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Author for correspondence:

L. D. Hayes

e-mail: loren-hayes@utc.edu

[†]Co-first authors.

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

A. V. Jaeggi^{1,†}, M. I. Miles^{2,†}, M. Festa-Bianchet³, C. Schradin^{4,5} and L. D. Hayes²

¹Institute of Evolutionary Medicine, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

²Department of Biology, Geology, and Environmental Science, University of Tennessee at Chattanooga, USA

³Département de Biologie, Université de Sherbrooke, Sherbrooke, Quebec, Canada J1K 2R1

⁴School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, WITS 2050 Johannesburg, South Africa

⁵IPHC, UNISTRA, CNRS, 23 rue du Loess, 67200 Strasbourg, France

id AVJ, 0000-0003-1695-0388; MF-B, 0000-0002-2352-3379; CS, 0000-0002-2706-2960; LDH, 0000-0003-0713-416X

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

1. Introduction

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

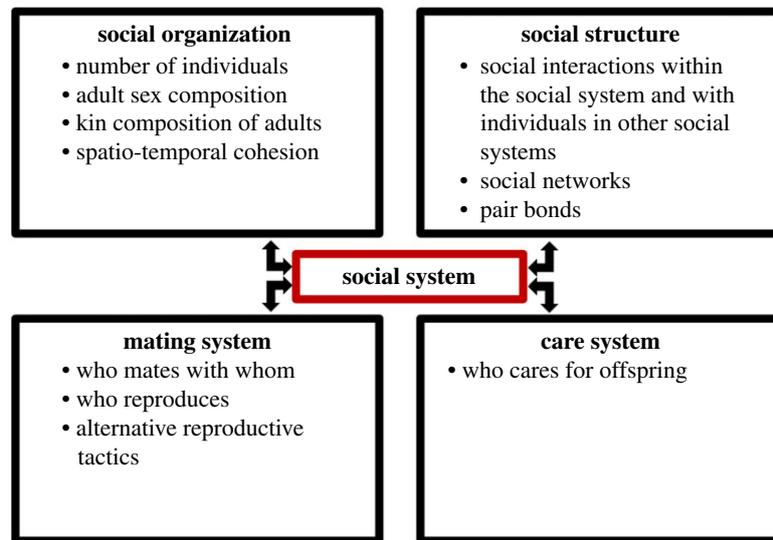


Figure 1. Representation of animal social systems, including the four components (SO, mating system, social structure, care system). Double arrows indicate that the four components shape the entire social system and can be shaped by other components. Adapted from [1,6]. (Online version in colour.)

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

Most comparative studies of mammalian SO characterized each species as solitary, pair-living or (different forms of) group-living [8,10,12]. However, many species have more than one form of SO, at both the population and the species levels. At the population level (the unit of analysis in our study), *variable SO* is the occurrence of multiple forms of SO within a population. At the species level, variation can occur both within and between populations, and has been called intraspecific variation in social organization (IVSO) [7,9,16,17]. Determining the extent of IVSO is important because it is predicted to influence reproductive competition and social interaction, and thus other components of the social system [7].

In mammals, IVSO has been reported in numerous species from different orders [9,18–21], transforming our understanding of mammalian social evolution. For example, in carnivorans and shrews, it was long believed that the ancestral SO was solitary. Two observations challenge the validity of this assumption. Phylogenetic reconstructions did not support a solitary ancestor in Carnivora [9]. In shrews, group-living and variable SO occurs in 36% and 27% of species [21]. More broadly, ignoring intraspecific variation can increase statistical type II error rates [22–24] and lead to spurious conclusions

about social evolution [7,25]. Thus, comparative studies of SO should include intraspecific variation by using modern statistical methods, such as phylogenetic mixed-effects (aka multilevel) models or measurement-error models [23,26].

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

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

First, we investigated how often variable SO has been reported within- and between-populations in field studies on artiodactyls and used this information to describe the extent of IVSO (electronic supplementary material, tables S1 and S2). Second, we inferred the ancestral SO of artiodactyls, testing whether the previous assumption of a pair-living ancestor [14,19] is correct. Third, we evaluated the extent to which factors previously suggested to be key determinants of

artiodactyl social evolution [14,19] influence SO, predicting that (i) group-living would be associated with open habitats and with sexual dimorphism. In addition, based on earlier work on IVSO [7], we predicted that the likelihood of variable SO increases with (ii) number of habitats and (iii) breeding seasonality. Even though SO was defined at the population level, since this was the unit of observation, most of the predictors of SO (body size, sexual dimorphism, breeding seasonality) were only available at the species level. Hence, an effect of body size on SO, for example, represents a between- rather than within-species effect; if body size were available at the population level these two effects could be disentangled [26,33].

