



The evolution of marsupial social organization

J. Qiu, C A Olivier, A. Jaeggi, C. Schradin

► To cite this version:

J. Qiu, C A Olivier, A. Jaeggi, C. Schradin. The evolution of marsupial social organization. Proceedings of the Royal Society B: Biological Sciences, 2022, 289 (1985), 10.1098/rspb.2022.1589 . hal-03880760

HAL Id: hal-03880760

<https://cnrs.hal.science/hal-03880760>

Submitted on 1 Dec 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

The Evolution of Marsupial Social Organization

Qiu, J.^{1,2}, Olivier, C.A.^{1,2}, Jaeggi, A.V.³ & Schradin, C.^{1,2}

Published as

Qiu, J., Olivier, C. A., Jaeggi, A. V. & Schradin, C. 2022. The evolution of marsupial social organization. *Proceedings of the Royal Society B: Biological Sciences*, 289, 20221589.

¹ School of Animal, Plant & Environmental Sciences, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, South Africa

² IPHC, UNISTRA, CNRS, 23 rue du Loess, 67200 Strasbourg, France

³ Institute of Evolutionary Medicine, University of Zurich, Wintherthurerstr. 190, 8057 Zurich, Switzerland

Abstract: It is generally believed that marsupials are more primitive mammals than placentals and mainly solitary living, representing the ancestral form of social organization of all mammals. However, field studies have observed pair and group-living in marsupial species, but no comparative study about their social evolution was ever done. Here we describe the results of primary literature research on marsupial social organization which indicate that most species can live in pairs or groups and many show intra-specific variation in social organization. Using Bayesian phylogenetic mixed-effects models with a moderate phylogenetic signal of 0.18 we found that solitary living is the most likely ancestral form (35% posterior probability), but has high uncertainty, and the combined probability of a partly sociable marsupial ancestor (65%) should not be overlooked. For Australian marsupials, group-living species were less likely to be found in climate representing tropical rainforest, and species with a variable social organization were associated with low and unpredictable precipitation representing deserts. Our results suggest that modern marsupials are more sociable than previously believed and that there is no strong support that their ancestral state was strictly solitary living, such that the assumption of a solitary ancestral state of all mammals may also need reconsideration.

Key words: Marsupial, social organization, ancestral state, social

Introduction

Social systems are believed to evolve from a simple state of solitary living to more complex forms, including pairs, and groups, some of which show communal or even cooperative breeding [1, 2]. The environment is seen as a major driver of social evolution [3]. In birds [4], mammals [5] and humans [6], cooperative breeding occurs more often in harsh environments with low rainfall and variable climate. However, so far no comparative study tested whether the association between environmental harshness and sociality is also found in taxa which do not contain cooperative breeders.

Animals' social systems are composed of four parts [7]: social organization (group size and composition), social structure (the interaction between individuals), mating system (who mates with whom) and the care system (who takes care of the offspring). These components are connected in complex ways [7]. Most information is available for social organization [8], which can influence social structure, mating and care system, and therefore the entire social system [7]. Social organization differs not only between species, but also within species. Intra-specific variation in social organization (IVSO) occurs when the composition of social units of a species can vary, for example between solitary, pairs and / or different forms of group living [8]. Several mammalian taxa have a more variable social organization than we used to believe [9, 10, 11]. Consideration of IVSO is important when studying social evolution because it more accurately describes the social organization than a simple categorisation [8].

Social organization is the product of individual social tactics that evolved to maximise inclusive fitness in natural habitats [12]. The habitat type may have an effect on individual social tactics, affecting the social organization of the population. For example, arid environments may favour sociality by limiting dispersal opportunities [13, 14, 15, 4], while moist and temperate habitats are often the home of solitary species [15]. Thus, the social organization might be habitat specific, and species occupying multiple habitats may show IVSO as a response to different types of habitats.

Habitats vary depending on the local climatic conditions. From tropical rainforests to arid deserts, climate plays an important role in controlling the environment and drives species evolution [16]. Seasonal changes in local climate might cause periodic changes in habitat quality, which may lead to seasonal variation in social organization. Many studies found a link between climate-related environmental harshness and sociality [5, 15, 17]. Arid environments with low and unpredictable rainfall are positively correlated with the care system, i.e. the occurrence of non-breeding helpers in birds [17] and mammals [5], but we know little about how environmental variations influences variation in social organization.

As a diverse clade of animals, mammals show high variability in social organization, possibly depending on habitat and climate, as studied in some placental taxa [15, 18]. Marsupials are the only extant members of Metatheria, which is one of the three extant clades of mammals, together with monotremes and eutherians (= placental mammals). Fossil records suggested the divergence between the ancestors of placentals and marsupials happened about 160 million years ago [19]. The care system of marsupials is normally exclusive maternal care with paternal care being very rare, and there are no reports of cooperative breeding [20]. This makes marsupials a good system to study the relationship between climate, environmental harshness and social organization independent from variation in the care system. Most marsupial species are believed to be solitary living, but other forms of social organization have also been observed [21]. For example, some kangaroo species like *Macropus parryi* and *Macropus giganteus* can form fission-fusion societies or permanent social groups of up to 50 individuals [22]. While many field studies on marsupials have been published in the last decades, no recent review about their social organization exists. Recently, using modern statistical approaches, marsupials were used as a model to study brain size [23] and life

history evolution [24] in mammals with a supposedly relatively simple social system. However, their social evolution is poorly understood, though there is indication that in large generalist grass feeders like kangaroos (macropods) occupying open-habitats are more social than cryptic, nocturnal, selectively browsing fruit and fungus feeders [25]. However, to our knowledge no phylogenetically comparative study about the evolution of marsupial social organization was ever done.

