

1 **Title: Contrasts in kinship structure in mammalian societies**

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8 **Lay Summary:** Cooperative behavior in mammals is most often seen in species that live in groups of  
9 closely related individuals. It is therefore important to establish how and why the kinship structure of  
10 mammal groups varies between species. Using mathematical modelling, we show that these  
11 differences are a consequence of differences in litter size, dispersal, reproductive skew and the  
12 number of breeding adults of each sex.

13  
14 **Abstract:** Comparative studies of mammals confirm Hamilton's prediction that differences in  
15 cooperative and competitive behavior across species will be related to contrasts in kinship between  
16 group members. While theoretical models have explored the factors affecting kinship within social  
17 groups, few have analyzed the causes of contrasts in kinship among related species. Here, we describe  
18 interspecific differences in average kinship between group members among social mammals and  
19 show that a simple mathematical model which includes the number of breeding females, male  
20 reproductive skew and litter size successfully predicts ~95% of observed variation in average kinship  
21 between group members across a sample of mammals. Our model shows that a wide range of  
22 conditions can generate groups with low average relatedness but only a small and rather specific set of  
23 conditions are likely to generate high average levels of relatedness between their members, providing  
24 insight into the relative rarity of advanced forms of cooperation in mammalian societies.

25  
26 **Key words:** Kinship, cooperation, mammal societies, social organization, relatedness

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28

## 1. Introduction

29

The theory of kin selection (Hamilton 1964) suggests that individuals can derive fitness benefits from aiding close genetic kin. Hamilton (1971) also suggested that asymmetrical forms of cooperation, like alloparental care of dependent young, should be most common in species where average relatedness between group members is high while competitive behavior should be most frequent where relatedness is low. Recent comparative studies of social mammals have confirmed that asymmetrical or 'altruistic' forms of cooperation are most developed in species where average coefficients of relatedness are high while competitive interactions, the formation of competitive coalitions between group members and complex forms of manipulative behavior are most frequent in species where average relatedness is low (Griffin and West 2003; Silk 2009; Lukas and Clutton-Brock 2018).

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39

The relationship between variation in average kinship between group members and the frequency of competitive and cooperative interactions across mammal species emphasizes the need to understand the factors responsible for interspecific differences in relatedness between group members in social species. Gene-based estimates of average coefficients of relatedness between members of natural groups are still scarce but are now available for a small sample of social mammals and comparisons show how widely they vary – from close to 0 in chimpanzees to over 0.45 in some social mole-rats (Burland et al. 2002; Lukas et al. 2005; Langergraber et al. 2007) (Fig 1, Table 1).

46

47

[Figure 1 here]

48

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Theoretical studies have identified the effects of several parameters on kinship within animal groups, including group size (Altmann 1979; Lukas et al. 2005; Lehmann and Rousset 2010), male reproductive skew (Lukas et al. 2005; Johnstone 2008; Schülke and Ostner 2008), and dispersal (Rousset 2004; Johnstone and Cant 2008; Lehmann and Rousset 2010). However, as yet there have

52

53 been few systematic investigations of the causes of interspecific differences in kinship in different  
54 animal groups and none for mammals. Here, we develop and test a simple model that predicts  
55 relatedness within mammal groups in order to explore and compare the influence of different factors  
56 on average kinship between group members.

57  
58 We anticipated that four life history factors are likely to play a particularly important role. First,  
59 increases in the number of breeding females and reductions in reproductive skew or breeding tenure  
60 among females are likely to dilute maternal kinship and reduce kinship between group members  
61 (Lukas et al. 2005; Johnstone 2008). Second, increases in the number of breeding males per group and  
62 reductions in male breeding tenure and reproductive skew will reduce paternal kinship (Altmann  
63 1979; Lukas et al. 2005; Schülke and Ostner 2008). Third, increases in litter size and reductions in the  
64 period for which offspring remain in their natal groups are likely to increase the proportion of natal  
65 recruits that are full siblings and so increase average kinship between group members (Altmann  
66 1979). Finally, increases in the frequency of immigration by unrelated individuals of either sex into  
67 established breeding groups and levels of kinship between immigrants are likely to influence the  
68 kinship structure of groups (Johnstone and Cant 2008; Silk 2009; Lehmann and Rousset 2010).

