comparative studies of mammalian SO characterized each species as solitary, pair-living or
80 (different forms of) group-living [8, 10, 12]. However, many species have more than one form of

81 SO, both on the population and on the species levels. At the population level (the unit of analysis
82 in our study), *variable social organisation* is the occurrence of multiple forms of SO within a
83 population. At the species level, variation can occur both within- and between-populations, and
84 has been called *intraspecific variation in social organisation (IVSO)* [7, 9, 16, 17]. Determining
85 the extent of IVSO is important because it is predicted to influence reproductive competition and
86 social interactions and thus other components of the social system [7].

87

88 In mammals, IVSO has been reported in numerous species from different orders [9, 18-21]
89 transforming our understanding of mammalian social evolution. For example, in carnivorans and
90 shrews, it was long believed that the ancestral SO was solitary. Two observations challenge the
91 validity of this assumption. Phylogenetic reconstructions did not support a solitary ancestor in
92 Carnivora [9]. In shrews, group-living and variable social organisation occurs in 36% and 27%
93 of species [21]. More broadly, ignoring intraspecific variation can increase statistical type II
94 error rates [22-24] and lead to spurious conclusions about social evolution [7, 25]. Thus,
95 comparative studies of SO should include intraspecific variation by using modern statistical
96 methods, such as phylogenetic mixed-effects (a.k.a. multilevel) models or measurement-error
97 models [23, 26].

98

99 Variable SO is likely associated with several inter-related factors, including spatiotemporal
100 variation in ecology and life history [7, 16, 27-29]. Consequently, variable SO may occur due to
101 environmental heterogeneity and thereby, the likelihood of variable SO may depend on life
102 history and body size. Short-lived, small bodied individuals may experience less environmental
103 variation over a lifetime, resulting in adaptive responses in SO to prevailing conditions [7]. In
104 contrast, large-bodied, long-lived species may have larger home ranges [30] spanning more
105 habitat types and encounter more diverse ecological conditions over their life course [7].
106 Variable kinds of groups are specifically expected in seasonal breeders, as reproductive
107 competition during the breeding season can exclude some individuals from social units [29]; by
108 contrast, the survival benefits of living in large groups (e.g., anti-predator strategies; [19, 31])
109 may prevail during the non-breeding season.

110

111 Artiodactyl social evolution has historically been explained by habitat heterogeneity, body size,
112 sexual dimorphism, and breeding seasonality [14, 19, 32]. Jarman [19] argued that (i) ancestral
113 artiodactyls lived in male-female pairs in closed habitats and were monomorphic and that (ii)
114 group-living evolved as species radiated into open habitats, favouring the evolution of larger
115 body sizes, polygyny and sexual dimorphism. A subsequent comparative analysis supported
116 these predictions [14]. However, neither study accounted for IVSO and both assumed pair-living
117 as the ancestral state instead of inferring it. Thus, the ancestral SO and the extent to which
118 environmental heterogeneity, body size, and breeding strategies (proxied by sexual dimorphism)
119 play a role in artiodactyl social evolution needs to be re-evaluated.

120

121 First, we investigated how often variable SO has been reported within- and between populations
122 in field studies on artiodactyls and used this information to describe the extent of IVSO
123 (Supplemental Tables S1 and S2). Second, we inferred the ancestral SO of artiodactyls, testing
124 whether the previous assumption of a pair-living ancestor [14, 19] is correct. Third, we evaluated
125 the extent to which factors previously suggested to be key determinants of artiodactyl social
126 evolution [14, 19] influence SO, predicting that (i) group-living would be associated with open
127 habitats and with sexual dimorphism. In addition, based on earlier work on IVSO [7] we
128 predicted that the likelihood of variable SO increases with (ii) number of habitats and (iii) with
129 breeding seasonality. Even though SO was defined at the population level, since this was the unit
130 of observation, most of the predictors of SO (body size, sexual dimorphism, breeding
131 seasonality) were only available at the species level. Hence, an effect of body size on SO, for
132 example, represents a between- rather than within-species effect; if body size were available at
133 the population level these two effects could be disentangled [26, 33].

134

135 **2. Methods**

136

137 (a) Data collection

138

139 We searched the Web of Science and Google Scholar for primary sources on SO for all 226
140 extant species of Artiodactyla [34]. The initial search consisted of the scientific name (genus and
141 species) and a keyword ('social', 'herd', or 'group'). If no sources were found, a final search

142 used only the scientific name. In *Web of Science*, search results were refined by selecting three
143 research areas: ‘zoology’, ‘behavioral science’, and ‘environmental science/ecology’, and
144 document type ‘article’. Lab-based studies, studies in enclosures smaller than 1,000-hectares,
145 and studies that included manipulation of individuals, groups, or resources were discarded. We
146 recorded and analysed all information on SO at the level of the population, as defined by the
147 original authors.

