

1 Intraspecific variation in Artiodactyla social organisation: A Bayesian phylogenetic multilevel
2 analysis of detailed population-level data

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20

21 **Abstract**

22

23 Understanding *inter*-specific variation in social systems is a major goal of behavioural ecology.
24 Previous comparative studies of mammalian social organisation produced inconsistent results,
25 possibly because they ignored *intra*-specific variation in social organisation (IVSO). The
26 Artiodactyla have been the focus of many comparative studies as they occupy a wide diversity of
27 habitats and exhibit large variation in life history patterns as well as other potential correlates of
28 social organisation. Here we present the first systematic data on IVSO among Artiodactyla, infer
29 their ancestral social organisation, and test whether habitat, sexual dimorphism, seasonal
30 breeding, and body size predict inter- and intraspecific variation in social organisation. We found
31 data on social organisation for 110 of 226 artiodactyl species, of which 74.5% showed IVSO.
32 Using Bayesian phylogenetic multilevel models, the ancestral artiodactyl population was
33 predicted to have a variable social organisation with significantly higher probability (0.77, 95%
34 CI 0.29-1.00) than any non-variable form (i.e. solitary, pair-living, group-living). Greater sexual
35 dimorphism and smaller body size both predicted more IVSO; smaller body size also predicted a
36 higher likelihood of pair-living. Our results challenge the long-held assumption that ancestral
37 Artiodactyla were pair-living and strongly imply that taking IVSO into account is crucial for
38 understanding mammalian social evolution.

39

40 Key words: Intraspecific variation, Social organisation, Artiodactyla, phylogenetic mixed-effects
41 model

42 **1. Introduction**

43

44 Animals show remarkable *inter*-specific variation in social systems [1, 2], and understanding the
45 sources of this diversity is a major goal of behavioural ecology. Social systems are characterized
46 by four components [3, 4]: i) social organisation: the size, sex-age, and kin composition of
47 groups, ii) mating system, iii) social structure: relationships emerging from repeated interactions
48 among individuals, and iv) parental and allo-parental care. These components are interdependent.
49 For example, the number and spatial distribution of individuals characterize their social
50 organisation but also constrain their mating tactics [4].

51

52 There have been numerous comparative analyses of mammalian social organisation [6-8].
53 However, inconsistent results have emerged from these studies for several taxa, including
54 primates and carnivorans. In primates, it has been suggested that pair-living species evolved
55 exclusively from solitary [7] or from both solitary and group-living ancestors [8, 9]. In
56 carnivorans, the long-held hypothesis that social evolution involved transitions in social
57 organisation from a solitary ancestor into more advanced forms of group living [solitary ancestor
58 hypothesis: 10, 11] has been questioned [6].

59

60 These inconsistent results likely occurred for several reasons. First, studies have relied on
61 different datasets, methods of analysis, and conceptual frameworks [3]. In an effort to account
62 for as many species as possible, some studies relied on information from secondary sources and
63 taxonomic inference, such as the untested assumption that members of the same genus share the
64 same social organisation [12]. Other studies used confusing terminology or failed to distinguish
65 between social organisation and mating system [3]. For example, some studies inferred
66 monogamy (mating system) from the observation of male-female pairs (social organisation) [9,
67 13]. To resolve these issues, comparative studies should rely exclusively on data from primary
68 sources, and distinguish social organisation from other social system components.

69

70 Most comparative studies of mammalian social organisation relied on a single trait value for each
71 species, yet social systems can be dynamic [14-16]. *Intraspecific* variation in social organisation
72 (IVSO) occurs when adults of a species show two or more forms of social organisation [6, 14,

73 17]. Variation can also occur in the composition of groups, such that a species may live in
74 different types of groups, e.g., unisex vs. multi-sex groups. In mammals, IVSO has been reported
75 in numerous species from different orders [6, 18-22], transforming our understanding of
76 mammalian social evolution. For example, in carnivorans (Order: Carnivora) and shrews (Order:
77 Euliptophya), it was long believed that the ancestral state was solitary. However, a variable
78 ancestral state was found to be equally likely after taking IVSO into account (Carnivora: [6];
79 Euliptophya: [21]). More broadly, ignoring intraspecific variation can increase statistical type II
80 error rates [23-25] and lead to spurious conclusions about social evolution [17, 26]. Modern
81 comparative methods such as phylogenetic mixed-effects (a.k.a. multilevel) models or
82 measurement-error models [24, 27] can easily incorporate intraspecific variation. Thus,
83 comparative studies should include intraspecific variation in social organisation.