2. Methods

(a) Data collection

We searched the Web of Science and Google Scholar for primary sources on SO for all 226 extant species of Artiodactyla [34]. The initial search consisted of the scientific name (genus and species) and a keyword (social, herd, or group). If no sources were found, a final search used only the scientific name. In Web of Science, search results were refined by selecting three research areas—‘zoology’, ‘behavioral science’ and ‘environmental science/ecology’—and document type ‘article’. Laboratory-based studies, studies in enclosures smaller than 1000 hectares, and studies that included manipulation of individuals, groups or resources were discarded. We recorded and analysed all information on SO at the level of the population, as defined by the original authors.

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

The concept of IVSO is only meaningful if it captures hitherto unconsidered variation and allows us to differentiate between populations where all individuals live in the same form of SO from those where more forms of SO occur. Thus, the following cases were not regarded as variable SO. (i) Reports of solitary individuals of only one sex, since every species has dispersers that are typically solitary and dispersal is often sex-specific. (ii) Different kinds of male groups or alternative reproductive tactics in species that form single-male/multi-female groups or where some males otherwise monopolize access to females. In such cases, the remaining males (sex ratio of birth is close to 1:1 in mammals) must necessarily be somewhere else, such as in bachelor groups. It is

critical to note that studies focusing on dispersal and alternative reproductive tactics are important and related to studies on IVSO, but they do not represent studies on how and why the composition of social units varies in many species. For further details on the dataset, see the electronic supplementary material, text S1 and accompanying data file (<https://github.com/adrianjaeggi/artiodactyl.socialorg>).

(b) Predictor variables

Each species was categorized as either seasonal or non-seasonal breeder. Sexual dimorphism was calculated as the ratio of adult male to female body mass using data reported by Pérez-Barbería & Gordon [35]. Categorical classifications of sexual dimorphism were determined based on Pérez-Barbería & Gordon [14,35]. Mean adult female body mass was used as a measure of body size. Habitat type was derived from the primary sources and categorized based on IUCN classification (www.iucn.org) as desert, forest, rocky areas, savannah, grassland, shrubland, wetlands or artificial. There were 45 populations with missing data on female body size and sexual dimorphism, though for many of these we had data on average body size and/or a categorical measure of dimorphism, and one population with missing data on habitat type(s); these missing values were imputed (see §2d).

(c) Phylogeny

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

(d) Statistical analysis

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

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

In Model 2, we separated out the specific forms of variable SO to further test the assumption that pair-living was important in ancestral artiodactyls, including perhaps as a part of variable SOs. This resulted in the following categories: (i) solitary, (ii) pair-living, (iii) sex-specific SO, (iv) non-variable group-living (one

type of group within a population), (v) variable group-living (multiple types of groups within a population), (vi) solitary and pair-living, (vii) solitary and group-living, (viii) pair-living and group-living and (ix) solitary and pair-living and group-living. Given the much larger number of parameters, Model 2 only included those predictors that strongly predicted SO in Model 1, and no random effects (other than species).

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

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

We fit all models in a Bayesian framework [42] in Stan [43] through the RStan interface [44] using *brms* v. 2.5.1. [45]. Rather than removing populations with missing data (see S2b), i.e. complete-case analysis, we ran analyses on 10 datasets imputed using *mice* [46], which uses all other variables (including a binary measure of dimorphism, male- and average body size) to predict missing values (e.g. female body size, or dimorphism) and pooled parameter estimates [47]. This approach makes the same assumptions about missingness as complete-case analysis but has the advantage of preserving valuable information, and of propagating the uncertainty of the imputation into the final parameter estimates [42]. Complete-case analyses showed no qualitative differences (details not reported). Bayesian estimation produces a posterior probability distribution for each parameter, which can be summarized in various ways; here we report the mean and 95% credible intervals for the likelihoods of different SOs (figure 2 and electronic supplementary material, figure S1) and the proportion of the posterior distribution supporting a given association with a predictor (figure 3; electronic supplementary material, figure S2); this ‘posterior probability’ [PP] can be directly interpreted as the level of confidence in a given result,