148
149 To determine the forms of SO present in each population, we used data available for all
150 individuals in the population during both the breeding and non-breeding season, using the
151 classical definitions from Kappeler and van Schaik [1, 6]. For each population, we recorded all
152 forms of SO reported for all studied individuals. We found 7 different forms of SO: 1) Both
153 sexes were solitary and only met for mating (M, F), 2) Pair-living (MF), 3) Single male / multi-
154 female groups (MFF), 4) Multi male / single female groups (MMF), 5) Multi male / multi female
155 groups (MMFF), 6) Both sexes lived in unisex groups (MM, FF), 7) Sex-specific SO (M, FF). If
156 more than one of the above 7 forms of SO was observed within the same population, the
157 population was scored as having a variable SO. In addition to variation occurring *within*
158 populations, a species could exhibit variation in SO *between* populations; the latter form of
159 variable SO did not enter our statistical analyses, but is presented for descriptive purposes in the
160 Results and in Table S2. Note that if IVSO were to occur mostly between populations, then our
161 phylogenetic model could not infer variable SO as the ancestral state; instead, the ancestral state
162 would likely be unresolved since different populations of the same species contribute conflicting
163 information. Unlike some previous comparative studies [24], we did not consider variation in
164 group size as variable SO; variation in group size does not indicate variable SO if the relative
165 number of breeders of each sex does not change [7].

166
167 The concept of IVSO is only meaningful if it captures hitherto unconsidered variation and allows
168 us to differentiate between populations where all individuals live in the same form of SO from
169 those where more forms of SO occur. Thus, the following cases were not regarded as variable
170 SO: (i) Reports of solitary individuals of only one sex, since every species has dispersers that are
171 typically solitary, and dispersal is often sex specific. (ii) Different kinds of male groups or
172 alternative reproductive tactics in species that form single-male / multi-female groups or where

173 some males otherwise monopolize access to females. In such cases, the remaining males (sex
174 ratio of birth is close to 1:1 in mammals) must necessarily be somewhere else, such as in
175 bachelor groups. It is critical to note that studies focusing on dispersal and alternative
176 reproductive tactics are important and related to studies on IVSO, but they do not represent
177 studies on how and why the composition of social units varies in many species. For further
178 details on the dataset see the Supplementary Text S1 and accompanying data file
179 (<https://github.com/adrianjaeggi/artiodactyl.socialorg>).

180

181 (b) Predictor variables

182

183 Each species was categorized as either seasonal or non-seasonal breeder. Sexual dimorphism was
184 calculated as the ratio of adult male to female body mass using data reported in Pérez-Barbería &
185 Gordon [35]. Categorical classifications of sexual dimorphism were determined based on Pérez-
186 Barbería & Gordon [14, 35]. Mean adult female body mass was used as a measure of body size.
187 Habitat type was derived from the primary sources and categorized based on IUCN classification
188 (www.iucn.org) as desert, forest, rocky areas, savanna, grassland, shrubland, wetlands, or
189 artificial. There were 45 populations with missing data on female body size and sexual
190 dimorphism, though for many of these we had data on average body size and/or a categorical
191 measure of dimorphism, and one population with missing data on habitat type(s); these missing
192 values were imputed (see d).

193

194 (c) Phylogeny

195

196 We used the mammal supertree from Bininda-Emonds et al. [36]. Some species names in the
197 database had to be amended to match the phylogeny as detailed in the accompanying R code. In
198 virtually all cases, a name mismatch could be resolved by finding a pseudonym for that species
199 through www.iucn.org, or by using a sister species that was not included in the database. In one
200 case, two closely-related taxa missing from the supertree (*Moschus leucogaster* and *Moschus*
201 *cupreus*) were proxied by the same sister species (*Moschus chrysogaster*).

202

203 (d) Statistical analysis

204

205 We used Bayesian phylogenetic mixed-effects models, accounting for the multilevel structure of
206 the data (populations nested within species) and the phylogenetic relationships among species, to
207 simultaneously (i) infer the ancestral SO and (ii) test hypotheses for factors influencing SO [23,
208 26]. Thus, our models can adjust for values of the predictors when estimating ancestral SO,
209 which is particularly relevant given potential associations between SO and body size, and the
210 general trend towards larger size in mammalian evolution [15]. To model the likelihood of
211 several mutually exclusive categorical traits (e.g.: solitary, pair-living, group-living, sex-specific
212 or variable SO) and how the likelihood of each trait was affected by predictor variables we used
213 multinomial models [37] (see Supplementary Text S2i for more details). We chose solitary as the
214 reference category in all models.

215

216 To maximize statistical power, we first combined all cases where only one form of group living
217 (either only MFF, only MMF or only MMFF) was observed to one category (“non-variable
218 group-living”), leaving five categories for analysis (Model 1): (i) Solitary, (ii) pair-living, (iii)
219 sex-specific SO, (iv) non-variable group-living, and (v) variable SO (more than one of the 7
220 possible forms of SO, see (a. Data collection)). Model 1 included all predictor variables – sexual
221 dimorphism, female body size, breeding seasonality, and number of habitats. Furthermore,
222 number of studies was included to control for research effort, and habitat type and continent were
223 modelled as random intercepts.