84

85 IVSO may arise, for example, if individuals of both sexes can respond to unpredictable or
86 changing ecological conditions by changing their social tactic [16, 17]. Further, IVSO may vary
87 with body size, which correlates strongly with life-history pace [34] as well as available anti-
88 predator strategies [35]. Intraspecific variation in group size and composition is also expected in
89 seasonal breeders. During the breeding season, reproductive competition can exclude some
90 individuals from groups, thus causing IVSO [36]. Alternatively, relaxed competition during the
91 non-breeding season may allow the formation of larger groups, particularly if grouping has
92 survival benefits [e.g., anti-predator strategies; 18, 37]. Thus, we expect greater variability in
93 social organisation among species occupying a wider range of habitats and among seasonal
94 breeders.

95

96 The order Artiodactyla is well suited for comparative studies of social evolution because its
97 members exhibit both inter- and intraspecific variation in social organisation, occupy a wide
98 diversity of habitat types, and exhibit a range of body sizes, sexual dimorphism, as well as both
99 seasonal and non-seasonal breeding [18, 38]. Habitat heterogeneity and availability of protective
100 cover are associated with *interspecific* variation in social organisation of many artiodactyls [18].
101 Generally, groups are larger in open areas [18, 39], with solitary species mostly living in dense
102 forests [40]. Group-living and large body size are adaptations to open habitats characterized by
103 high predation risk [41]. Sexual dimorphism in body size and seasonal breeding, common in

104 artiodactyls, are also associated with interspecific variation in social organisation [18]. Most
105 sexually dimorphic species live in unisex groups or as solitary individuals, forming mixed sex
106 groups only in the breeding season [42, 43], [but see 44, 45]. Monomorphic species live alone, in
107 pairs, or mixed sex groups [46]. Sexual dimorphism is also correlated with body size [18]. We
108 therefore expected these factors to influence IVSO.

109

110 We first describe *interspecific* and *intraspecific* variation in artiodactyl social organisation, using
111 only data from published studies on wild populations. Our second objective was to infer the
112 ancestral social organisation of artiodactyls. We used a detailed phylogeny and modern
113 comparative methods to evaluate competing hypotheses about artiodactyl social evolution,
114 namely 1) from pair-living to group-living [7] or 2) from IVSO to single types of social
115 organisation [6]. Our third objective was to determine the extent to which habitat, sexual
116 dimorphism, body size and breeding seasonality predict variation in social organisation.
117 Specifically, we predicted that the likelihood of IVSO and the total number of social
118 organisations in a species (i) increase with greater number of habitats, (ii) decrease in open
119 habitats due to predation pressure favoring group-living, (iii) sexually dimorphic than
120 monomorphic species and (iv) are greater in seasonal breeders than non-seasonal breeders.

121

122 **2. Methods**

123

124 (a) Data collection

125

126 Searches were conducted using Web of Science and Google Scholar to find primary sources
127 reporting social organisation for all 226 extant species of Artiodactyla [47]. The initial search
128 consisted of the scientific name (genus and species) and a keyword ('social', 'herd', or 'group').
129 If no sources were found, a final search used only the scientific name. In *Web of Science*, search
130 results were refined by selecting three research areas: 'zoology', 'behavioral science', and
131 'environmental science/ecology', and document type 'article'. Lab-based studies, studies in
132 enclosures smaller than 1,000-hectares, and studies that included manipulation of individuals,
133 groups, or resources were discarded. From the 267 primary sources, we coded the following
134 social organisation(s): 1) Solitary, 2) Pair-living, 3) Sex-specific social organisation 4) Unisex

135 groups, 5) Single female/multi-male, 6) Multi-female/single male, and 7) Multi-female/multi-
136 male (Supplementary Material Table S1).

137

138 (b) Determining variable social organisation

139

140 Variable social organisation was identified when 1) both sexes had more than one form of social
141 organisation in the same population [e.g., solitary and pair-living; 17] or between populations or
142 2) multiple types of groups occurred within the same population or in different populations (e.g.,
143 FFM and FFMM groups). For statistical analyses, overall population-level social organisations
144 were categorized as: 1) Solitary, 2) Pair-living, 3) Sex-specific, 4) Non-variable group-living,
145 and 5) variable, including populations with multiple forms of group-living. We categorized cases
146 where one sex was solitary and the other was in unisex groups as a specific form of social
147 organisation (sex-specific) and cases in which both sexes lived in unisex groups as a form of
148 group-living. Additional details are provided in Supplementary Material S2.

