



HAL
open science

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.

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

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

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

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

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

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

101

102 **Material and methods**

103 *Ancestral state of social organization of all marsupials*

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

111 We searched for publications about social organization of marsupials on Web of Science and
112 Google Scholar from June 2020 until April 2021. Our search included all 345 marsupial
113 species categorized by the IUCN (International Union for Conservation of Nature) database in
114 2021 (<https://www.iucnredlist.org/>). Each species was searched by its scientific name (genus
115 and species) and the keyword “social” (e.g., *Acrobates pygmaeus* AND social). If no results
116 were found, a second search was conducted using only the scientific name (genus and
117 species). For each study, title and abstract were read to determine whether the study was based
118 on a wild population and if it might contain data about social organization. By reading the
119 article titles from the search results we marked 697 articles, and downloaded 456 of them
120 after reading the abstract. For 105 articles (mainly old articles from local journals) we were
121 not able to obtain a PDF or copy; thus, we could not check them for suitability nor add them

122 to our database (DRYAD ref)

123 To address our main interest of identifying primary data on IVSO (deviation from the main
124 form of social organization), methods, results, figures and tables of all 456 articles were
125 checked. Further, the full text was searched for the following keywords: "social", "solitary",
126 "pair", "group". 253 articles did not contain useable data on social organization. Based on our
127 criteria, 83 articles could not be included in the analyses (DRYAD ref), as the authors only
128 stated the main form of social organization, but did not present the data on the composition of
129 social units, the sex of individuals, occupancy of sleeping sites, home range overlap or the
130 proportion of the individuals marked and studied in the study area [26]. In other words, these
131 studies were excluded because either IVSO was ignored as a possibility, or if the existence of
132 IVSO was reported, it was impossible to determine the degree of it. Supplementary materials
133 8 presents an alternative analysis focussing only on the main form of social organization
134 ignoring IVSO, including these studies excluded from our main analysis. As would be
135 predicted, this model overemphasizes the probability of solitary living being ancestral.

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

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

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

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

196 *Ancestral state of social organization and climate in Australian marsupials*

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

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

214 *Statistical analysis*

215 Phylogenetic comparative analyses were conducted by R v.3.6.1, using the R packages brms
216 [31, 32], RStan [33] and Rethinking. All R codes and data are available at
217 <https://github.com/JingyuQ/MarsupialSO>.

218 Climate data are often correlated with each other. Thus, we first performed a principal
219 component analysis (PCA) to reduce the six climate variables (see above) to a smaller number
220 of components. The first two principal components (PC1 and PC2) explained 82% of the
221 variation (Supplementary materials S2, Table S2). PC 1 was positively related with annual
222 temperature (eigenvector=0.506) and within-year variation of precipitation (eigenvector
223 =0.449), and negatively related with within-year variation of temperature (eigenvector=-0.497)
224 and between-year variation of temperature (eigenvector=-0.494; Table S2). High PC1 values
225 match with the climate of tropical rainforest in Australia. PC2 was positively related with
226 annual precipitation (eigenvector=0.693) and negatively with between-year variation of
227 precipitation (eigenvector=-0.639; Table S2). Low PC2 values match with the climate of the
228 desert in central Australia.

229 We used Bayesian generalized linear mixed-effects models (GLMMs) to control for
230 phylogeny and estimate the associations between social organization and predictor variables
231 [34]. The probability of each kind of social organization was modelled using a categorical
232 likelihood, allowing gradual changes in the probability of each kind of social organization
233 along the phylogeny; the intercept of such a model represents the phylogenetically-controlled
234 mean of extant species, and, in the absence of any directional trends, the ancestral state [34,
235 35]. This approach corresponds to a multi-factorial model of trait inheritance, as opposed to
236 alternative approaches to inferring ancestral states of categorical traits based on nucleotide
237 substitution models [36, 37]; in substitution models evolutionary change is not gradual but
238 occurs in “jumps” between states, which has been deemed less plausible than polygenic
239 inheritance [34, 38] (and in our opinion rightfully so). Furthermore, these models often have
240 many more free parameters, require treating the species rather than the population as the unit
241 of observation (thus failing to account for intra-specific variation), and cannot include
242 covariates when inferring ancestral states. We therefore prefer the quantitative genetic
243 approach implemented by our GLMMs.