We established a marsupial social organization database based on primary literature reporting field data, taking the occurrence of intra-specific variation in social organization into account for the first time. Our first objective was to infer the ancestral form of marsupial social organization and whether species living in multiple habitats are likely to show a high percentage of IVSO. Our second objective was to test the prediction that sociality is favoured in harsh environments, predicting more social species living in environments with high ambient temperature and low rainfall (arid and semi-arid environments) and high variation in both. For Australian rodents, it was previously found that sociality evolved in response to harsh environment of low rainfall and high temperature variability [15]. Our study represents an independent test of this hypotheses, by focussing on other mammalian taxa living in the same environment, using the same climate data source. Therefore, while objective 1 considered all marsupials, for objective 2 we focused on Australian marsupials only.

Material and methods

Ancestral state of social organization of all marsupials

Our aim was to create a database based exclusively on published primary data, without consideration of interpretations or generalisations of the authors, and in doing so contribute to improving the quality of future comparative studies. We only considered primary literature that reported actual field data on social organization in their methods or results section. This was important for the main aim of our study which is to consider IVSO and not only the most common form of social organization believed to occur in one species. Reviews making generalisations were not considered.

We searched for publications about social organization of marsupials on Web of Science and Google Scholar from June 2020 until April 2021. Our search included all 345 marsupial species categorized by the IUCN (International Union for Conservation of Nature) database in 2021 (<https://www.iucnredlist.org/>). Each species was searched by its scientific name (genus and species) and the keyword “social” (e.g., *Acrobates pygmaeus* AND social). If no results were found, a second search was conducted using only the scientific name (genus and species). For each study, title and abstract were read to determine whether the study was based on a wild population and if it might contain data about social organization. By reading the article titles from the search results we marked 697 articles, and downloaded 456 of them after reading the abstract. For 105 articles (mainly old articles from local journals) we were not able to obtain a PDF or copy; thus, we could not check them for suitability nor add them

to our database (DRYAD ref)

To address our main interest of identifying primary data on IVSO (deviation from the main form of social organization), methods, results, figures and tables of all 456 articles were checked. Further, the full text was searched for the following keywords: "social", "solitary", "pair", "group". 253 articles did not contain useable data on social organization. Based on our criteria, 83 articles could not be included in the analyses (DRYAD ref), as the authors only stated the main form of social organization, but did not present the data on the composition of social units, the sex of individuals, occupancy of sleeping sites, home range overlap or the proportion of the individuals marked and studied in the study area [26]. In other words, these studies were excluded because either IVSO was ignored as a possibility, or if the existence of IVSO was reported, it was impossible to determine the degree of it. Supplementary materials 8 presents an alternative analysis focussing only on the main form of social organization ignoring IVSO, including these studies excluded from our main analysis. As would be predicted, this model overemphasizes the probability of solitary living being ancestral.

We found data on social organization that matched our criteria for inclusion in 120 of all articles. The data in these articles were recorded at the population level (N=149 populations, DRYAD ref) and covered 65 species. The phylogenetic distribution of those species (Supplementary materials S10) shows that while there is very limited knowledge for the Ameridelphia, the available data for the Australidelphia are relatively evenly distributed among families. We also compared our database with two previously published databases (Supplementary materials S4).

We were able to classify the social organization of each social unit reported in the 120 articles as one of six possible forms: (1) solitary, (2) pair-living, and four forms of group-living: (3) single male multiple female group, (4) single female multiple male group, (5) sex-specific group (group of only males or only females), and (6) multi-male multi-female group. For analyses we used the category "stable group" if all social units showed the same category of group-living, while if more than one category occurred, this was categorised as IVSO (see details below). Social organisation was only based on the number of adults present and we did not consider pups and juveniles (Joeys). Solitary individuals were recorded separately by sex; a social unit was recorded as solitary only when both sexes were solitary. Many species show sex specific dispersal. Thus, when solitary living was only reported for individuals of one sex, this was not considered as evidence for a solitary social organization, since the data might represent dispersing individuals. As most species have dispersing individuals that for a short time are solitary, including this transitional phase as a separate social organisation would basically mean that all species show IVSO, in which case it would not make sense to study why and when it occurs. Instead, apart from studies on IVSO, separate studies on the proximate causes and ultimate function of dispersal are needed. To facilitate comparison to pairs (one male and one female), the number of solitary social units was determined by the sex with the smaller number of solitary individuals (e.g., when 10 solitary males and five solitary females were observed, we recorded five solitary social units). The same method was applied for sex-specific groups.