149

150 (c) Predictor variables

151

152 Each species was categorized as either seasonal or non-seasonal breeder [38]. The extent of
153 sexual dimorphism was calculated as the ratio of adult male to female body mass using data
154 reported in Pérez-Barbería & Gordon [38]. Body size was included as mean adult female body
155 mass. Habitat type was derived from the primary source and categorized based on IUCN
156 classification (www.iucn.org) as desert, forest, rocky areas, savanna, grassland, shrubland,
157 wetlands, or artificial.

158

159 (d) Phylogeny

160

161 We used the mammal supertree from Bininda-Emonds et al. [48]. Some species names in the
162 database had to be amended to match the phylogeny as detailed in the accompanying R code. In
163 virtually all cases, a name mismatch could be resolved by finding a pseudonym for that species
164 through www.iucn.org, or by using a sister species that was not included in the database. In one

165 case, two closely-related taxa missing from the supertree (*Moschus leucogaster* and *Moschus*
166 *cupreus*) were proxied by the same sister species (*Moschus chrysogaster*).

167

168 (e) Statistical analysis

169

170 We used Bayesian phylogenetic mixed-effects models, accounting for the multilevel structure of
171 the data (populations nested within species) and the phylogenetic relationships among species
172 [24, 27]. Predictors included sexual dimorphism, female body size, breeding seasonality, and
173 number of habitats. Type of habitat was modeled as a random intercept. All models controlled
174 for research effort by including the number of studies. To control for potential geographical
175 biases continent was included as a random intercept.

176

177 Prior to fitting the model, we estimated the likely ancestral state for body size, sexual
178 dimorphism, and breeding seasonality (see Supplementary Material 3). We then centered body
179 size and sexual dimorphism on these estimated ancestral states and chose the likely ancestral
180 breeding seasonality as the reference category. Consequently, the estimated ancestral social
181 organisation (i.e. the global intercepts of the multilevel models) is contingent on predictors that
182 are *also* at their likely ancestral state.

183

184 To model the likelihood of several mutually exclusive categorical traits (i.e. different social
185 organisations) and how the likelihood of each trait was affected by other variables we used a
186 multinomial model [52] (see Supplementary Material 3). We highlight any covariates that
187 influence the likelihood of different social organisations, and thus may explain evolutionary
188 transitions from the ancestral state. Additional details are in Supplementary Material 4.

189

190 We fit all models in a Bayesian framework [53] in Stan [54] through the RStan interface [55]
191 using *brms* v. 2.5.1. [56]. Bayesian estimation produces a posterior probability distribution for
192 each parameter, which can be summarized in various ways; here we report the mean and 95%
193 credible intervals and occasionally the proportion of the posterior that lies above or below a
194 certain value (“PP”). Phylogenetic signal was calculated as the proportion of variance captured
195 by the phylogenetic random effect(s) following [57]. All models converged as assessed with the

196 potential scale reduction factor (all ≤ 1.01), effective sample sizes (all > 500), and by visually
197 examining trace plots of the Markov chains. Details on model fitting can be gleaned from the
198 accompanying R code (available at <https://github.com/adrianjaeggi/artiodactyl.socialorg>).

199

200 **3. Results**

201

202 We found data on social organisation for 247 populations from 110 of the 226 extant artiodactyl
203 species. The majority of these species showed variation in their social organisation at the species
204 level (74.5%, 82 out of 110). Five species were strictly solitary (4.5%), only one was strictly
205 pair-living (0.9%), one showed sex-specific social organisation (0.9%), and eleven showed only
206 one form of group-living (Table 1). A more detailed breakdown of variable social organisation is
207 available in Supplementary Material Table S5. At the population level, 62% (155/247) of all
208 populations also had variable social organisation. Of the 82 species showing variable social
209 organisation, five (6.1%) showed variation between populations, twenty-nine (35.4%) showed
210 variation within a population, and forty-eight (58.5%) showed variable social organisation both
211 between populations and within a population.

212

213 A summary of the phylogenetic multilevel model is available in the Supplementary Material S6.
214 The intercepts reflect a non-seasonally-breeding species of ancestral body size and sexual
215 dimorphism that lives in only one habitat and was studied once. An ancestral population with
216 these characteristics was predicted to have a variable social organisation with significantly higher
217 probability (0.77, 95% CI 0.29-1.00) than any non-variable form (Figure 1).