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

262

263 **Results**

264 *Ancestral state of social organization of all marsupials*

265 Out of the 65 marsupial species with data, three species were excluded from this model for
266 lack of life history and / or habitat heterogeneity information. Only one population of
267 *Macropus giganteus* (the species with most data available) shows IVSO of solitary + group
268 and it was excluded from the analysis for lack of habitat information. In the remaining 62
269 species, 30.6% (19 species) were strictly solitary, 14.5% (9 species) only live in pairs, and
270 11.3% (7 species) were stable group-living (e.g., always MMFF; DRYAD ref), 43.5% (27
271 species) showed IVSO, with 23 species showing two or more forms of
272 solitary/pair-living/group-living, 4 species with two or more different forms of group-living
273 (Supplementary materials S3) DRYAD ref.

274 Social organization was moderately influenced by phylogenetic history ($\lambda = 0.18$, 95% CI =
275 0.06 – 0.31). The most probable ancestral state was solitary living (mean=0.35, 95% CI = 0 –
276 0.88) and IVSO (SP+PG+SPG+VG; mean = 0.35), with the IVSO form of
277 pair-living+group-living (PG) having the second highest probability (mean=0.26, 95% CI = 0
278 – 0.97). The following were pair-living (mean = 0.22, 95% CI = 0 – 0.90) and group-living
279 (mean=0.09, 95% CI = 0 – 0.53) (Figure 1, Table S5.1). There was no significant effect of
280 habitat heterogeneity nor number of studies per populations on social organization (Table
281 S5.2). In addition, when the analysis was done at the species level with only the main form of
282 social organization and no IVSO, the probability of solitary ancestor increased (mean = 0.61,
283 95% CI 0 – 1.00) (Supplementary materials S7).

285 For the 51 Australian marsupials, the phylogenetic signal was 0.20 (95% CI = 0.07 – 0.34).
286 The most probable ancestral state was the IVSO form of pair-living+group-living (PG) but
287 with high uncertainty (mean=0.26, 95% CI = 0 – 0.97), followed by group-living (mean =
288 0.21, 95% CI = 0 – 0.95), solitary living (mean = 0.20, 95% CI = 0 – 0.79) and pair-living
289 (mean = 0.18, 95% CI = 0 – 0.96) (Figure 2, Table S6.1). All forms of IVSO combined
290 (SP+PG+SPG+VG) had a mean probability of 0.41.