Intra-specific variation in social organization (IVSO) was recorded when more than one form of social organization was observed in the same population. Populations where 2 or more forms of group-living but no other forms of social organisation occurred were categorised as “variable group”. Otherwise, to reduce the numbers of IVSO categories for the statistical analysis, we combined the four forms of group living as “group” when the population had both group-living and non-group-living social units. Therefore, IVSO consisted of five categories: (1) solitary + pair (SP), (2) solitary + group (SG), (3) pair + group (PG), (4) solitary + pair + group (SPG), (5) variable group (VG). Together with the 3 non-IVSO categories: solitary (S), pair (P) and stable group (G, only one forms of group-living reported), we have theoretically 8 combinations of social organization, but as SG did not occur in any population, this was effectively reduced to 7. If males and females live separately in two different forms of social organization (for example, group-living females and solitary males), this population was classified as having a sex-specific social organization and not IVSO, since there was no variation within either sex. Fission-fusion groups characterized by temporal variation in group size and composition [27] are common in some kangaroo species [28]. All observed variation in social organization in a fission-fusion population was recorded. Environmental disruption events, such as the accidental death of a group member, represent external incidents that can change the social organization of the social unit. Three cases of social organization change due to environmental disruptor were not considered for further analysis (DRYAD ref) because they do not represent a change in social organization in response to ancestrally relevant conditions.

To better estimate the ancestral state and the possible ecological factors that may have an influence on the evolution of social organization, we obtained body mass from the Handbook Mammals of the World [29] and centred it to the body mass of Australia’s oldest known marsupial fossil [30]. By comparing the M2 mesiodistal length, we estimated the body mass of the 30 million years old ancestral species *Djarthia murgonensis* would be similar to *Antechinus stuartii* as 37.75g, which is smaller than most of the modern species in our database and much smaller than the mean (4871g). The number of studies per population was recorded to control for research effort. We determined the habitat type(s) in which the study took place, categorized and recorded based on IUCN classification (www.iucn.org) as desert, forest, rocky areas, savannah, grassland, shrubland, wetlands or artificial. Habitat heterogeneity was then determined as the maximum number of habitats occupied per population.

Ancestral state of social organization and climate in Australian marsupials

To test how climate would affect their social organization, we focused on Australian marsupial species to control for other environmental variable that differ between Australia and South America, such as competition with placentals that mainly occurs in South America but not Australia (apart from small rodents and bats). We obtained long-term climate data from the online dataset of Australian Bureau of Meteorology (<http://www.bom.gov.au/climate>). For each studied population, we obtained local climate data at the GPS coordinates reported in the articles. Climate data were obtained for 51 Australian marsupial species.

High-resolution (0.05x0.05 degree) grids downloaded from climate dataset were converted to raster grids in QGIS 3.10. Based on the monthly precipitation and monthly mean maximum temperature data from 1910 to 2019, we calculated six variables to represent climate conditions: annual mean precipitation (mm), annual mean maximum temperature (°C) and coefficient of variation to represent within-year variation (seasonality) and between-year variation (predictability) for both precipitation and temperature (for details see Supplementary materials S1). Six maps were generated in QGIS, one for each climate variable. For populations with precise GPS locations, data were directly obtained from the climate maps. When the location was not specified in the paper (one population of *Distoechurus pennatus* in the state of Victoria), we ran “zonal statistics” analysis to obtain mean value of the area.

Statistical analysis

Phylogenetic comparative analyses were conducted by R v.3.6.1, using the R packages brms [31, 32], RStan [33] and Rethinking. All R codes and data are available at <https://github.com/JingyuQ/MarsupialSO>.

Climate data are often correlated with each other. Thus, we first performed a principal component analysis (PCA) to reduce the six climate variables (see above) to a smaller number of components. The first two principal components (PC1 and PC2) explained 82% of the variation (Supplementary materials S2, Table S2). PC 1 was positively related with annual temperature (eigenvector=0.506) and within-year variation of precipitation (eigenvector=0.449), and negatively related with within-year variation of temperature (eigenvector=-0.497) and between-year variation of temperature (eigenvector=-0.494; Table S2). High PC1 values match with the climate of tropical rainforest in Australia. PC2 was positively related with annual precipitation (eigenvector=0.693) and negatively with between-year variation of precipitation (eigenvector=-0.639; Table S2). Low PC2 values match with the climate of the desert in central Australia.

We used Bayesian generalized linear mixed-effects models (GLMMs) to control for phylogeny and estimate the associations between social organization and predictor variables [34]. The probability of each kind of social organization was modelled using a categorical likelihood, allowing gradual changes in the probability of each kind of social organization along the phylogeny; the intercept of such a model represents the phylogenetically-controlled mean of extant species, and, in the absence of any directional trends, the ancestral state [34, 35]. This approach corresponds to a multi-factorial model of trait inheritance, as opposed to alternative approaches to inferring ancestral states of categorical traits based on nucleotide substitution models [36, 37]; in substitution models evolutionary change is not gradual but occurs in “jumps” between states, which has been deemed less plausible than polygenic inheritance [34, 38] (and in our opinion rightfully so). Furthermore, these models often have many more free parameters, require treating the species rather than the population as the unit of observation (thus failing to account for intra-specific variation), and cannot include covariates when inferring ancestral states. We therefore prefer the quantitative genetic approach implemented by our GLMMs.