## 69 70 **2. Methods**

### 71 *Modelling group relatedness*

72 Our model generates an estimate of average intragroup relatedness that is a function of the number of  
73 adult males ( $N_m$ ), the number of adult females ( $N_f$ ), litter size ( $\kappa$ ), male reproductive skew ( $\alpha$ ), the  
74 probability of a subordinate female reproducing ( $\beta$ ), male dominance tenure ( $\tau_m$ ), female dominance  
75 tenure ( $\tau_f$ ), the number of juvenile cohorts ( $n$ ), and the number of juveniles per adult ( $\theta$ ) (see *Methods*,  
76 Table 1). It also makes it possible to explore the effect of male and female dispersal on intragroup  
77 relatedness.

79 Our model first considers relatedness among juveniles among which the primary source of relatedness  
80 is through shared parentage; using simple pedigree relatedness, individuals who share one parent are  
81 half siblings ( $r = 0.25$ ) and individuals sharing both parents are full siblings ( $r = 0.5$ ). In a simple  
82 scenario, the mean relatedness of juveniles through shared parentage is therefore  $0.25(P + M)$  where  $P$   
83 is the probability of sharing a father and  $M$  is the probability of sharing a mother.

84  
85 What is the probability of two juveniles born in the same reproductive cohort sharing a father? Let us  
86 assume that a group contains  $N_m$  adult males and allow for the possibility that one male is  
87 reproductively dominant, taking a proportion of the reproductive success of others, determined by  $\alpha$   
88 such that the total proportion of offspring produced by the dominant ( $d$ ) is calculated as  $d = 1/N_m +$   
89  $\alpha(N_m - 1)/N_m$ . Therefore, if  $\alpha = 0$ , all males including the dominant have an equal probability of  
90 fathering an offspring ( $1/N_m$ ) while if  $\alpha = 1$ , the dominant male produces all offspring in that cohort.  
91 Given  $d$ , the probability of two individuals born in the same cohort sharing a father ( $p_0$ ) is  $d^2 + (1 -$   
92  $d)^2/(N_m - 1)$ .

93  
94 What is the probability of two juveniles born in *different* cohorts sharing a father? This depends on the  
95 likelihood of the dominant male retaining dominance between the production of juvenile cohorts (e.g.  
96 from one breeding season to the next among seasonal breeders). Let us say that the dominant male  
97 retains his reproductive dominance from one cohort to the next with probability  $\tau_m$ . Where this occurs,  
98 the probability of juveniles in different cohorts sharing a father will remain  $p_0$ . However, when there  
99 is a dominance challenge (with probably  $1 - \tau_m$ ) let us assume that all males have an equal chance of  
100 becoming dominant. In such a scenario, the expected probability of a random male fathering an  
101 offspring following a dominance challenge is  $1/N_m$ . Thus, the probability of individuals born  $i$  cohorts  
102 apart sharing a father ( $p_i$ ) is  $\tau_m^i p_0 + (1 - \tau_m^i)/N_m$ . Generalizing across a population of juveniles born  
103 across  $n$  cohorts, the total probability of juveniles sharing a father ( $P$ ) is therefore:

104  
105 
$$P = \frac{np_0 + \sum_{i=1}^{n-1} 2(n-i)p_i}{n^2} \quad (1)$$

106

107 What is the probability of two juveniles sharing a mother? Let us say that there are  $N_f$  adult females in  
 108 a group and that when females reproduce, they produce  $\kappa$  offspring. For example, if  $\kappa = 1$ , the species  
 109 is monotocous, producing single offspring and if  $\kappa = 6$ , the species is polytocous, producing litters of  
 110 six offspring. Let us assume that one female (the dominant) always reproduces and that the other  
 111 females (the subordinates) reproduce with probability  $\beta$ . The probability of two individuals born in the  
 112 same cohort having the same mother ( $m_0$ ) is:

113

$$114 \quad m_0 = \sum_{i=1}^{N_f} \binom{N_f-1}{i-1} \beta^{(i-1)} (1-\beta)^{(N_f-i)} \frac{\kappa-1}{i\kappa-1} \quad (2)$$

115

116 As with fathers, the probability of two juveniles born in different cohorts sharing a mother depends on  
 117 the probability of a change in female dominance. Let us say that there is probability  $\tau_f$  that the  
 118 dominant female maintains her reproductive dominance from the production of one reproductive  
 119 cohort to the next. Where this occurs, the probability of juveniles in different cohorts sharing a mother  
 120 ( $m_d$ ) is:

$$121 \quad m_d = \sum_{i=1}^{N_f} \binom{N_f-1}{i-1} \beta^{(i-1)} (1-\beta)^{(N_f-i)} \frac{1}{i} \quad (3)$$