224

225 In Model 2, we separated out the specific forms of variable SO to further test the assumption that
226 pair-living was important in ancestral artiodactyls, including perhaps as a part of variable SOs.
227 This resulted in the following categories: (i) Solitary, (ii) Pair-living, (iii) Sex-specific SO, (iv)
228 non-variable group-living (one type of group within a population), (v) Variable group-living
229 (multiple types of groups within a population), (vi) Solitary and pair-living, (vii) Solitary and
230 group-living, (viii) Pair-living and group-living, and (ix) Solitary and pair-living and group-
231 living. Given the much larger number of parameters, Model 2 only included those predictors that
232 strongly predicted SO in Model 1, and no random effects (other than species).

233

234 The likelihood of ancestral SOs are represented by the global intercepts of the multilevel models,
235 and as such are contingent on the values of the predictors. Specifically, the intercepts in these
236 multinomial models represent the probability of each type of SO when categorical predictors
237 (e.g. breeding seasonality) are at their baseline level, and all continuous predictors are at 0. To
238 make these values best represent the last common ancestor, we therefore centred body size (737
239 g; [38]) and sexual dimorphism (monomorphic=1.0; [39]) on the values from the oldest
240 artiodactyl known in the fossil record (*Diacodexis* [40]). Note that this species was substantially
241 smaller than any of the extant species in our dataset (smallest: *Madoqua kirkii*, 5.1 kg), hence
242 these estimates of ancestral SO rely upon extending associations between body size and SOs well
243 beyond the range of data used to fit the model (cf. Figure 3A-E), which increases uncertainty in
244 the predictions. Since breeding seasonality cannot be known from fossil evidence, we estimated
245 its likely ancestral state based on the extant species data (Supplementary Text S2ii and Table
246 S3), resulting in non-seasonal breeding as the baseline (though seasonal breeding was almost
247 equally likely). Since breeding seasonality was barely associated with SO (see Figure 3), this
248 choice of baseline should not make much difference; if anything, group-living would be even
249 less likely if seasonal breeding were the baseline. Number of studies and number of habitats were
250 both centred on their median, 1.

251
252 In addition to reporting the probability of SOs at the likely ancestral state, we also present the
253 likelihood of different SOs when ancestral body size (66 kg) and sexual dimorphism (1.21) were
254 inferred from extant species values (Supplementary Text S2ii and Table S3); given the known
255 trend of increasing body size, these values reflect the phylogenetically-controlled averages of
256 these predictors and consequently the *phylogenetic mean* SO of extant artiodactyls, rather than
257 the ancestral SO [15, 41]. This provides an important complement to the reported descriptive
258 prevalence of different SOs (see below), as it controls for potentially uneven sampling across the
259 phylogeny as well as the values of associated predictors. Given the uncertainty inherent in these
260 estimates, we also report the likelihoods of different SOs for the upper and lower 95% CI bounds
261 of the predictors (see Supplementary Tables S4 & S5).

262
263 We fit all models in a Bayesian framework [42] in Stan [43] through the RStan interface [44]
264 using *brms* v. 2.5.1. [45]. Rather than removing populations with missing data (see b, Predictor

265 variables), i.e. complete-case analysis, we ran analyses on 10 datasets imputed using *mice* [46],
266 which uses all other variables (including a binary measure of dimorphism, male- and average
267 body size) to predict missing values (e.g. female body size, or dimorphism), and pooled
268 parameter estimates [47]. This approach makes the same assumptions about missingness as
269 complete-case analysis but has the advantage of preserving valuable information, and of
270 propagating the uncertainty of the imputation into the final parameter estimates [42]. Complete-
271 case analyses showed no qualitative differences (details not reported). Bayesian estimation
272 produces a posterior probability distribution for each parameter, which can be summarized in
273 various ways; here we report the mean and 95% credible intervals for the likelihoods of different
274 SOs (see Figures 2 & S1) and the proportion of the posterior distribution supporting a given
275 association with a predictor (see Figures 3 & S2); this “posterior probability” [PP] can be
276 directly interpreted as the level of confidence in a given result, which allows inference to be
277 probabilistic rather than dichotomous (as with arbitrary significance thresholds) [42]. We
278 illustrate all associations between SOs and predictors graphically by plotting the predicted means
279 and surrounding uncertainty (Figures 3 & S2). Phylogenetic signal was calculated as the
280 proportion of variance captured by the phylogenetic random effect(s) [48]. All models converged
281 as the potential scale reduction factors were ≤ 1.01 , effective sample sizes > 500 , there were no
282 divergent transitions, and visual examination of the Markov chains showed good mixing. For
283 further details on model fitting see the accompanying R code.

284

285 **3. Results**

286

287 We found data on SO for 245 populations from 100 of the 226 extant artiodactyl species
288 (Supplemental Tables S1 and S2). 61.6% of these populations showed variable SO. 83% of
289 species thus showed IVSO, mostly due to within- (76 species) but also exclusive between-
290 population variability in SO (7 species).