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

299

300 **Discussion**

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

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

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

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

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

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

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

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

386 **Conclusions**

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

397

398 **Data accessibility**

399 R code and dataset available at XXX

400 **Funding**

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

402 **Acknowledgments**

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

406

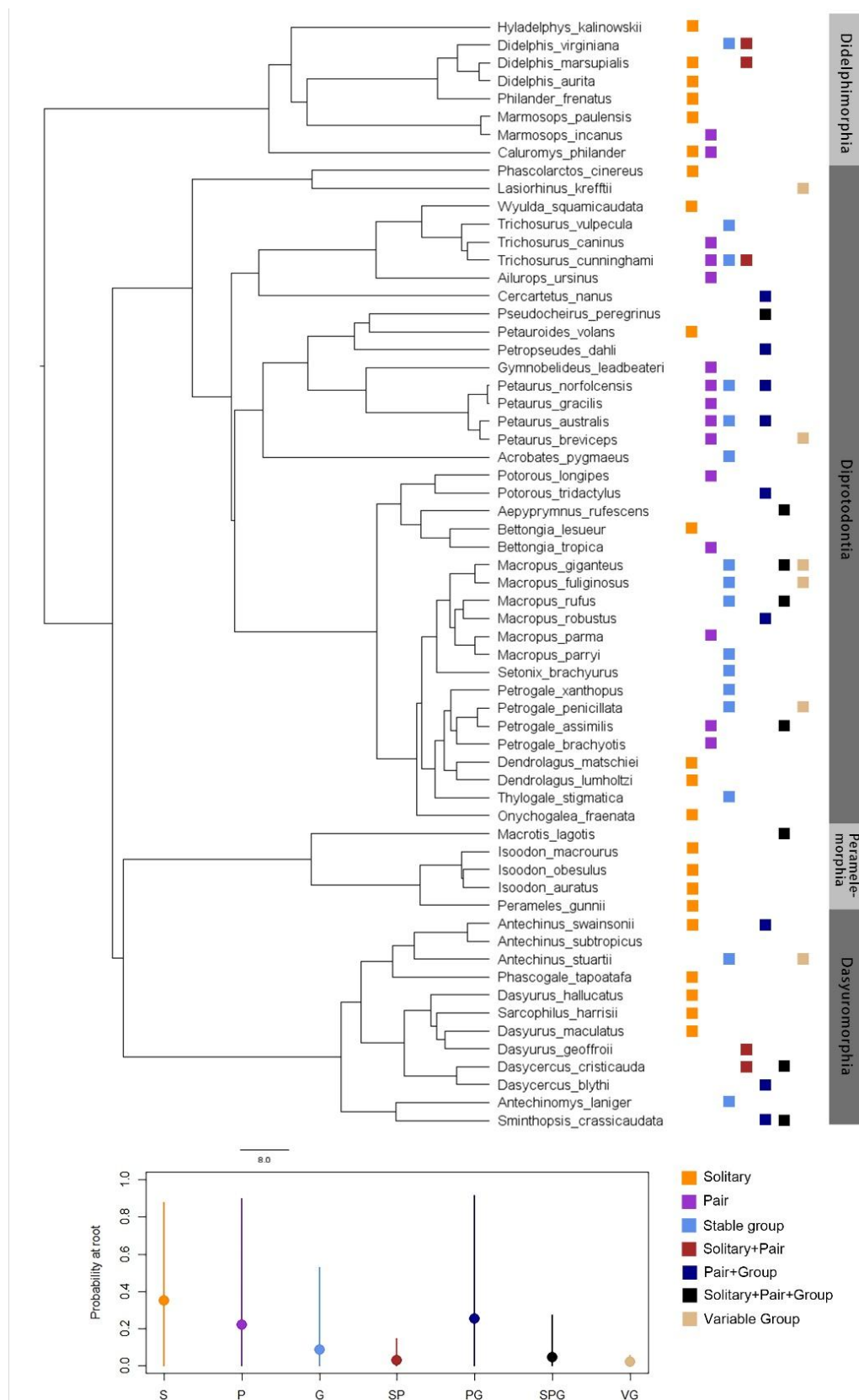
407 **References**

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

- 439 14. Ebensperger LA, Rivera DS, Hayes LD. 2012 Direct fitness of group living mammals
440 varies with breeding strategy, climate and fitness estimates. *Journal of Animal Ecology* 81,
441 1013–1023.
- 442 15. Firman RC, Rubenstein DR, Moran JM, Rowe KC, Buzatto BA. 2020 Extreme and
443 Variable Climatic Conditions Drive the Evolution of Sociality in Australian Rodents.
444 *Current Biology* 30, 691–697.e3. (doi:10.1016/j.cub.2019.12.012)
- 445 16. Lusseau D, Williams R, Wilson B, Grellier K, Barton TR, Hammond PS, Thompson PM.
446 2004 Parallel influence of climate on the behaviour of Pacific killer whales and Atlantic
447 bottlenose dolphins. *Ecology Letters* 7, 1068–1076.
448 (doi:10.1111/j.1461-0248.2004.00669.x)
- 449 17. Cornwallis CK, Botero CA, Rubenstein DR, Downing PA, West SA, Griffin AS. 2017
450 Cooperation facilitates the colonization of harsh environments. *Nat Ecol Evol* 1, 0057.
451 (doi:10.1038/s41559-016-0057)
- 452 18. Rymer TL, Pillay N, Schradin C. 2013 Extinction or Survival? Behavioral Flexibility in
453 Response to Environmental Change in the African Striped Mouse *Rhabdomys*.
454 *Sustainability* 5, 163–186. (doi:10.3390/su5010163)
- 455 19. Luo Z-X, Yuan C-X, Meng Q-J, Ji Q. 2011 A Jurassic eutherian mammal and divergence
456 of marsupials and placentals. *Nature* 476, 442–445. (doi:10.1038/nature10291)
- 457 20. Lukas D, Clutton-Brock TH. 2013 The Evolution of Social Monogamy in Mammals.
458 *Science* 341, 526–530. (doi:10.1126/science.1238677)
- 459 21. Russell EM. 1984 Social behaviour and social organization of marsupials. *Mammal*
460 *Review* 14, 101–154. (doi:10.1111/j.1365-2907.1984.tb00343.x)
- 461 22. Kaufmann JH. 1974 The Ecology and Evolution of Social Organization in the Kangaroo
462 Family (Macropodidae). *American Zoologist* 14, 51–62. (doi:10.1093/icb/14.1.51)
- 463 23. Todorov OS, Blomberg SP, Goswami A, Sears K, Drhlík P, Peters J, Weisbecker V. 2021
464 Testing hypotheses of marsupial brain size variation using phylogenetic multiple
465 imputations and a Bayesian comparative framework. *Proceedings of the Royal Society B:*
466 *Biological Sciences* 288, 20210394. (doi:10.1098/rspb.2021.0394)
- 467 24. Fisher DO, Owens IPF, Johnson CN. 2001 The Ecological Basis of Life History Variation
468 in Marsupials. *Ecology* 82, 3531–3540.
469 (doi:10.1890/0012-9658(2001)082[3531:TEBOLH]2.0.CO;2)
- 470 25. Croft, D. (Marsupial Behavior. 1998. In: *Comparative Psychology: A Handbook* (editors
471 Greenberg, G. & Haraway, M. M.) Garland reference library of social science vol 894.
- 472 26. Makuya L, Olivier C-A, Schradin C. In press. Field studies need to report essential
473 information on social organization – independent of the study focus. *Ethology* n/a.
474 (doi:10.1111/eth.13249)
- 475 27. Aureli F et al. 2008 Fission- Fusion Dynamics: New Research Frameworks. *Current*
476 *Anthropology* 49, 627–654. (doi:10.1086/586708)