122

123 In contrast, when a female dominance challenge does occur (with probability  $1 - \tau_f$ ) all females have  
 124 an equal chance of becoming dominant such that the expected probability of a female being the  
 125 mother of a given offspring after a dominance challenge is  $1/N_f$ . Generalizing across  $n$  cohorts, the  
 126 probability of two juveniles sharing a mother ( $M$ ) is:

127

$$128 \quad M = \frac{nm_0 + \sum_{i=1}^{n-1} 2(n-i) \left( \tau_f^i m_d + \frac{(1-\tau_f^i)}{N_f} \right)}{n^2} \quad (4)$$

129

130 Given  $P$  and  $M$ , expected relatedness among juveniles when considering only shared parentage is  
 131  $0.25(M + P)$ . However, sharing a parent is not the only way in which juveniles may be related; they

132 may be related by sharing grandparents, great-grandparents etc. We can incorporate this additional  
 133 source of relatedness by assuming that same-sex adults are related to each other by  $r_j$  when they have  
 134 either remained in their natal group or have dispersed with group-mates. When this is true for adult  
 135 females, for example, we can assume that even if two juveniles do not share mothers, their mothers  
 136 will be related to one another by  $r_j$ . The expected relatedness between juveniles once relatedness  
 137 through the grandparental generation has been added ( $r_{j'}$ ) is:

$$138$$

$$139 \quad r_{j'} = \frac{r_j}{2} + P \left( 0.25 - \frac{r_j}{4} \right) + M \left( 0.25 - \frac{r_j}{4} \right) \quad (5)$$

140

141 This can be simplified to form a general equation for estimating the relatedness between juveniles  
 142 given a pedigree that is  $g$  generations deep ( $r_{j^g}$ ):

$$143$$

$$144 \quad r_{j^g} = \frac{P+M}{4} \sum_{i=1}^g \left( \frac{2-P-M}{4} \right)^{i-1} \quad (6)$$

145

146 Alternative formulations for when adult males are related but adult females are unrelated are given in  
 147 Table S4. For all calculations in this paper, we use  $g = 5$  to estimate relatedness among juveniles ( $r_j$ ).  
 148 From this, we can build an estimate of relatedness among adults ( $r_A$ ) and relatedness between adults  
 149 and juveniles ( $r_B$ ). For adults, if we assume that same-sex adults are related by  $r_j$  and that different-sex  
 150 adults are unrelated, the mean relatedness among adults is:

$$151$$

$$152 \quad r_A = \frac{r_j ((N_m^2 - N_m) + (N_f^2 - N_f))}{(N_m + N_f)^2 - (N_m + N_f)} \quad (7)$$

153 where the numerator is the number of same-sex adult dyads and the denominator is the total number  
 154 of adult dyads. Again, Equation 7 can be formulated for scenarios where only one sex or neither are  
 155 related (Table S4).

156

157 What about relatedness between adults and juveniles ( $r_B$ )? Since the assumption of our model is that  
 158 juveniles will have both parents in the adult population, the sum of the total relatedness will always  
 159 include 1. They will be related to the other males by  $r_J/2$  and to the other females by  $r_J/2$ . So the total  
 160 mean relatedness between juveniles and adults will be:

161

$$162 \quad r_B = \frac{1+0.5r_J(N_f-1)+0.5r_J(N_m-1)}{N_f+N_m} \quad (8)$$

163

164 As above, this assumes relatedness between both adult males and between adult females, an  
 165 assumption that can be relaxed (Table S4), and which is varied in our simulations. Given all of the  
 166 above, and where  $N_A$  is the number of adults ( $N_f + N_m$ ) and  $N_J$  is the number of juveniles ( $N_J = \theta N_A$ ),  
 167 the mean relatedness between group members  $r_G$  will be:

168

$$169 \quad r_G = \frac{r_A N_A (N_A - 1) + 2r_B N_A N_J + r_J N_J (N_J - 1)}{(N_J + N_A)(N_J + N_A - 1)} \quad (9)$$

170 For simplicity, our model makes some assumptions. First, we assume pedigree relatedness in a diploid  
 171 population in which genetically unrelated individuals are  $r = 0$ . This differs from the relative measures  
 172 of relatedness used in some empirical analyses of relatedness in animal populations in which  
 173 individuals related by less than the population average have a negative coefficient of relatedness  
 174 (Queller and Goodnight 1989). As such, where we compare model predictions to empirical data  
 175 calculated using this method, our model may overestimate relatedness. The model also assumes that  
 176 all juveniles have both parents within the adult cohort, conditions unlikely to be met in species facing  
 177 high mortality. We also assume a lack of inbreeding, neutral demography, and non-overlapping  
 178 generations.