291

292 Model 1 estimated the probability of five different SOs (solitary, pair-living, group-living, sex-
293 specific, variable; see Table 1) and their associations with several predictors. The intercepts
294 represent a non-seasonally-breeding, small (737 g), monomorphic species, which lives in only
295 one habitat and was studied once. An ancestral population with these characteristics was

296 predicted to be pair-living with higher probability (mean=0.76, 95% CI = 0.00-1.00) than any
297 other SO, though variable SO also received considerable support (mean=0.19, 95% CI = 0.00-
298 0.99; Figure 2). Indeed, variable SO becomes the most likely state (0.74, 95% CI = 0.18-1.00;
299 Figure 2) when body size and dimorphism are at the phylogenetically-controlled averages of
300 extant species; in other words, variable SO is the phylogenetic mean SO of extant artiodactyla
301 (though see Tables S4 & S5 for likelihoods of SOs at the upper and lower 95% CI bounds of the
302 estimated phylogenetic averages).

303

304 Figure 3 illustrates changes in the probabilities of different SOs as a function of the predictors.
305 We highlight associations with posterior probabilities ≥ 0.9 , i.e. where the model is $\geq 90\%$
306 confident that a certain predictor is associated with SO. From the top row (A-E), it is clear that
307 SO readily evolves away from pair-living towards solitary, group-living, and variable as body
308 size reaches the range of values observed in extant species, with the likelihood of variable SO
309 dropping again at larger body size values. Greater sexual dimorphism (F-J) is associated with a
310 lower probability of solitary living and a higher probability of variable SO. A higher number of
311 studies (P-T) predicts a greater likelihood of sex-specific and variable SOs. Associations with
312 number of habitats (K-O) and breeding seasonality (U-Y) were more uncertain, with the
313 exception of non-variable group-living being less likely in populations occupying more habitats
314 and breeding seasonally, and the probability of pair-living declining with number of habitats
315 (PP=0.90).

316

317 In terms of habitat type, the prediction of variable SO being less likely in open (savanna and
318 native grasslands) than closed (forest) habitats was not supported (PP=0.35). Similarly, there was
319 little support for group-living being more likely in open habitats (PP=0.63) or pair-living in
320 closed habitats (PP=0.29). The phylogenetic signal (λ) in SO, after conditioning on all other
321 fixed and random effects, was weak but largely greater than 0 (mean = 0.05, 95% CI = 0.00 –
322 0.18, $PP_{>0.01} = 0.70$), suggesting valid but highly uncertain phylogenetic inference for this trait.

323

324 Model 2 further distinguished different kinds of variable SO (see Table 1), and included body
325 size (baseline = 737 g), sexual dimorphism (baseline = 1) and number of studies (baseline = 1) as
326 predictors. At these baseline levels, the most likely ancestral SO was again pair-living (0.48,

327 95%CI = 0.00-1.00), followed by solitary-pair (0.42, 95%CI = 0.00-1.00), pair-group (0.06,
328 95%CI = 0.00-0.73), and solitary-pair-group (0.03, 95%CI = 0.00-0.10; Figure S1). No other SO
329 had a likelihood whose upper 95%CI bound extended above 0.00. However, with body size and
330 dimorphism set to their phylogenetically-controlled averages, the highest probabilities were
331 assigned to SOs involving solitary or group-living (Figure S1), i.e. group-living (0.29, 95% CI =
332 0.00-0.82), solitary (0.24, 95% CI = 0.00-0.48), variable group (0.21, 95% CI = 0.00-0.63),
333 solitary-group (0.18, 95% CI = 0.00-0.44), or solitary-pair-group (0.06, 95% CI = 0.00-0.22),
334 with very low probability for other SOs (solitary-pair: 0.01, 95% CI = 0.00-0.02; Pair-group:
335 0.01, 95% CI = 0.00-0.03; Sex-specific: 0.01, 95% CI = 0.00-0.00; Pair-living: 0.00, 95% CI =
336 0.00-0.00). Figure S2 illustrates the influence of the predictors on the likelihoods of these SOs.
337 As in Model 1, the likelihood of pair-living declines with body size while the likelihoods of
338 solitary and group-living increase; in addition, solitary-pair declines while solitary-pair-group
339 peaks at intermediate body size. Greater sexual dimorphism is strongly associated with increases
340 in the probabilities of solitary-group and variable group-living, while a larger number of studies
341 predicts a greater likelihood of sex-specific SO and is strongly associated with most of the
342 variable forms; for instance, the likelihood of solitary-group increases linearly with study effort.
343 The phylogenetic signal in Model 2 was again weak but largely greater than 0 (mean = 0.06,
344 95% CI = 0.00 – 0.23, $PP_{>0.01} = 0.78$).