The phylogenetic history and its uncertainty were represented by a sample of 100 phylogenetic trees, downloaded from VertLife (<http://vertlife.org/phylosubsets/>). We created two models, the first one was to estimate the ancestral state of modern marsupials, therefore included data from all studied marsupial species: social organisation (with 7 categories) ~ species intercept + covariance for phylogeny + habitat heterogeneity + number of studies + body mass. The second model was aimed to estimate the ecological factors (climate and habitat) effects on Australian marsupial's social organization pattern: social organization ~ species intercept + covariance for phylogeny + habitat heterogeneity + number of studies + body mass + principle component 1 climate+ principle component 2 climate. Due to the limitation of climate data, this model only considered Australian marsupials. Both models were run at the population level, and included phylogeny and species as random factors. The number of studies per population was considered as a predictor of the occurrence of IVSO. Phylogenetic signal (λ) was calculated as the proportion of variance captured by the phylogenetic random effect [39], representing the tendency of related species to resemble each other more than species drawn at random from the same tree [40]. For analysis, the social organization of populations showing only one form of group living was categorised as stable group. For more details on model structure, see the PDF "Model details" on <https://github.com/JingyuQ/MarsupialSO>.

Results

Ancestral state of social organization of all marsupials

Out of the 65 marsupial species with data, three species were excluded from this model for lack of life history and / or habitat heterogeneity information. Only one population of *Macropus giganteus* (the species with most data available) shows IVSO of solitary + group and it was excluded from the analysis for lack of habitat information. In the remaining 62 species, 30.6% (19 species) were strictly solitary, 14.5% (9 species) only live in pairs, and 11.3% (7 species) were stable group-living (e.g., always MMFF; DRYAD ref), 43.5% (27 species) showed IVSO, with 23 species showing two or more forms of solitary/pair-living/group-living, 4 species with two or more different forms of group-living (Supplementary materials S3) DRYAD ref.

Social organization was moderately influenced by phylogenetic history ($\lambda = 0.18$, 95% CI = 0.06 – 0.31). The most probable ancestral state was solitary living (mean=0.35, 95% CI = 0 – 0.88) and IVSO (SP+PG+SPG+VG; mean = 0.35), with the IVSO form of pair-living+group-living (PG) having the second highest probability (mean=0.26, 95% CI = 0 – 0.97). The following were pair-living (mean = 0.22, 95% CI = 0 – 0.90) and group-living (mean=0.09, 95% CI = 0 – 0.53) (Figure 1, Table S5.1). There was no significant effect of habitat heterogeneity nor number of studies per populations on social organization (Table S5.2). In addition, when the analysis was done at the species level with only the main form of social organization and no IVSO, the probability of solitary ancestor increased (mean = 0.61, 95% CI 0 – 1.00) (Supplementary materials S7).

For the 51 Australian marsupials, the phylogenetic signal was 0.20 (95% CI = 0.07 – 0.34). The most probable ancestral state was the IVSO form of pair-living+group-living (PG) but with high uncertainty (mean=0.26, 95% CI = 0 – 0.97), followed by group-living (mean = 0.21, 95% CI = 0 – 0.95), solitary living (mean = 0.20, 95% CI = 0 – 0.79) and pair-living (mean = 0.18, 95% CI = 0 – 0.96) (Figure 2, Table S6.1). All forms of IVSO combined (SP+PG+SPG+VG) had a mean probability of 0.41.

There was no significant effect of habitat heterogeneity nor number of studies per populations on social organization (Table S6.2). Climate had a significant effect on social organization (Table S6.2). PC1 showed a negative relation with the occurrence of stable group-living (mean = -0.64, 95% CI = -1.38 – 0), which indicates that species living in groups with stable composition are less common in Australian tropical rainforest. PC2 had a negative relation with the occurrence of a IVSO characterised by a combination of solitary, pair and group-living (mean = -1.42, 95% CI = -2.51 – -0.31), indicating such populations are more common in desert area in Australia.

Discussion

Our literature review shows that marsupials are more social than previously believed. Only 31% of the 65 studied species were strictly solitary, with the remaining species living either sometimes (22%) or always (48%) in pairs or groups. Still, solitary living was the most likely ancestral state, but with high uncertainty. However, for Australian marsupials alone, solitary living was not the most likely ancestral state, and it is possible that solitary living in the South American marsupials is not an ancestral trait but an adaptation to living under competition with placentals. This means, for phylogenetic comparative studies on mammalian social evolution, one cannot assume with certainty that so far unstudied marsupials are solitary, nor that the common ancestor of modern marsupials was solitary. The result also shows the marsupial may have the ability of living in different forms of social organization, especially the mixture of pair and group-living. Like previously reported for Australian rodents [15], we found an effect of climate on sociality, indicating fewer group-living species in tropical rainforests and that species occupying harsh and unpredictable habitat like deserts are more likely to show a flexible form of social organization. Thus, our study indicates that marsupial social organization is not at primitive solitary default stage but represents complex and variable adaptations to climate.

While Russell regarded marsupials as being pre-dominantly solitary living, he also pointed out that the variability in social organization within species has been overlooked and that field data for most species were lacking [21]. With more observations on marsupial social organization having been published in recent decades, we found that most studied species can form social units of two or more individuals. Important to note is that nearly every other species showed variation in social organization, which often included solitary living. Our

study indicates that previous assumptions about marsupial social organization have been outdated by the addition of more field studies. This new understanding must be considered when conducting comparative studies on mammalian social organization.