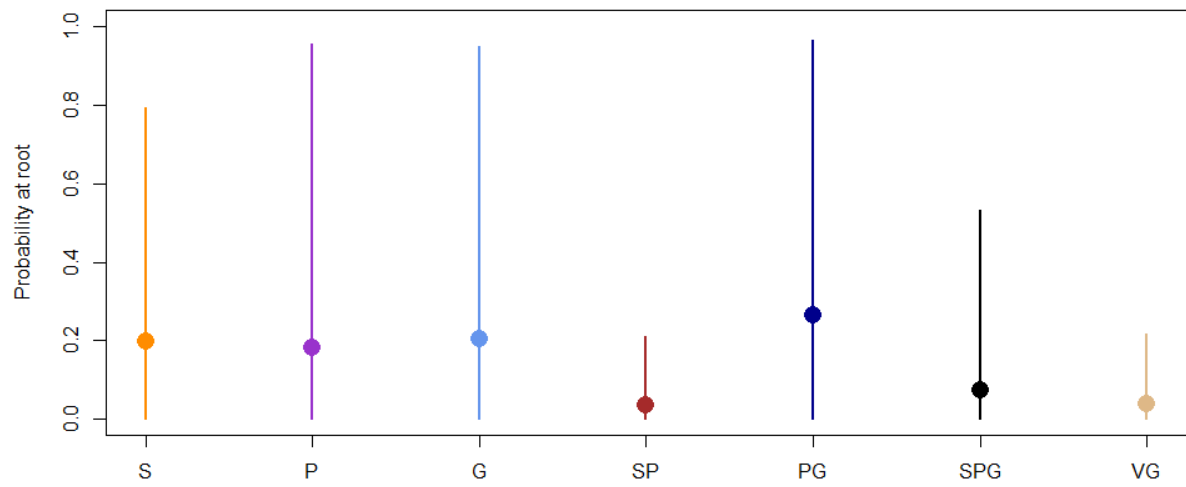
- 477 28. Best EC, Seddon JM, Dwyer RG, Goldizen AW. 2013 Social preference influences female
478 community structure in a population of wild eastern grey kangaroos. *Animal Behaviour* 86,
479 1031–1040. (doi:10.1016/j.anbehav.2013.09.008)
- 480 29. Wilson, D,E, & Mittermeier, R,A. 2015 *Handbook of the Mammals of the World Volume*
481 *5: Monotremes and Marsupials*. Lynx Edicions, Barcelona.
- 482 30. Beck RMD, Godthelp H, Weisbecker V, Archer M, Hand SJ. 2008 Australia's Oldest
483 Marsupial Fossils and their Biogeographical Implications. *PLoS ONE* 3, e1858.
484 (doi:10.1371/journal.pone.0001858)
- 485 31. Bürkner P. C. 2017 brms: An R Package for Bayesian Multilevel Models Using Stan.
486 *Journal of Statistical Software* 80, 1–28. (doi:10.18637/jss.v080.i01)
- 487 32. Bürkner P. C. 2018. Advanced Bayesian Multilevel Modeling with the R Package brms.
488 *The R Journal* 10(1), 395–411. (doi.org/10.32614/RJ-2018-017)
- 489 33. Stan Development Team. 2020 RStan: the R interface to Stan. R package version 2.21.2.
490 (<http://mc-stan.org/>)
- 491 34. Hadfield JD, Nakagawa S. 2010 General quantitative genetic methods for comparative
492 biology: phylogenies, taxonomies and multi-trait models for continuous and categorical
493 characters. *Journal of Evolutionary Biology* 23, 494–508.
494 (doi:10.1111/j.1420-9101.2009.01915.x)
- 495 35. Lynch M. 1991 *Methods for the Analysis of Comparative Data in Evolutionary Biology*.
496 *Evolution* 45, 1065–1080. (doi:10.1111/j.1558-5646.1991.tb04375.x)
- 497 36. Pagel M. 1994 Detecting correlated evolution on phylogenies: a general method for the
498 comparative analysis of discrete characters. *Proceedings of the Royal Society of London.*
499 *Series B: Biological Sciences* 255, 37–45. (doi:10.1098/rspb.1994.0006)
- 500 37. Pagel M, Meade A. 2006 Bayesian Analysis of Correlated Evolution of Discrete
501 Characters by Reversible- Jump Markov Chain Monte Carlo. *The American Naturalist*
502 167, 808–825. (doi:10.1086/503444)
- 503 38. Felsenstein J. 2005 Using the quantitative genetic threshold model for inferences between
504 and within species. *Philosophical Transactions of the Royal Society B: Biological*
505 *Sciences* 360, 1427–1434. (doi:10.1098/rstb.2005.1669)
- 506 39. Nakagawa S, Schielzeth H. 2012 The mean strikes back: mean–variance relationships and
507 heteroscedasticity. *Trends in Ecology and Evolution*
- 508 40. Münkemüller T, Lavergne S, Bzeznik B, Dray S, Jombart T, Schifffers K, Thuiller W. 2012
509 How to measure and test phylogenetic signal. *Methods in Ecology and Evolution* 3,
510 743–756. (doi:10.1111/j.2041-210X.2012.00196.x)
- 511 41. Ladevèze S, de Muizon C, Beck RMD, Germain D, Céspedes-Paz R. 2011 Earliest
512 evidence of mammalian social behaviour in the basal Tertiary of Bolivia. *Nature* 474,
513 83–86. (doi:10.1038/nature09987)
- 514 42. Fisher DO, Lara MC. 1999 Effects of body size and home range on access to mates and