345

346 **4. Discussion**

347

348 Our dataset revealed that IVSO occurred in 83% of Artiodactyla species, mostly due to within-
349 population variation in SO (61.6% of the studied populations). Model 1 confirmed that variable
350 SO is the phylogenetic mean SO of extant artiodactyl, i.e. the most typical SO when controlling
351 for phylogeny and predictors (Figure 2). This ubiquity of variable SO is consistent with previous
352 descriptions of IVSO in other mammals including Carnivora [27% of species; [9]], Eulipotyphla
353 [43.8% of species; [21]], and strepsirrhine primates [60.5% of species; [18]]. Contingent on body
354 size estimates and sexual monomorphism from the fossil record, we found that the SO of the
355 ancestral artiodactyl population was most likely pair-living and/or variable (Figures 2 & S1). The
356 evolution of larger body size, as characteristic of extant artiodactyls, and increased (male-biased)
357 sexual dimorphism were likely associated with transitions towards group-living and variable SO

358 (Figure 3) including combinations of solitary and group-living (Figures S1 & S2). Given the
359 relatively weak phylogenetic signal in our models, these inferences were mainly driven by the
360 association of SO with socio-ecological predictors rather than by phylogenetic inertia; this
361 highlights the adaptability of SO and allows good predictions for species with unknown
362 phylogenetic status, such as new fossil discoveries.

363 However, our ancestral state estimation also highlights the high uncertainty surrounding
364 predictions that extend beyond the range of data observed in extant species.

365

366 Our results suggest that the conceptual framework for the social evolution of artiodactyls
367 requires revision. We statistically confirmed Jarman's [19] assumption that the ancestral
368 artiodactyl lived in pairs. However, the body sizes of extant species exhibiting pair-living are
369 6.5-112 times greater (4.8-83.8 kg) than that of the ancestral artiodactyl (737 g; [38]). Thus, the
370 extrapolation of SO to body size values well outside the extant range remains tentative. Our
371 results further suggest that variable kinds of SO were either already part of the ancestral state or
372 evolved with increases to intermediate body sizes. As expected [19], stable social groups evolved
373 in populations with the largest body sizes. Further, we found minimal support for associations
374 previously described for artiodactyl social evolution: (i) sexual monomorphism and closed
375 habitats did not predict pair-living and (ii) sexual dimorphism, breeding seasonality and open
376 habitats did not predict transitions to stable social groups. Our findings also contradict the
377 argument that the ancestral artiodactyl was solitary [10]. A revised framework for artiodactyl
378 social evolution now has a well-grounded inference of a pair-living ancestor with a likely
379 capacity for variable SO. Moreover, our results shift the focus to the conditions favouring the
380 evolution of different kinds of variable SO and the role of body size and its associated factors in
381 these transitions (e.g. predation pressure or life-history pace, neither of which were modelled
382 directly here). We also found strong evidence that the likelihood of reporting sex-specific and
383 variable SOs increases with study effort, suggesting much undiscovered variation in artiodactyl
384 SO.

385

386 Our study generated different results from previous studies [10, 14] in part because we had an
387 improved dataset, more information about the ancestral artiodactyl, and modern phylogenetic
388 methods at our disposal. We collated data at the level of populations rather than species,

389 allowing us to describe and analyse SO at the level at which it is observed and reported in the
390 primary literature. In general, previous studies in which species were categorized into a single
391 SO inflated the prevalence of some SOs (e.g., solitary in 56% of species reported in [10]).
392 Likewise, we did not rely on taxonomic inference (the same SO inferred for unobserved species
393 of the same genus) to build our dataset; this explains, in part, why we had fewer species (100;
394 Supplemental Tables S1 and S2) compared to 187 species in [10]. Our model also accounted for
395 predictors associated with SO, most importantly body size. This allowed us to make our estimate
396 of the ancestral SO contingent on the body size of the oldest artiodactyl known from the fossil
397 record [38]. This value was smaller (737 g) than any observed in extant species (5100 g or more)
398 and that Pérez-Barbería et al. [14, 35] used to classify species as sexually dimorphic or not.
399 Should new fossil evidence become available, this information can easily be incorporated into
400 the model predictions.

401
402 Group-living in open habitats and large body size are considered possible adaptations in
403 artiodactyls to reduce predation risk [19, 49, 50]. Indeed, in our models the probability of pair-
404 living decreased and the probability of group-living increased with larger body size, suggesting
405 that predation risk indeed acted as a selection pressure on SO. However, group-living was not
406 likelier in open compared to closed habitats. The probability of variable SO also did not increase
407 with number of habitat types and did not differ between open and closed habitats. Ecological
408 conditions, such as the spatiotemporal distribution of food resources resulting from
409 environmental (un)predictability, may have a greater effect than habitat type on artiodactyl SO
410 [27, 51]. Contrary to expectations [29], breeding seasonality was not associated with variable
411 SO. The expected relationship might have been observed if we had explicitly included changes
412 in social organisation between breeding and non-breeding periods. However, only a few detailed
413 studies have collected this information. Finally, we found that greater sexual dimorphism was
414 associated with a higher probability of variable SO, specifically solitary-group and variable
415 group-living. This observation is in line with previously reported associations between sexual
416 dimorphism and group-living in artiodactyls [14, 19]. However, the causal relationship between
417 dimorphism and SO is unclear because dimorphism could be a cause or a consequence of
418 changes in SO.