which allows inference to be probabilistic rather than dichotomous (as with arbitrary significance thresholds) [42]. We illustrate all associations between SOs and predictors graphically by plotting the predicted means and surrounding uncertainty (figure 3 and electronic supplementary material, figure S2). Phylogenetic signal was calculated as the proportion of variance captured by the phylogenetic random effect [48]. All models converged as the potential scale reduction factors were less than or equal to 1.01, effective sample sizes greater than 500, there were no divergent transitions, and visual examination of the Markov chains showed good mixing. For further details on model fitting, see the accompanying R code.

3. Results

We found data on SO for 245 populations from 100 of the 226 extant artiodactyl species (electronic supplementary material, tables S1 and S2). 61.6% of these populations showed variable SO. 83% of species thus showed IVSO, mostly due to within-(76 species) but also exclusive between-population variability in SO (seven species).

Model 1 estimated the probability of five different SOs (solitary, pair-living, group-living, sex-specific, variable; table 1) and their associations with several predictors. The intercepts represent a non-seasonally breeding, small (737 g), monomorphic species, which lives in only one habitat and was studied once. An ancestral population with these characteristics was predicted to be pair-living with higher probability (mean = 0.76, 95% CI = 0.00–1.00) than any other SO, though variable SO also received considerable support (mean = 0.19, 95% CI = 0.00–0.99; figure 2). Indeed, variable SO becomes the most likely state (0.74, 95% CI = 0.18–1.00; figure 2) when body size and dimorphism are at the phylogenetically controlled averages of extant species; in other words, variable SO is the phylogenetic mean SO of extant Artiodactyla (though see electronic supplementary material, tables S4 and S5 for likelihoods of SOs at the upper and lower 95% CI bounds of the estimated phylogenetic averages).

Figure 3 illustrates changes in the probabilities of different SOs as a function of the predictors. We highlight associations with posterior probabilities greater than or equal to 0.9 (i.e. where the model is at least 90% confident that a certain predictor is associated with SO). From the top row (*a–e*), it is clear that SO readily evolves away from pair-living towards solitary, group-living and variable as body size reaches the range of values observed in extant species, with the likelihood of variable SO dropping again at larger body size values. Greater sexual dimorphism (*f–j*) is associated with a lower probability of solitary living and a higher probability of variable SO. A higher number of studies (*p–t*) predicts a greater likelihood of sex-specific and variable SOs. Associations with number of habitats (*k–o*) and breeding seasonality (*u–y*) were more uncertain, with the exception of non-variable group-living being less likely in populations occupying more habitats and breeding seasonally, and the probability of pair-living declining with number of habitats.

In terms of habitat type, the prediction of variable SO being less likely in open (savannah and native grasslands) than closed (forest) habitats was not supported (PP = 0.35). Similarly, there was little support for group-living being more likely in open habitats (PP = 0.63) or pair-living in closed habitats (PP = 0.29). The phylogenetic signal (λ) in SO, after