- 515 paternity in male bridled nailtail wallabies. *Animal Behaviour* 58, 121–130.
516 (doi:10.1006/anbe.1999.1119)
- 517 43. Newell GR. 1999 Home range and habitat use by Lumholtz's tree-kangaroo
518 (*Dendrolagus lumholtzi*) within a rainforest fragment in north Queensland. *Wildl. Res.* 26,
519 129–145. (doi:10.1071/wr98016)
- 520 44. Pays O, Goulard M, Blomberg SP, Goldizen AW, Sirot E, Jarman PJ. 2009 The effect of
521 social facilitation on vigilance in the eastern gray kangaroo, *Macropus giganteus*.
522 *Behavioral Ecology* 20, 469–477. (doi:10.1093/beheco/arp019)
- 523 45. Makuya L, Olivier C, Schradin C. 2022 Field studies need to report essential information
524 on social organization—independent of the study focus. *Ethology* 128, 268–274.
- 525 46. Ellis WAH, Melzer A, Carrick FN, Hasegawa M. 2002 Tree use, diet and home range of
526 the koala (*Phascolarctos cinereus*) at Blair Athol, central Queensland. *Wildl. Res.* 29, 303.
527 (doi:10.1071/WR00111)
- 528 47. Schradin C. 2017 Comparative studies need to rely both on sound natural history data and
529 on excellent statistical analysis. *Royal Society Open Science* 4, 170346.
530



531
 532 **Figure 1:** Phylogeny of 62 marsupial species with available data and the probability of each kind of
 533 social organization at the root of the phylogeny, i.e. the last common ancestor of all marsupials. The
 534 different forms of social organization recorded for each species at the population level are shown on
 535 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.