179

### 180 *Simulations and model validation*

181 A standard approach to exploring the effect of multiple parameters on an outcome is to use a set of  
 182 default parameters and to vary each in turn in order to understand its effect on the outcome. However,  
 183 this approach is sensitive to the default parameter values and may be an ineffective way to fully

184 explore parameter space. Following Gallagher *et al.* (2015), we use a Fitting to Idealized Outcomes  
185 (FIO) approach in which we randomly set our parameter values within defined limits (Table 1) and  
186 use the model to estimate group relatedness. We repeat this a large number of times ( $1.2 \times 10^7$ ,  
187 following Gallagher *et al.* (2015)) and explore the parameter values that produce a mean group  
188 relatedness greater than two thresholds:  $r > 0.125$  and  $r > 0.25$  which correspond to the mean  
189 relatedness between cousins and half-siblings respectively. Both simulations and data analysis were  
190 conducted in R.3.3.3 with some additional analyses run in Mathematica. An R script of the model is  
191 provided in the Supplementary Material.

192

193 In order to test the ability of our model to predict empirical observations of mean intragroup  
194 relatedness, we conducted a search of the literature and compiled data from mammal species in which  
195 we were able to find published estimates of both mean intragroup relatedness and the social and  
196 demographic parameters required by our model. Estimates of relatedness among all group members  
197 (rather than only among females and/or adults) are relatively rare and this resulted in a sample of  
198 eleven species. Parameter values and references to the supporting literature for each species are given  
199 in Tables S1-3. The eleven species range in mean intragroup relatedness from  $r = 0.01$  in chimpanzees  
200 (Langergraber *et al.* 2007) to  $r = 0.46$  in Damaraland mole-rats (Burland *et al.* 2002). Where possible,  
201 parameters refer specifically to the study population for which the estimate of relatedness was  
202 produced, rather than the species in general. For example, the intragroup relatedness estimate for  
203 chimpanzees is taken from the Ngogo population which have an unusually large group size of ~150  
204 individuals (Langergraber *et al.* 2007); the group size parameters for chimpanzees reflect this group  
205 and not the species-wide average group size. The power of our model in predicting the observed data  
206 was determined by estimating the variation explained by cross-validation ( $VE_{cv}$ ) (Li 2017).

207

208 **Table 1.** Model parameters, value ranges used in the FIO modelling, and the Spearman's rank  
209 correlation coefficients ( $\rho$ ) between the parameter and mean relatedness across all simulations.



Parameter	Symbol	Range/values	Spearman's rank correlation coefficients ( $\rho$ )
Number of breeding males	$N_m$	$\{N_m \in \mathbb{Z} \mid 2 \leq N_m \leq 10\}$	-0.31
Number of breeding females	$N_f$	$\{N_f \in \mathbb{Z} \mid 2 \leq N_f \leq 10\}$	-0.38
Number of juvenile cohorts	$n$	$\{n \in \mathbb{Z} \mid 1 \leq n \leq 6\}$	-0.11
Male reproductive skew	$\alpha$	$\{\alpha \in \mathbb{R} \mid 0 \leq \alpha \leq 1\}$	0.34
Probability of a subordinate female reproducing	$\beta$	$\{\beta \in \mathbb{R} \mid 0 \leq \beta \leq 1\}$	-0.23
Mean litter size	$\kappa$	$\{\kappa \in \mathbb{Z} \mid 1 \leq \kappa \leq 6\}$	0.08
Likelihood of dominant male retaining dominance	$\tau_f$	$\{\tau_f \in \mathbb{R} \mid 0 \leq \tau_f \leq 1\}$	0.08
Likelihood of dominant female retaining dominance	$\tau_m$	$\{\tau_m \in \mathbb{R} \mid 0 \leq \tau_m \leq 1\}$	0.06
Number of juveniles per adult	$\theta$	$\{\theta \in \mathbb{R} \mid 0.5 \leq \theta \leq 2.5\}$	0.20
Adult females related?	-	{Yes, No}	-
Adult males related?	-	{Yes, No}	-