218

219 The likelihood of variable social organisation increased with degree of sexual dimorphism (odds
220 ratio for 1SD change = 2.91, 95% CI = 1.16 – 8.94), and decreased as female body mass
221 increased (odds ratio for 1SD change = 0.39, 95% CI = 0.16 – 0.80; Figure 2). Pair-living was
222 more likely with lower female body mass (Figure 2). Unsurprisingly, the probability of variable
223 and sex-specific social organisations increased with study effort. No other associations were
224 “significant” at the 95% CI level, but transitions to group-living were likelier with greater sexual
225 dimorphism (PP=0.85) and seasonal breeding (PP=0.87). In terms of habitat type, the prediction
226 of variable social organisation being less likely in open (savanna and native grasslands) than

227 closed (forest) habitats was not supported (PP=0.37). Similarly, support for group-living being
228 more likely in open habitats was weak (PP=0.63). The phylogenetic signal in social organisation
229 was weak but greater than 0 (mean = 0.24, 95% CI = 0.05 – 0.48).

230

231 The model for number of social organisations is summarized in Supplementary Materials S5.
232 The predicted number of social organisations for the ancestor of all Artiodactyla was 1.73 (95%
233 CI = 1.19 - 2.41), with no predictor influencing the number of social organisations at the 95% CI
234 level. However, a decrease in number of social organisations with greater mean female body
235 mass was relatively well supported (PP=0.91, consistent with Figure 2A). The prediction of
236 fewer social organisations in open habitats compared to closed ones was again only weakly
237 supported (PP=0.70). The phylogenetic signal was low (mean = 0.13, 95% CI = 1 e-5 – 0.29).

238

239 **4. Discussion**

240

241 Our dataset revealed that IVSO occurred in 75% of Artiodactyla species. For species showing
242 IVSO, social organisation was variable within 62% of populations. These trends are consistent
243 with previous descriptions of IVSO in artiodactyls [58] and other mammals including Carnivora
244 [27% of species classified as 'flexible'; 6], Eulipotyphla [43.8% of species with data; 21],
245 Rodentia [16, 20], and strepsirrhine primates [60.5% of species with data; 22]. Mounting
246 evidence of extensive IVSO in mammals challenges the common assumption in comparative
247 studies that all species have only one social organisation [7, 59-61]. Failing to account for
248 intraspecific variation will likely result in spurious conclusions about social evolution, slowing
249 theoretical advancement [17, 25]. Using modern phylogenetic methods, we can now easily
250 account for IVSO by analyzing data at the population rather than the species level. Moreover,
251 greater effort should be made to build datasets from high-quality, primary sources rather than
252 relying on secondary sources and taxonomic inference.

253

254 Our results change our understanding of social evolution. Both Jarman [18] and Pérez-Barbería
255 et al. [13] assumed in their early comparative studies that the ancestral artiodactyl was socially
256 monogamous (pair-living) with evolutionary transitions to polygyny and group-living. In
257 contrast, Lukas & Clutton-Brock [7] argued that solitary living was the ancestral condition for

258 most mammalian orders, including Artiodactyla. Contrary to these studies, our analysis estimated
259 the ancestral social organisation to be variable, with possible transitions to both pair-living or
260 group-living depending on body size, or sexual dimorphism and breeding seasonality,
261 respectively (or possible unmeasured variables that cause variation in these factors). Thus, our
262 study supports the argument that IVSO plays an important role in the evolution of mammalian
263 social systems [6, 17].

264
265 Group-living and large body size are possible adaptations for artiodactyls living in open habitats
266 [18, 40, 41] and to reduce predation risk [1]. Positive associations between group size and habitat
267 openness have been observed in artiodactyls [62] and other mammals [e.g., 63]. Thus, we
268 expected reduced IVSO in large bodied, group-living species in open habitats. In support of this
269 hypothesis, both the probability of variable social organisation and the number of social
270 organisations was low for species with large (and with very low) body mass but highest for
271 species of intermediate body mass.

272
273 Contrary to expectations, IVSO did not increase with increasing number of habitat types,
274 suggesting that IVSO is not the result of selection for habitat-specific social organisations.
275 Furthermore, neither the probability of variable social organisation or group-living nor the
276 number of social organisations differed between open (savannas and grasslands) and closed
277 habitats (forests). Ecological conditions, such as the spatiotemporal distribution of food
278 resources as a result of unpredictable and/or variable precipitation and temperature, may have a
279 greater effect than habitat type on the social organisation, as was suggested for artiodactyls [64].

280
281 Reproductive competition changes seasonally in species that breed seasonally which in turn, can
282 lead to greater variation in social organisation [36, 65]. Contrary to this expectation, artiodactyls
283 that breed seasonally did not exhibit greater IVSO than non-seasonal breeders. Seasonal
284 variation in local ecological conditions, such as the spatiotemporal variation in rainfall and food
285 [17] may be more important predictors of IVSO than seasonality of breeding alone. The
286 likelihood of IVSO increased with degree of sexual dimorphism. In polygynous systems, a large
287 percentage of males may not breed [66]. Some males may live with other males in bachelor
288 groups, increasing the prevalence of IVSO. In some species, such as African buffalo (*Syncerus*

289 *caffer*) there is a rotation system in which breeding males join herds of breeding females for a
290 period of time [67]. During this time, the males breed and fight, but then re-join bachelor groups
291 to recover from the energetic costs of breeding [67].