To our knowledge, we did the first statistical model to estimate the ancestral social organization of marsupials, which so far were assumed to have evolved from a solitary ancestor [21]. While solitary living had the highest probability, this was associated with a very wide confidence interval, and only a minority of species (31%) was strictly solitary living. In other words, the ancestral state cannot be accurately estimated with the current information we have and leaves the possibility that the ancestor was more sociable than previously believed. This is also supported by fossils found in Bolivia indicating a gregarious lifestyle for marsupials 60 million years ago [41]. In sum, our study does not support nor reject the assumption that the ancestor of all marsupials was solitary living; a more sociable ancestral state was virtually just as likely.

Ecological factors can shape sociality in macropods: large, diurnal generalist grass feeding species living in open-habitat are more social than cryptic, nocturnal, selectively browsing fruit and fungus feeders [25]. In our study we did not find support for the prediction that habitat heterogeneity is associated with social organization. Like in artiodactyls [10], more habitats occupied per species/population didn't increase the occurrence of IVSO, suggesting that IVSO did not evolve as an adaptation to habitat heterogeneity in the two taxa. The number of papers published per species/population also had no effect, i.e. IVSO was not more commonly reported for better studied populations. However, climate had a significant effect. Harsh environments characterised by low rainfall, high ambient temperature, and high variation in these climate factors, favour sociality in a variety of taxa [5, 15, 17]. Australia is a continent of environmental extremes and contrasts, with significant variation of precipitation and temperatures. We found group-living to be less common under the climate condition of tropical rainforest, which are home to many solitary species [42, 43]. For Australian rodents, it was previously reported that sociality evolved in harsh environments [15]. Our independent study in the same environments with other mammalian taxa partly supports this result. We did not find a direct relationship between group-living and harshness, but a negative relationship between group-living and benign environments. Our criteria for determining social organization was more restricted and clearer than the definition of "sociality" by Firman, which for example excluded territorial species from social species [15]. In sum, our study which strictly focussed on the composition of social units as a measure of social organization adds to previous studies showing that climate is related to sociality.

Instead of only considering the main social organization at the species level, we took variation within and between populations into account. We found IVSO to be more common in climates with low and highly unpredictable precipitation (variation between-years), which in Australia is characteristic of central deserts. Here, populations that have (and thus probably can switch between) multiple forms of social organization among solitary, pair and group-living were more common than in other climate situations. IVSO might offer a buffer against environmental unpredictability, many kangaroos are a prime example for this, as depending on food availability, a function of previous rainfall and bush fires, they can forage solitarily, in

small or large groups [44]. While for Australian rodents [15], mammals in general [5] and birds [8], it was found that sociality evolved under harsh climatic conditions, our study indicates that having a flexible social organization might also be an adaptation to harshness.

Evolutionary change needs variation in traits. This is why intra-specific variation is important for understanding social evolution. Unfortunately, many papers we found failed to present their field data in a way that they could be included into our database [45]. Often no data but only a general statement about the assumed main form of social organization was reported, especially in mainly solitary species such as the Tasmanian devil or the koala. Ignoring such studies might lead to an underestimation of solitary living, but including such studies might lead to an underestimation of IVSO. For example, koalas are generally believed to be solitary living, but possible deviation (pairs) has been reported, unfortunately in a way that it could not be incorporated in our database, as it was not clear how many pairs were observed and whether these were stable or not [46]. An alternative analysis, which was including studies only reporting the main form of social organization found, as one would predict, have stronger support for solitary living as the ancestral state (Supplementary materials S8) than our model considering IVSO. We believe that comparative analyses which are based on real data are more meaningful than ones based on assumptions. Similarly, overgeneralisations, like assuming that most species of a taxon are solitary living, can lead to conclusions that are in contrast to the existing data [11] which might then bias comparative studies [47]. In sum, we are not at the end of empirical science, but we need more field studies [47] that report data in a way they can be used in meta-analysis including comparative analyses [45].

Conclusions

Our study estimated the ancestral social organization of marsupials using Bayesian phylogenetic mixed-effect models based on a new and accurate database accounting for variation within and between populations. Our analysis demonstrates that the previous assumption of a solitary marsupial ancestor has low confidence, and many modern species are found to be more sociable than was believed. In summary, the ancestral form of social organization of marsupials and as such of all mammals demands further investigation, for which more field data from more species are needed. While previous studies found arid environments with low and unpredictable rainfall to be positively correlated with the care system in birds [17] and mammals [5], our study suggests that when studying the influence of variable and unpredictable climate on sociality, one should also consider variation in sociality.

Data accessibility

R code and dataset available at XXX

Funding

This work was supported by the XXX [grant numbers xxx, yyyy]; ...

Acknowledgments

We thank Anna Kurkierewicz for helping in collecting data for American marsupials.
Important comments by N. Pillay, E. Fernandez-Duque and L. Makuya improved the methods
section.