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### 3. Results

213

To test the predictive power of our model, we used life history data for eleven group-living mammal species to estimate intragroup relatedness according to our model and compared this to genetic estimates of relatedness for those species (Figure 2, Tables S1-3). The greatest absolute difference between expected and observed related was for lions (observed = 0.11, predicted = 0.18). Overall, there was a strong correspondence between the predicted and observed estimates of group relatedness, with the model accounting for ~95% of variation (Fig 2, Variance explained by cross-validation  $VE_{cv} = 0.949$ ; Pearson's correlation coefficient = 0.974, 95% CI = [0.90,0.99],  $R^2 = 0.949$ ).

220

221

[Figure 2 here]

222

223 Across our simulations, relatedness ranged from  $r = 0.01$  to  $0.40$ . However, less than 1% of  
224 combinations of variables in our model resulted in average values of relatedness of  $r > 0.25$  (the  
225 average coefficient of relatedness between half siblings), suggesting that high group relatedness  
226 results from a very narrow set of social and demographic traits. We also used our model to explore the  
227 relative contributions of different life history parameters to variation in kinship. In line with our  
228 expectations, average group relatedness was higher in smaller groups, with negative relationships  
229 between relatedness and the number of adult males ( $N_m$ ) and adult females ( $N_f$ ) (Fig 3a-b). After group  
230 size, variation in reproductive skew had the greatest influence on average relatedness between group  
231 members with greater skew in both males and females (characterized by high  $\alpha$  and low  $\beta$ ,  
232 respectively) associated with higher mean group relatedness (Fig 3d-e, Fig 4c). Although the absolute  
233 effects of male and female dominance tenure were modest (Fig 3g-h), high group relatedness was  
234 more likely when there was both high male skew and tenure ( $\alpha$  and  $\tau_m$ ) or high female skew and  
235 tenure ( $\beta$  and  $\tau_f$ ; in females low  $\beta$  represented high skew). In mammals, this effect is reflected in the  
236 fact that in some species living in highly related groups, such as meerkats (Griffin et al. 2003),  
237 dominant males and females may maintain their dominance for many years, while in many  
238 polygynous species of more intermediate relatedness, there is frequent turnover in male dominance  
239 (Clutton-Brock 2016).

240

241 [Figure 3 here]

242

243 Since litters produce sets of maternal siblings related by at least  $r = 0.25$ , we also expected that litter  
244 size would have a positive effect on group relatedness. Our results suggest that increases in litter size  
245 are indeed associated with higher average kinship but that there is a threshold effect: the initial move  
246 from monotoccy ( $\kappa = 1$ ) to the production of twins ( $\kappa = 2$ ) resulted in a ~5-fold increase in the  
247 probability of a simulation producing relatedness of  $r > 0.25$  (Fig 3f, Fig 4a) while increases in litter  
248 size beyond 2 had only a modest effect on the probability of a simulation producing high mean  
249 relatedness (Fig 3f). We also found that high intragroup relatedness was more likely to evolve when

250 the ratio of juveniles to adults was high (Fig 3i) and when the juvenile population was composed of  
251 relatively few cohorts (Fig 3c), as is common in species with a short juvenile period.

252

253 In many group-living mammals, members of one sex (usually males) leave their natal group after  
254 reaching sexual maturity to search for breeding opportunities elsewhere while members of the other  
255 sex (usually females) remain and breed in their natal group (Greenwood 1980; Silk 2009; Clutton-  
256 Brock 2016). Contrasts in dispersal have an important effect on relatedness among adults of the same  
257 sex who may be closely related either because they remain in their natal group to breed or because  
258 they disperse as part of a coalition of individuals from the same group (Clutton-Brock 2016). For  
259 males, coalitional dispersal occurs among species such as lions and banded mongooses where groups  
260 may include multiple breeding males (Packer and Pusey 1982; Packer et al. 1988; Cant et al. 2016). In  
261 contrast, in many cercopithecine primates males emigrate and immigrate independently and few co-  
262 resident males are close relatives (Alberts and Altmann 1995; Clutton-Brock 2016). Our results show  
263 that, compared to a scenario of no relatedness among adults of either sex, average intragroup  
264 relatedness in a group is around 50% higher when adults of one sex are related and around 120%  
265 higher when both adult males and adult females are related to same-sex adults (Fig 4b).