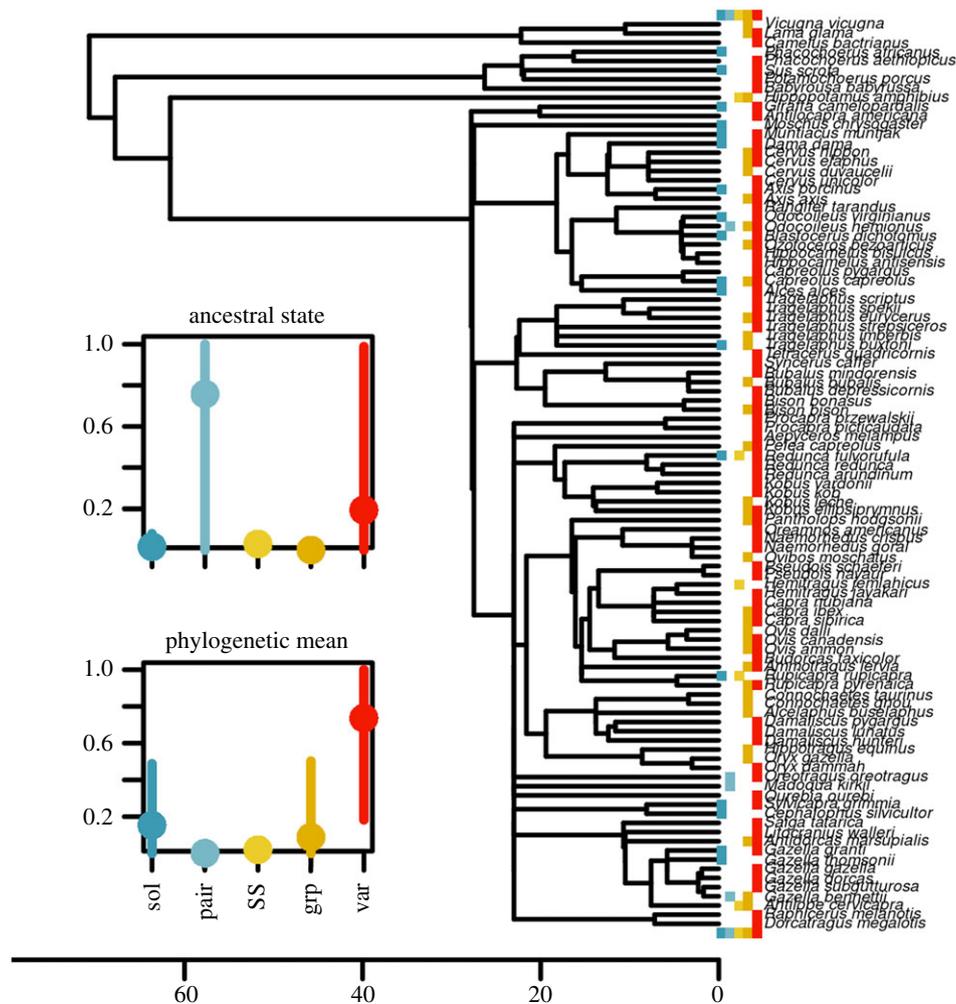


Figure 2. Phylogeny of extant artiodactyls with data on SO, with the coloured boxes at the tips of the phylogeny show SOs observed in different populations of the same species. As a reference, the five possible states (solitary, pair-living, sex-specific, group-living, variable) are plotted above and below the phylogeny in this order. Using the same colours, the inset figures show the probabilities (from Model 1) of each SO (sol, solitary; pair, pair-living; SS, sex-specific; grp, non-variable group-living; var, variable) when body size and dimorphism are at the levels known from the fossil record (ancestral state), or the phylogenetically controlled averages estimated from extant species (phylogenetic mean); number of habitats and studies as well as breeding seasonality are kept at their baselines of 1 and non-seasonal, respectively. The scale bar shows million years before present. For the same figure with variable split into different categories (Model 2), see electronic supplementary material, figure S1. (Online version in colour.)

conditioning on all other fixed and random effects, was weak but largely greater than 0 (mean = 0.05, 95% CI = 0.00–0.18, $PP_{>0.01} = 0.70$), suggesting valid but highly uncertain phylogenetic inference for this trait.

Model 2 further distinguished different kinds of variable SO (table 1), and included body size (baseline = 737 g), sexual dimorphism (baseline = 1) and number of studies (baseline = 1) as predictors. At these baseline levels, the most likely ancestral SO was again pair-living (0.48, 95% CI = 0.00–1.00), followed by solitary–pair (0.42, 95% CI = 0.00–1.00), pair–group (0.06, 95% CI = 0.00–0.73) and solitary–pair–group (0.03, 95% CI = 0.00–0.10; electronic supplementary material, figure S1). No other SO had a likelihood whose upper 95%CI bound extended above 0.00. However, with body size and dimorphism set to their phylogenetically controlled averages, the highest probabilities were assigned to SOs involving solitary or group-living (electronic supplementary material, figure S1), i.e. group-living (0.29, 95% CI = 0.00–0.82), solitary (0.24, 95% CI = 0.00–0.48), variable group (0.21, 95% CI = 0.00–0.63), solitary–group (0.18, 95% CI = 0.00–0.44), or solitary–pair–group (0.06, 95% CI = 0.00–0.22), with very low probability for other SOs (solitary–pair: 0.01, 95%