References

1. Chak STC, Duffy JE, Hultgren KM, Rubenstein DR. 2017 Evolutionary transitions towards eusociality in snapping shrimps. *Nat Ecol Evol* 1, 1–7. (doi:10.1038/s41559-017-0096)
2. Rubenstein DR, Abbot P. 2017 Comparative Social Evolution. Cambridge University Press.
3. Shen S-F, Emlen ST, Koenig WD, Rubenstein DR. 2017 The ecology of cooperative breeding behaviour. *Ecology Letters* 20, 708–720. (doi:10.1111/ele.12774)
4. Jetz W, Rubenstein DR. 2011 Environmental Uncertainty and the Global Biogeography of Cooperative Breeding in Birds. *Current Biology* 21, 72–78. (doi:10.1016/j.cub.2010.11.075)
5. Lukas D, Clutton-Brock T. 2017. Climate and the distribution of cooperative breeding in mammals. *Royal Society Open Science* 4, 160897. (doi:10.1098/rsos.160897)
6. Martin JS, Ringen EJ, Duda P, Jaeggi AV. 2020 Harsh environments promote alloparental care across human societies. *Proc. R. Soc. B.* 287, 20200758. (doi:10.1098/rspb.2020.0758)
7. Kappeler PM. 2019 A framework for studying social complexity. *Behav Ecol Sociobiol* 73, 13. (doi:10.1007/s00265-018-2601-8)
8. Schradin C, Hayes LD, Pillay N, Bertelsmeier C. 2018 The evolution of intraspecific variation in social organization. *Ethology* 124, 527–536. (doi:10.1111/eth.12752)
9. Agnani P, Kauffmann C, Hayes LD, Schradin C. 2018 Intra-specific variation in social organization of Strepsirrhines. *Am J Primatol* 80, e22758. (doi:10.1002/ajp.22758)
10. Jaeggi AV, Miles MI, Festa-Bianchet M, Schradin C, Hayes LD. 2020 Variable social organization is ubiquitous in Artiodactyla and probably evolved from pair-living ancestors. *Proceedings of the Royal Society B: Biological Sciences* 287, 20200035. (doi:10.1098/rspb.2020.0035)
11. Valomy M, Hayes LD, Schradin C. 2015 Social organization in Eulipotyphla: evidence for a social shrew. *Biology Letters* 11, 20150825. (doi:10.1098/rsbl.2015.0825)
12. Southwood TRE. 1977 Habitat, the Templet for Ecological Strategies? *Journal of Animal Ecology* 46, 337–365. (doi:10.2307/3817)
13. Brashares JS, Arcese P. 2002 Role of Forage, Habitat and Predation in the Behavioural Plasticity of a Small African Antelope. *Journal of Animal Ecology* 71, 626–638.

14. Ebensperger LA, Rivera DS, Hayes LD. 2012 Direct fitness of group living mammals varies with breeding strategy, climate and fitness estimates. *Journal of Animal Ecology* 81, 1013–1023.
15. Firman RC, Rubenstein DR, Moran JM, Rowe KC, Buzatto BA. 2020 Extreme and Variable Climatic Conditions Drive the Evolution of Sociality in Australian Rodents. *Current Biology* 30, 691–697.e3. (doi:10.1016/j.cub.2019.12.012)
16. Lusseau D, Williams R, Wilson B, Grellier K, Barton TR, Hammond PS, Thompson PM. 2004 Parallel influence of climate on the behaviour of Pacific killer whales and Atlantic bottlenose dolphins. *Ecology Letters* 7, 1068–1076. (doi:10.1111/j.1461-0248.2004.00669.x)
17. Cornwallis CK, Botero CA, Rubenstein DR, Downing PA, West SA, Griffin AS. 2017 Cooperation facilitates the colonization of harsh environments. *Nat Ecol Evol* 1, 0057. (doi:10.1038/s41559-016-0057)
18. Rymer TL, Pillay N, Schradin C. 2013 Extinction or Survival? Behavioral Flexibility in Response to Environmental Change in the African Striped Mouse *Rhabdomys*. *Sustainability* 5, 163–186. (doi:10.3390/su5010163)
19. Luo Z-X, Yuan C-X, Meng Q-J, Ji Q. 2011 A Jurassic eutherian mammal and divergence of marsupials and placentals. *Nature* 476, 442–445. (doi:10.1038/nature10291)
20. Lukas D, Clutton-Brock TH. 2013 The Evolution of Social Monogamy in Mammals. *Science* 341, 526–530. (doi:10.1126/science.1238677)
21. Russell EM. 1984 Social behaviour and social organization of marsupials. *Mammal Review* 14, 101–154. (doi:10.1111/j.1365-2907.1984.tb00343.x)
22. Kaufmann JH. 1974 The Ecology and Evolution of Social Organization in the Kangaroo Family (Macropodidae). *American Zoologist* 14, 51–62. (doi:10.1093/icb/14.1.51)
23. Todorov OS, Blomberg SP, Goswami A, Sears K, Drhlík P, Peters J, Weisbecker V. 2021 Testing hypotheses of marsupial brain size variation using phylogenetic multiple imputations and a Bayesian comparative framework. *Proceedings of the Royal Society B: Biological Sciences* 288, 20210394. (doi:10.1098/rspb.2021.0394)
24. Fisher DO, Owens IPF, Johnson CN. 2001 The Ecological Basis of Life History Variation in Marsupials. *Ecology* 82, 3531–3540. (doi:10.1890/0012-9658(2001)082[3531:TEBOLH]2.0.CO;2)
25. Croft, D. (Marsupial Behavior. 1998. In: *Comparative Psychology: A Handbook* (editors Greenberg, G. & Haraway, M. M.) Garland reference library of social science vol 894.
26. Makuya L, Olivier C-A, Schradin C. In press. Field studies need to report essential information on social organization – independent of the study focus. *Ethology* n/a. (doi:10.1111/eth.13249)
27. Aureli F et al. 2008 Fission- Fusion Dynamics: New Research Frameworks. *Current Anthropology* 49, 627–654. (doi:10.1086/586708)