266 [Figure 4 here]

#### 267 **4. Discussion**

268 We produced a mathematical model that allowed us to explore the relative importance of various  
269 social and demographic factors in determining intragroup relatedness in mammals. Our results show  
270 that the principle factors affecting intragroup relatedness are differences in group size, male and  
271 female reproductive skew, litter size, and dispersal patterns. Some of these factors are intuitive and  
272 have previously been predicted by theoretical work or demonstrated in empirical studies (e.g.  
273 Altmann 1979; Rousset 2004; Lukas et al. 2005; Schülke and Ostner 2008). For example, our model  
274 predicts that intragroup relatedness will be lower in larger groups except in cases where there is high  
275 reproductive skew among both males and females. Among our test species, this is the case for both

276 meerkats and Damaraland mole-rats: although both species frequently live in groups of more than  
277 twenty individuals, high reproductive skew in both sexes means that the majority of individuals born  
278 in the group are siblings and mean intragroup relatedness is accordingly high at  $r = 0.35$  for meerkats  
279 (Griffin et al. 2003; Duncan et al. 2019) and  $r = 0.46$  for Damaraland mole-rats (Burland et al. 2002).

280

281 Our model also generates novel insights, highlighting litter size as a hitherto neglected but important  
282 determinant of intragroup relatedness. Specifically, producing single young (monotoccy) precludes the  
283 possibility of maternal siblings being born in the same cohort and places a constraint on group  
284 relatedness: in our simulations intragroup relatedness was ~5 times less likely to exceed  $r = 0.25$  with  
285 monotoccy compared to production of litters of two or more offspring. In mammals, contrasts in litter  
286 size may have played a particularly important role in social evolution since the formation of breeding  
287 groups that include multiple breeding females has evolved more frequently in monotocous species  
288 than in species that produce litters (Lukas and Clutton-Brock 2018). Where the aggregation of  
289 breeding females into cohesive social groups is also associated with polygamous mating systems,  
290 competition between males reduces the breeding tenure of successful individuals (Clutton-Brock and  
291 Isvaran 2007; Lukas and Clutton-Brock 2014) and will further reduce kinship between group  
292 members.

293

294 Differences in intragroup relatedness generated by social, demographic, and life-history traits may  
295 have far reaching consequences for patterns of competitive and cooperative behavior (Queller 2000;  
296 West et al. 2002; Fisher et al. 2013). Where average kinship between group members is high, conflicts  
297 of interest between group members are likely to be reduced, competitive interactions over resources or  
298 breeding opportunities may be infrequent, altruistic forms of cooperative behavior are more likely to  
299 evolve, and assistance may be less frequently directed selectively at an individual's closest kin  
300 (Hamilton 1971; Griffin and West 2003). As expected, the evolution of cooperative breeding systems  
301 where young are reared by non-breeding group members appears to have been restricted in mammals  
302 to polytocous species where reproductive skew is high in both sexes and most group members are

303 closely related (Lukas and Clutton-Brock 2012). Selective assistance of close kin is seldom highly  
304 developed in mammals that breed cooperatively (Griffin and West 2003; Cornwallis et al. 2009;  
305 Duncan et al. 2019) and aggressive interactions between group members are relatively infrequent  
306 except where individuals are competing for the breeding position in their group (Lukas and Clutton-  
307 Brock 2018). In contrast, in species where average kinship between group members is low, aggressive  
308 interactions, threats, manipulative strategies and the formation of competitive coalitions between  
309 group members are more frequent while altruistic forms of cooperation are relatively rare and are  
310 usually directed at close kin (Silk 2009; Lukas and Clutton-Brock 2018).