CI = 0.00–0.02; pair–group: 0.01, 95% CI = 0.00–0.03; sex-specific: 0.01, 95% CI = 0.00–0.00; pair-living: 0.00, 95% CI = 0.00–0.00). electronic supplementary material, figure S2 illustrates the influence of the predictors on the likelihoods of these SOs. As in Model 1, the likelihood of pair-living declines with body size while the likelihoods of solitary and group-living increase; in addition, solitary–pair declines while solitary–pair–group peaks at intermediate body size. Greater sexual dimorphism is strongly associated with increases in the probabilities of solitary–group and variable group-living, while a larger number of studies predicts a greater likelihood of sex-specific SO and is strongly associated with most of the variable forms; for instance, the likelihood of solitary–group increases linearly with study effort. The phylogenetic signal in Model 2 was again weak but largely greater than 0 (mean = 0.06, 95% CI = 0.00–0.23, $PP_{>0.01} = 0.78$).

4. Discussion

Our dataset revealed that IVSO occurred in 83% of Artiodactyla species, mostly due to within-population variation in SO

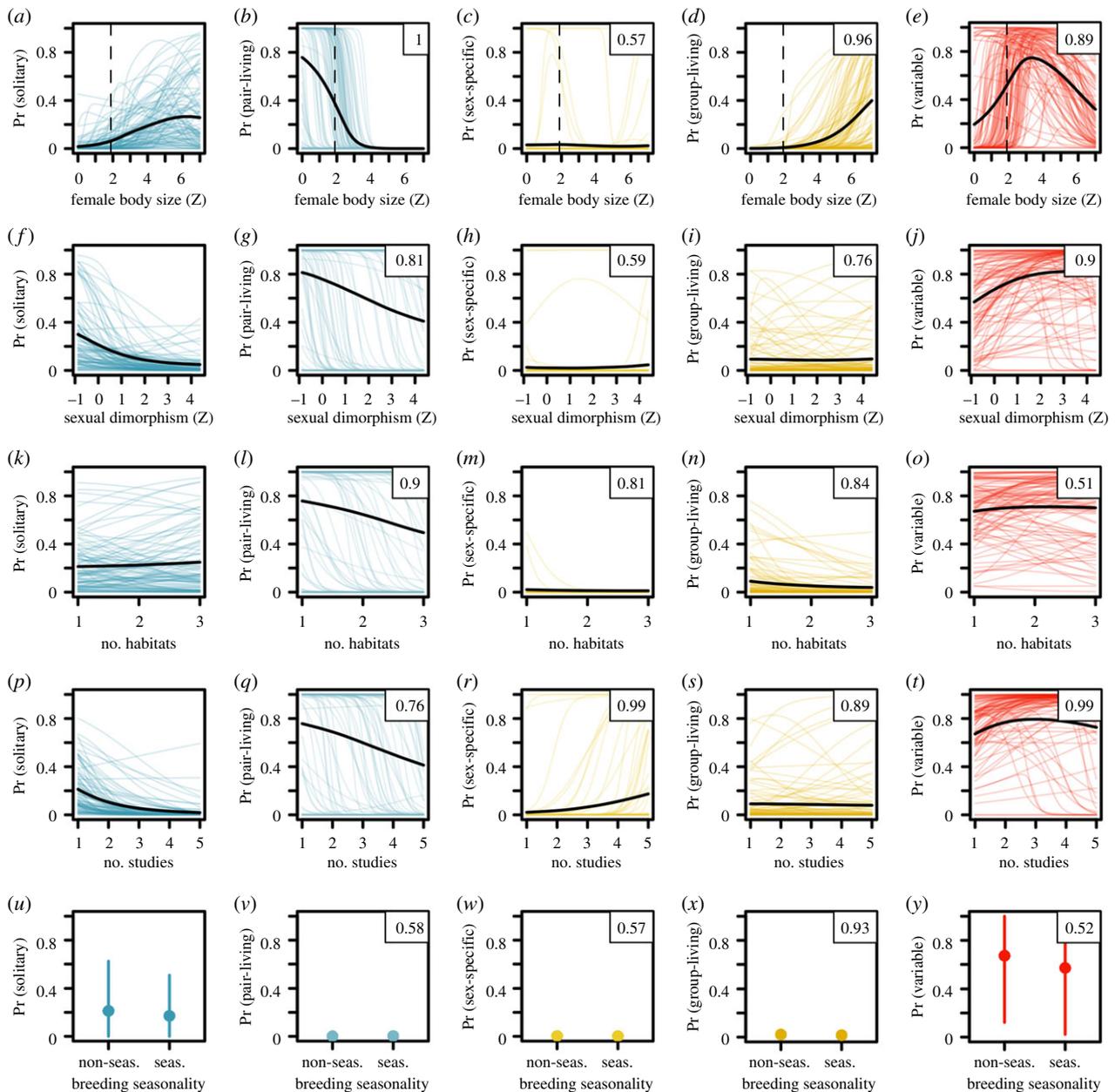


Figure 3. Illustrating evolutionary transitions in SO as a function of the predictors (from Model 1). Columns show (from left to right) the probability of solitary, pair-living, sex-specific, group-living and variable SO—using the same colours as in figure 2—while rows show (from top to bottom) predicted changes in those probabilities as a function of female body size (a–e), sexual dimorphism (f–j), number of habitats (k–o), number of studies (p–t) and breeding seasonality (u–y). The numbers in the legends are the posterior probabilities (PP), i.e. the proportion of the posterior distribution that supports a given association; these were not available for solitary, as this was the reference category. Within each row, all other predictors were held at their baseline value, except for body size; for pair-living, body size was kept at the ancestral state, for all others it was kept at the phylogenetic mean for better visibility. Solid black lines are the predicted means, thin coloured lines are 100 random samples drawn from the posterior to illustrate uncertainty. For breeding seasonality (u–y), points are predicted means and lines are 95% CIs. (Online version in colour.)

(61.6% of the studied populations). Model 1 confirmed that variable SO is the phylogenetic mean SO of extant Artiodactyl (i.e. the most typical SO when controlling for phylogeny and predictors; figure 2). This ubiquity of variable SO is consistent with previous descriptions of IVSO in other mammals including Carnivora (27% of species [9]), Eulipotyphla (43.8% of species [21]), and strepsirrhine primates (60.5% of species [18]). Contingent on body size estimates and sexual monomorphism from the fossil record, we found that the SO of the ancestral artiodactyl population was most likely to be pair-living and/or variable (figure 2; electronic supplementary material, figure S1). The evolution of larger body size, as characteristic of extant artiodactyls, and increased (male-