28. Best EC, Seddon JM, Dwyer RG, Goldizen AW. 2013 Social preference influences female community structure in a population of wild eastern grey kangaroos. *Animal Behaviour* 86, 1031–1040. (doi:10.1016/j.anbehav.2013.09.008)
29. Wilson, D,E, & Mittermeier, R,A. 2015 Handbook of the Mammals of the World Volume 5: Monotremes and Marsupials. Lynx Edicions, Barcelona.
30. Beck RMD, Godthelp H, Weisbecker V, Archer M, Hand SJ. 2008 Australia's Oldest Marsupial Fossils and their Biogeographical Implications. *PLoS ONE* 3, e1858. (doi:10.1371/journal.pone.0001858)
31. Bürkner P. C. 2017 brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software* 80, 1–28. (doi:10.18637/jss.v080.i01)
32. Bürkner P. C. 2018. Advanced Bayesian Multilevel Modeling with the R Package brms. *The R Journal* 10(1), 395–411. (doi.org/10.32614/RJ-2018-017)
33. Stan Development Team. 2020 RStan: the R interface to Stan. R package version 2.21.2. (<http://mc-stan.org/>)
34. Hadfield JD, Nakagawa S. 2010 General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology* 23, 494–508. (doi:10.1111/j.1420-9101.2009.01915.x)
35. Lynch M. 1991 Methods for the Analysis of Comparative Data in Evolutionary Biology. *Evolution* 45, 1065–1080. (doi:10.1111/j.1558-5646.1991.tb04375.x)
36. Pagel M. 1994 Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 255, 37–45. (doi:10.1098/rspb.1994.0006)
37. Pagel M, Meade A. 2006 Bayesian Analysis of Correlated Evolution of Discrete Characters by Reversible- Jump Markov Chain Monte Carlo. *The American Naturalist* 167, 808–825. (doi:10.1086/503444)
38. Felsenstein J. 2005 Using the quantitative genetic threshold model for inferences between and within species. *Philosophical Transactions of the Royal Society B: Biological Sciences* 360, 1427–1434. (doi:10.1098/rstb.2005.1669)
39. Nakagawa S, Schielzeth H. 2012 The mean strikes back: mean–variance relationships and heteroscedasticity. *Trends in Ecology and Evolution*
40. Münkemüller T, Lavergne S, Bzeznik B, Dray S, Jombart T, Schiffers K, Thuiller W. 2012 How to measure and test phylogenetic signal. *Methods in Ecology and Evolution* 3, 743–756. (doi:10.1111/j.2041-210X.2012.00196.x)
41. Ladevèze S, de Muizon C, Beck RMD, Germain D, Céspedes-Paz R. 2011 Earliest evidence of mammalian social behaviour in the basal Tertiary of Bolivia. *Nature* 474, 83–86. (doi:10.1038/nature09987)
42. Fisher DO, Lara MC. 1999 Effects of body size and home range on access to mates and

paternity in male bridled nailtail wallabies. *Animal Behaviour* 58, 121–130.
(doi:10.1006/anbe.1999.1119)

43. Newell GR. 1999 Home range and habitat use by Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*) within a rainforest fragment in north Queensland. *Wildl. Res.* 26, 129–145. (doi:10.1071/wr98016)

44. Pays O, Goulard M, Blomberg SP, Goldizen AW, Sirot E, Jarman PJ. 2009 The effect of social facilitation on vigilance in the eastern gray kangaroo, *Macropus giganteus*. *Behavioral Ecology* 20, 469–477. (doi:10.1093/beheco/arp019)

45. Makuya L, Olivier C, Schradin C. 2022 Field studies need to report essential information on social organization—independent of the study focus. *Ethology* 128, 268–274.

46. Ellis WAH, Melzer A, Carrick FN, Hasegawa M. 2002 Tree use, diet and home range of the koala (*Phascolarctos cinereus*) at Blair Athol, central Queensland. *Wildl. Res.* 29, 303. (doi:10.1071/WR00111)

47. Schradin C. 2017 Comparative studies need to rely both on sound natural history data and on excellent statistical analysis. *Royal Society Open Science* 4, 170346.