419

420 In conclusion, our study demonstrated three major points regarding artiodactyl social evolution:
421 (i) the ancestral SO was most likely pair-living and/or variable (Figure 2), (ii) the likelihoods of
422 different SOs change most dramatically with body size (Figures 3, S2), and (iii) variable SO is
423 most common for extant species. These findings highlight the importance of accounting for
424 IVSO [9, 18, 21] and body size in comparative studies and of including the general trend towards
425 increased body size and its downstream effects on SO in narratives on mammalian social
426 evolution. As the availability of different social partners influences social and mating
427 interactions and thereby impacts other social system components (Figure 1), our study should
428 motivate future efforts to understand the importance of IVSO in animal social evolution.
429 Specifically, while comparative studies are useful for highlighting general trends and open up
430 new questions, detailed field studies on individual populations are needed to answer questions on
431 mechanisms and function of within- and between-population variability in SO.

432

433 **Data accessibility.** R code and dataset available at
434 <https://github.com/adrianjaeggi/artiodactyl.socialorg>.

435

436 **Authors' contributions.** L.D.H. and C.S. conceived of the project and contributed to manuscript
437 writing. M.I.M. collected data under the supervision of L.D.H. and contributed to manuscript
438 writing. A.J. designed and conducted the statistical analysis and contributed to manuscript
439 writing. M.F.B. provided insight into artiodactyls and contributed to manuscript writing.

440

441 **Competing interests.** The authors declare that they have no competing interests.

442

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457 **Tables**

458

459 **Table 1. Social organisations of artiodactyl populations**

| <i>Category</i> | <i>No. and percentage of populations</i> |
|--|--|
| Stable forms of social organization (38.4%) | |
| Solitary | 26 (10.6%) |
| Pair-living | 6 (2.5%) |
| Sex-specific | 5 (2.0%) |
| Non-variable Group-living | 57 (23.3%) |
| Variable Social Organisation (61.6%) | |
| Variable Group-living | 61 (24.9%) |
| Solitary & Pair-living | 15 (6.1%) |
| Solitary & Group-living | 40 (16.3%) |
| Pair-living & Group-living | 11 (4.5%) |
| Solitary, Pair-living, & Group-living | 24 (9.8%) |