292

293 In conclusion, our study demonstrated three major points regarding social evolution: 1) ancestral
294 artiodactyl social organisation was variable and not pair-living, as was long assumed, 2) in
295 artiodactyls, the frequency of IVSO increased with increasing sexual dimorphism and decreased
296 with body size, and 3) taking IVSO into account and using a high-quality dataset significantly
297 changes our understanding of social evolution. Our study should motivate future efforts to
298 understand the importance of IVSO in animal social evolution.

299

300

301 **Data accessibility.** R code and dataset available at

302 <https://github.com/adrianjaeggi/artiodactyl.socialorg>.

303

304 **Authors' contributions.** L.D.H. and C.S. conceived of the project and contributed to manuscript
305 writing. M.I.M. collected data and contributed to manuscript writing. A.J. conducted the
306 statistical analysis and contributed to manuscript writing. M.F.B. provided insight into
307 artiodactyls and contributed to manuscript writing.

308

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310

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495 **Tables**

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497 **Table 1. Social organisations of Artiodactyla species**

Category	No. and percentage
Solitary	5 (4.5%)
Pair-living	1 (0.9%)
Sex-specific	1 (0.9%)
Group-living, only, but split into:	
- No variation in group composition	11 (10.0%)
- Variable group composition*	21 (19.1%)
- Unknown composition	10 (9.1%)
Species with more than one social organisation	61 (55.5%)
Species with variable group composition	42 (38.2%)
Species with any form of IVSO, including variable group composition	82 (74.5%)
Species with data	110 (48.7%)
Species with no data	116 (51.3%)

498 * *Variable includes more than one of the following: single male, multiple females (MFF); single*
 499 *female, multiple males (FFM); multiple males, multiple females (MMFF); unisex groups, both*
 500 *male-only and female-only in the same population.*

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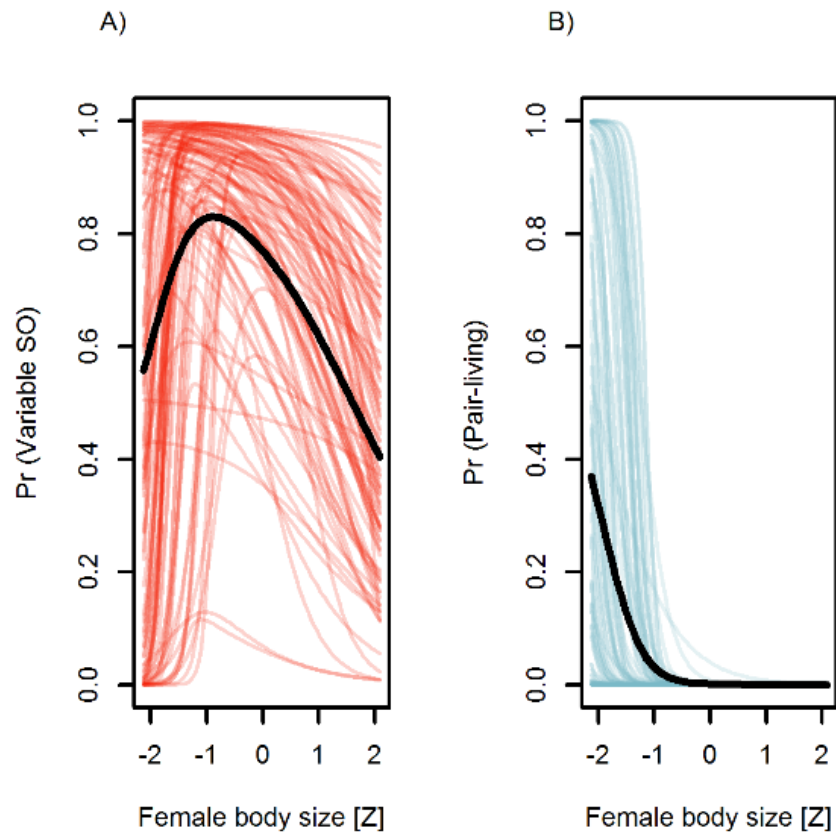
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523 **Figure 2.** Probability of A) variable social organisation and B) pair-living as a function of female
524 body size. Solid black lines indicate mean predicted values; thin lines represent 100 randomly
525 drawn posterior samples to illustrate uncertainty.

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