311

312 Contrasts in kinship generated by variation in life history patterns may also be responsible for broad  
313 differences in social behavior between major mammalian taxa. For example, they may offer some  
314 insight into the unusual characteristics of higher primates. Monotocy is normal in these species and  
315 levels of kinship between group members are typically low (Harvey and Clutton-Brock 1985; Lukas  
316 et al. 2005). As would be expected, competitive interactions between group members are relatively  
317 frequent and selfish and manipulative strategies are widespread while the more costly forms of  
318 altruistic cooperation, such as provisioning young born to others, are relatively rare and directed at  
319 close relatives (Silk 2009; Lukas and Clutton-Brock 2018). In contrast, the retention of polytocy in  
320 social carnivores and rodents may have contributed to the evolution of groups where dominants  
321 suppress reproduction in subordinates and asymmetrical forms of cooperation are frequent (Clutton-  
322 Brock 2016). For humans, parsimony suggests that we have had a deep evolutionary history of living  
323 in multi-male multi-female groups with low female reproductive skew and monotocy (Chapais 2013),  
324 all of which would have led to groups of low average relatedness similar to those seen among  
325 contemporary foraging societies (Hill et al. 2011; Dyble et al. 2015). Although this would suggest a  
326 context in which reproductive competition and manipulative tactics would be common and  
327 cooperative behavior would rely on mutualistic or reciprocal benefits, the formation of closely related  
328 family groups within these wider groups of low relatedness may have facilitated cooperation in food  
329 sharing and raising offspring (Kaplan et al. 2000; Dyble et al. 2016). At the same time, the evolution

330 of increased social intelligence, language, and cultural norms and institutions that facilitate  
331 cooperation may have stabilized cooperation between non-kin (Richerson and Boyd 2005; Herrmann  
332 et al. 2007; Pinker 2010).

333

334 We produced a simple mathematical model which, in combination with a powerful method for  
335 exploring parameter space (Gallagher et al. 2015), demonstrates that only a small and rather specific  
336 set of social, demographic, and life-history traits are likely to generate the high levels of intragroup  
337 relatedness thought to be required for the evolution of advanced forms of cooperation in mammals  
338 (Hamilton 1971; Lukas and Clutton-Brock 2018). However, it is important to note that our model  
339 makes no comment on why these traits evolve. Although headway has been made on understanding  
340 the evolution of some of these traits (e.g. reproductive skew: Cant 1998; Beekman et al. 2006; Hager  
341 and Jones 2009), further research is required to establish why the traits considered here vary in  
342 mammals and how they co-evolve.

343

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352 manuscript.

353

354 **Data accessibility:** All data are available in the main text or supplementary materials.

355

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455

456 **Figure 1. Contrasts in intragroup relatedness among social mammals. (a-c)** Among group-living  
457 mammals intragroup genetic relatedness varies from low levels in species such as (a) chimpanzees

458 (*Pan troglodytes*) where multiple individuals of both sexes breed and reproductive skew is relatively  
459 low, through groups of intermediate relatedness like (b-c) African wild dogs (*Lycaon pictus*) and  
460 banded mongooses (*Mungos mungo*), to very highly related and cooperatively breeding species such  
461 as (d) Damaraland mole-rats (*Fukomys damarensis*). (a), (b) and (d) made available under Creative  
462 Commons attribution licenses.

463

464 **Figure 2: Comparison of empirically observed estimates of intragroup relatedness for eleven**  
465 **mammal species against values predicted by our model.** The dotted line represents a 1:1  
466 correspondence between expected and observed values. Parameter values and references to the  
467 supporting literature for each species are given in Tables S1-3.

468

469 **Figure 3. Factors affecting group relatedness.** Plots of the relative frequency of parameter values  
470 for simulations in which relatedness was  $r > 0.125$  (blue) and  $r > 0.25$  (red). Horizontal dashed lines  
471 show the distribution expected if the parameter had no effect on group relatedness. Correlations  
472 between parameter values and predicted group relatedness are given in Table 1.

473

474 **Figure 4. Litter size, adult relatedness, and reproductive skew.** (a) simulations were much more  
475 likely to yield a relatedness estimate of  $r > 0.25$  when females produce litters (polytocry;  $\kappa \geq 2$ ) rather  
476 than single young (monotocry;  $\kappa = 1$ ), (b) predicted mean intragroup relatedness with and without  
477 kinship between same-sex adults, (c) contour plot showing the combined effect of male and female  
478 reproduce skew on within group relatedness ( $r$ ), with all other parameters set at intermediate values ( $n$   
479  $= 2$ ,  $\tau_m = 0.5$ ,  $\tau_f = 0.5$ ,  $\kappa = 2$ ,  $\theta = 1$ ,  $N_m = 8$ ,  $N_f = 8$ ). Values inside the plot denote the coefficients of  
480 relatedness at each contour line, with darker shades representing higher coefficients of relatedness.

481