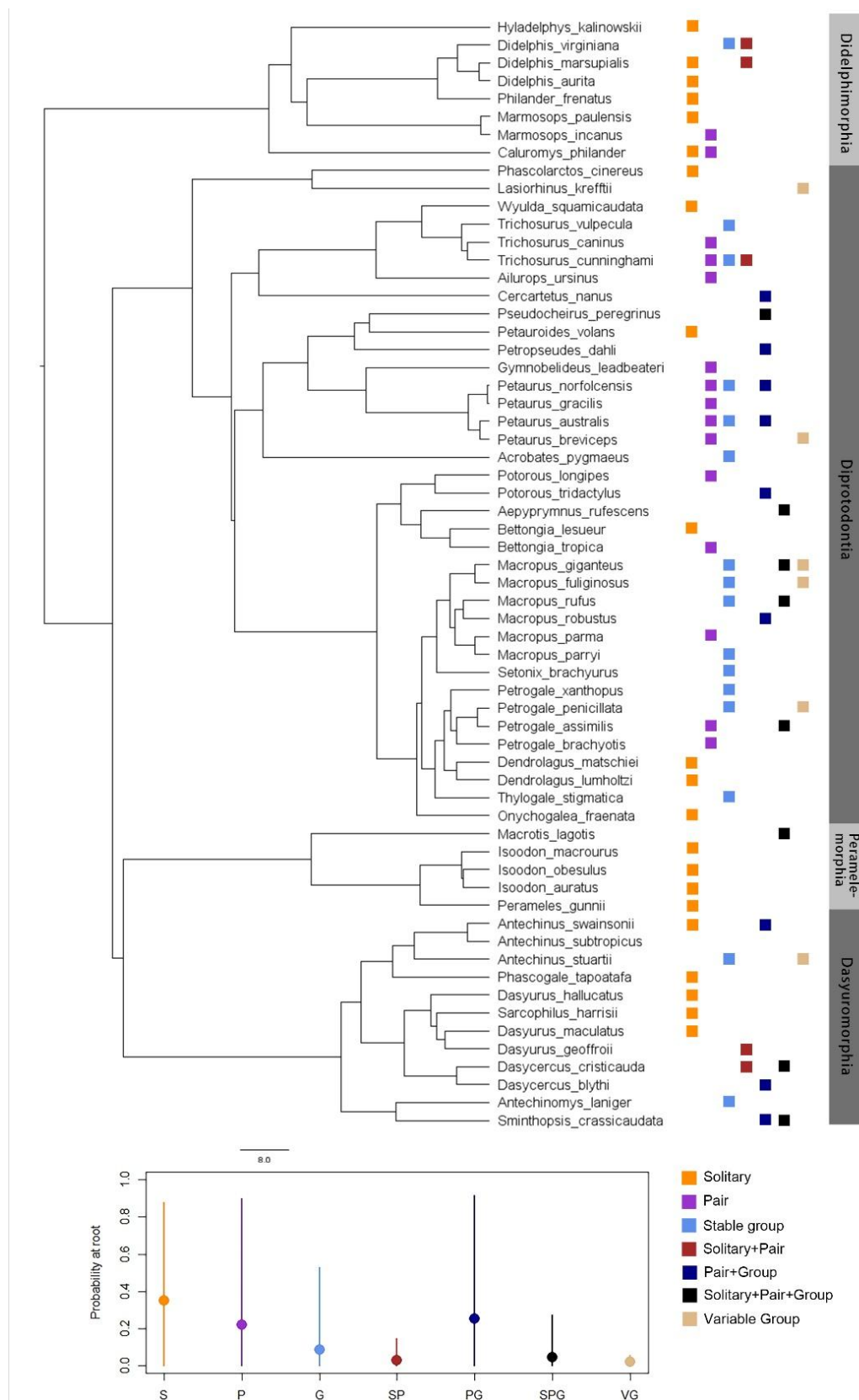
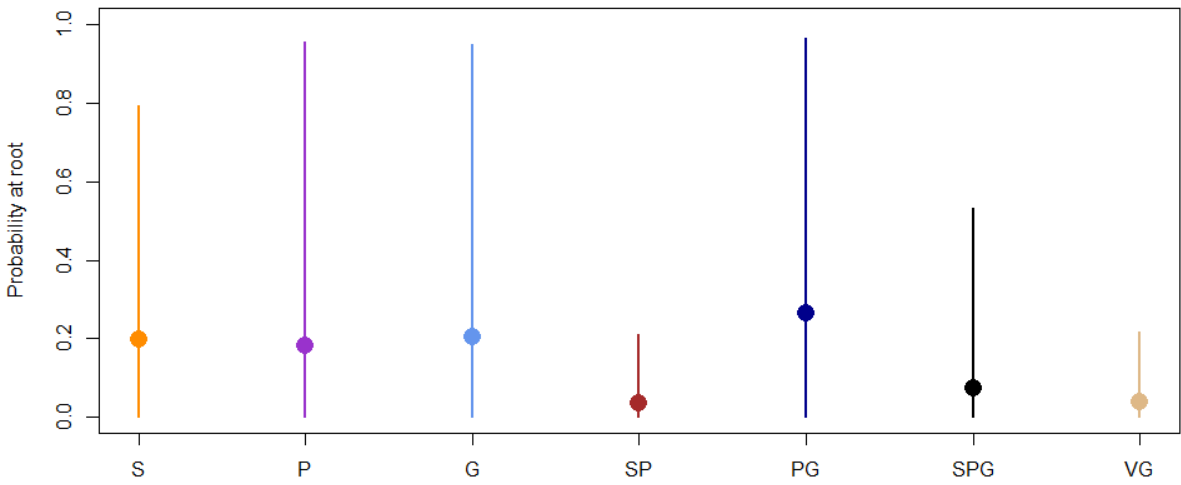


Figure 1: Phylogeny of 62 marsupial species with available data and the probability of each kind of social organization at the root of the phylogeny, i.e. the last common ancestor of all marsupials. The different forms of social organization recorded for each species at the population level are shown on the right, using the colour indicated in the legend.

536



537

538

539

540

541

542

Figure 2: The probability of different kinds of social organization for the last common ancestor of Australian marsupials. S: solitary, P: pair, G: stable group, SP: solitary + pair, PG: pair + group, VG: variable group.