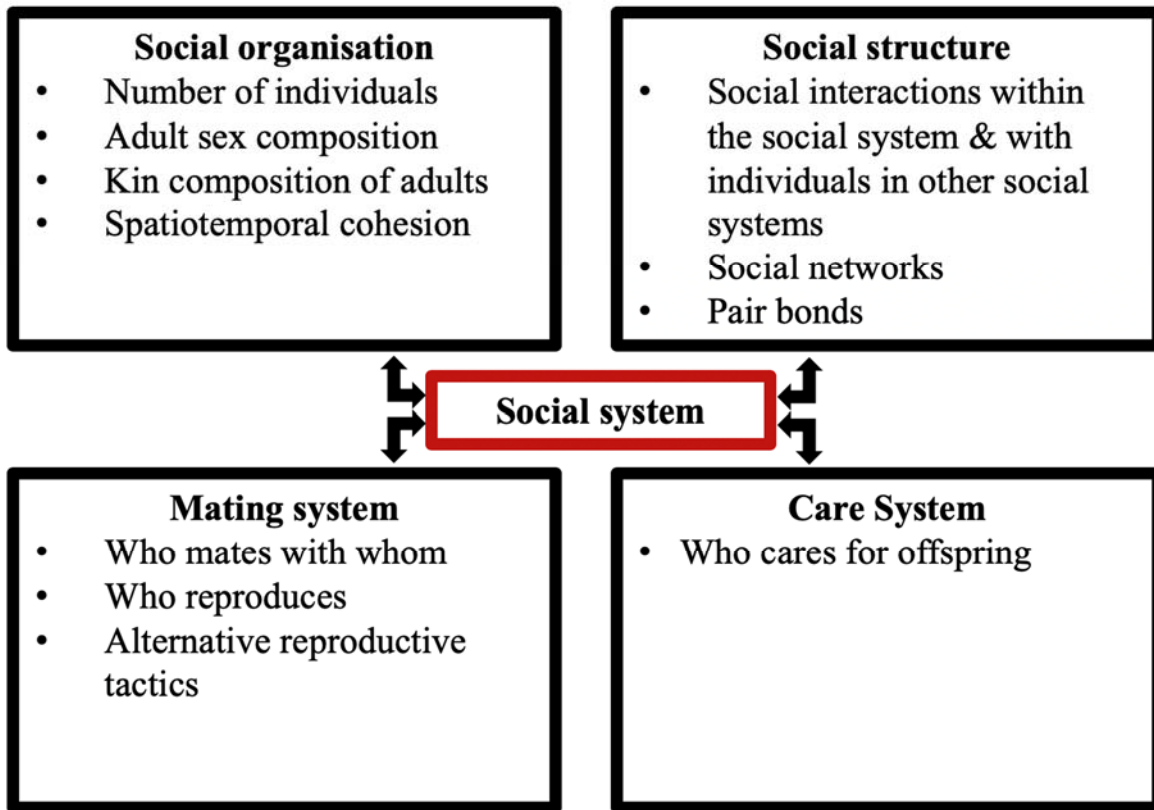
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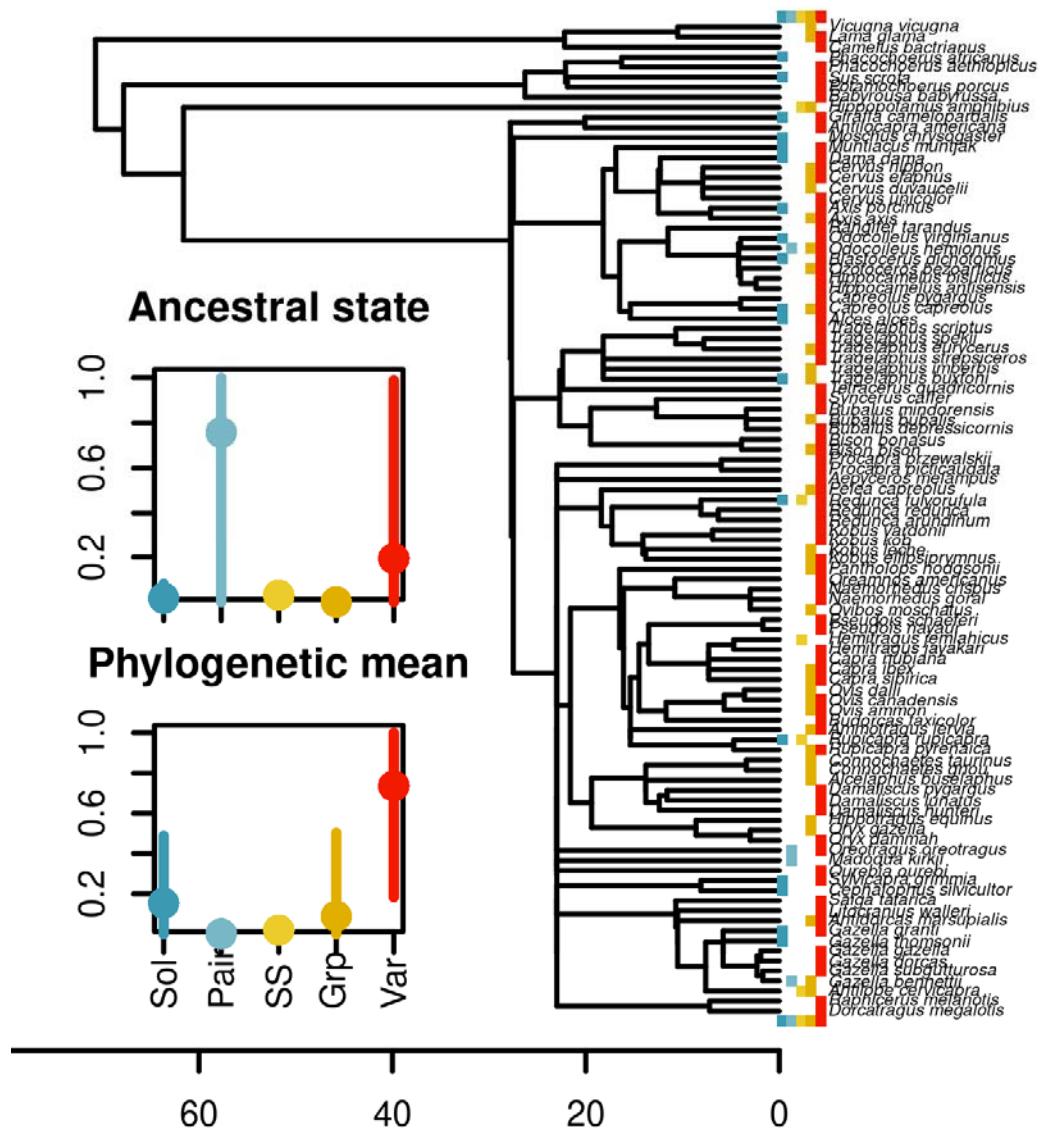
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464 **Figures**
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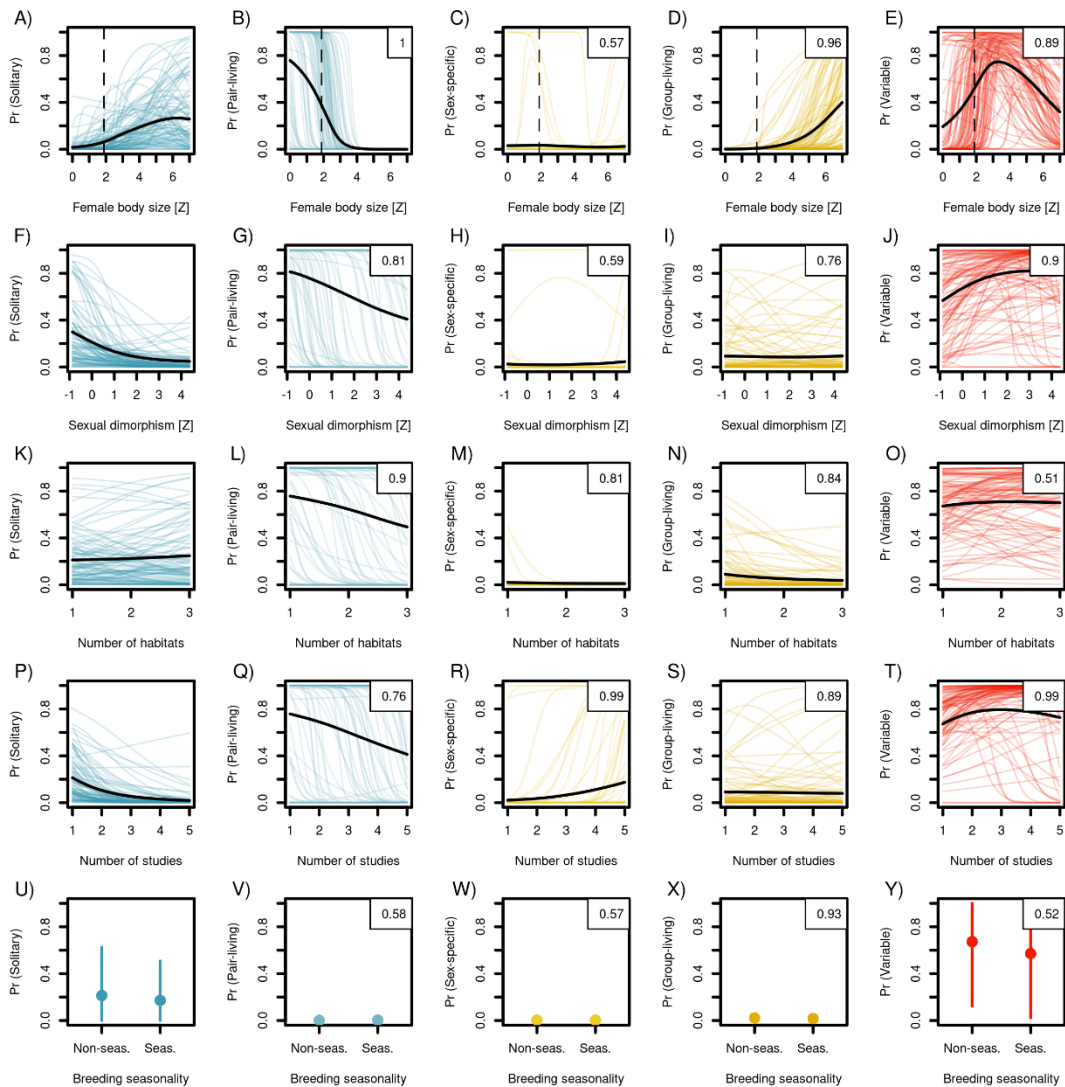