biased) sexual dimorphism were probably associated with transitions towards group-living and variable SO (figure 3) including combinations of solitary and group-living (electronic supplementary material, figures S1 and S2). **Given the relatively weak phylogenetic signal in our models, these inferences were mainly driven by the association of SO with socio-ecological predictors rather than by phylogenetic inertia; this highlights the adaptability of SO and allows good predictions for species with unknown phylogenetic status, such as new fossil discoveries.** However, our ancestral state estimation also highlights the high uncertainty surrounding predictions that extend beyond the range of data observed in extant species.

Table 1. Social organizations of artiodactyl populations.

category	no. and percentage of populations
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 organization (61.6%)	
variable group-living	61 (24.9%)
solitary and pair-living	15 (6.1%)
solitary and group-living	40 (16.3%)
pair-living and group-living	11 (4.5%)
solitary, pair-living and group-living	24 (9.8%)

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

Our study generated different results from previous studies [10,14], in part because we had an improved dataset, more information about the ancestral artiodactyl and modern phylogenetic methods at our disposal. We collated data at the level of populations rather than species, allowing us to describe and analyse SO at the level at which it is observed and reported in the primary literature. In general, previous studies in which species were categorized into a single SO inflated the prevalence of some SOs (e.g. solitary in 56% of species reported in [10]). Likewise, we did not rely on taxonomic inference (the same SO inferred for unobserved species of the same genus) to build our dataset; this explains, in part, why we had fewer species (100; electronic

supplementary material, tables S1 and S2; compared with 187 species in [10]). Our model also accounted for predictors associated with SO, most importantly body size. This allowed us to make our estimate of the ancestral SO contingent on the body size of the oldest artiodactyl known from the fossil record [38]. This value was smaller (737 g) than any observed in extant species (5100 g or more) and that used by Pérez-Barbería *et al.* [14,35] to classify species as sexually dimorphic or not. Should new fossil evidence become available, this information can easily be incorporated into the model predictions.

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

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

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

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

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