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Figure 1. Representation of animal social systems, including the four components (social organisation, mating system, social structure, care system). Double arrows indicate that the four components shape the entire social system and can be shaped by other components. Adapted from [1, 6].



479
 480 **Figure 2:** Phylogeny of extant artiodactyls with data on social organisation (SO), with the coloured boxes
 481 at the tips of the phylogeny show SOs observed in different populations of the same species. As a
 482 reference, the five possible states (solitary, pair-living, sex-specific, group-living, variable) are plotted
 483 above and below the phylogeny in this order. Using the same colours, the inset figures show the
 484 probabilities (from Model 1) of each SO (Sol=Solitary, Pair=Pair-living, SS=Sex-specific, Grp=Non-
 485 variable group-living, Var=Variable) when body size and dimorphism are at the levels known from the
 486 fossil record (“ancestral state”), or the phylogenetically-controlled averages estimated from extant species
 487 (“phylogenetic mean”); number of habitats and studies as well as breeding seasonality are kept at their
 488 baselines of 1 and non-seasonal, respectively. The scale bar shows million years before present. For the
 489 same figure with variable split into different categories (Model 2), see Figure S1.



491

492 **Figure 3:** Illustrating evolutionary transitions in social organisation (SO) as a function of the predictors

493 (from Model 1). Columns show (from left to right) the probability of solitary, pair-living, sex-specific,

494 group-living, and variable SO – using the same colours as in Figure 2 – while rows show (from top to

495 bottom) predicted changes in those probabilities as a function of female body size (A-E), sexual

496 dimorphism (F-J), number of habitats (K-O), number of studies (P-T), and breeding seasonality (U-Y).

497 The numbers in the legends are the posterior probabilities [PP], i.e. the proportion of the posterior

498 distribution that supports a given association; these were not available for solitary, as this was the

499 reference category. Within each row, all other predictors were held at their baseline value, except for

500 body size; for pair-living, body size was kept at the ancestral state, for all others it was kept at the

501 phylogenetic mean for better visibility. Solid black lines are the predicted means, thin coloured lines are

502 100 random samples drawn from the posterior to illustrate uncertainty. For breeding seasonality (U-Y),
503 points are predicted means and lines are 95% CIs.

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