1   **Title**

2   Patterns and consequences of age-linked change in local relatedness in animal societies

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Patterns and consequences of age-linked change in local relatedness in animal societies

39   **Abstract**

40   The ultimate payoff of behaviours depends not only on their direct impact on an individual but also on
41   the impact on their relatives. Local relatedness – the average relatedness of an individual to their
42   social environment – therefore has profound impacts on social and life history evolution. Recent work
43   has begun to show that local relatedness has the potential to change systematically over an
44   individual's lifetime, a process called kinship dynamics. However, it is unclear how general these
45   kinship dynamics are, whether they are predictable in real systems and their impacts on behaviour and
46   life history evolution. In this study, we combine modelling with data from real systems to explore the
47   extent and impact of kinship dynamics. We use data from seven group-living mammals with diverse
48   social and mating systems to demonstrate not only that kinship dynamics occur in animal systems, but
49   also that the direction and magnitude of kinship dynamics can be accurately predicted using a simple
50   model. We use a theoretical model to demonstrate that kinship dynamics can profoundly impact
51   lifetime patterns of behaviour and can drive sex differences in helping and harming behaviour across
52   the lifespan in social species. Taken together this work demonstrates that kinship dynamics are likely
53   to be a fundamental dimension of social evolution, especially when considering age-linked changes
54   and sex differences in behaviour and life history.

55

56

57   **Main text**

58   <u>Introduction</u>

59   The behavioural decisions and life history strategies of group-living animals are influenced both by
60   their direct impact on an individual's own survival and reproduction and their impact on the fitness of
61   group-mates and relatives[1–4]. The inclusive fitness consequences of interacting with related group-
62   mates represent a balance between the benefits of helping relatives and the costs of competition with
63   those same relatives[5–7]. The average relatedness of an individual to their social group – their local
64   relatedness – therefore sets the foundations for selection on helping and harming behaviour.
65   Reflecting this, local relatedness is a key predictor of social behaviours and social organisation in
66   group-living species[8–13].

67   Until recently, local relatedness has tended to be treated as a static property of a group or species.
68   However, there has been an increasing appreciation that in some social species, each individual's
69   local relatedness can change systematically with age – a process we refer to as kinship dynamics[14–19].
70   Kinship dynamics concepts and models were initially developed to explain the taxonomically rare
71   phenomenon of extended female post-reproductive lifespans (menopause)[14,20]. The models
72   demonstrated that, under some patterns of sex-specific dispersal and rates of local mating, female
73   local relatedness can increase with age and that this will lead to selection for older females to decrease
74   the harm they cause to the reproductive success of other, increasingly related, group members by
75   ceasing their own reproduction[14,20]. Subsequent empirical work in killer whales (*Orcinus orca*) and
76   humans has demonstrated that the cessation of reproduction by older females is indeed linked to the
77   increasing local relatedness of females to their group as they age[21–23]. Kinship dynamics can change
78   selective landscapes and shape behaviour and life history evolution, and treating local relatedness as
79   static may miss fundamental drivers of evolution in social species[19]. Currently, however, the presence
80   and causes of kinship dynamics have not been investigated outside of species exhibiting menopause.

81   There is no reason why the influence of kinship dynamics should be limited to the evolution of post-
82   reproductive lifespans, indeed it would be a surprise if they were. Local relatedness influences many
83   aspects of behaviour. For example, in spotted hyenas (*Crocuta crocuta*) local relatedness predicts the
84   amount of social support an individual will receive which in turn predicts their probability of winning
85   an agonistic interaction and, ultimately, their social rank[24]. Differences in local relatedness can also
86   translate into direct fitness outcomes. For example, in red howler monkeys (*Alouatta seniculus*)
87   females in groups with high local relatedness have greater reproductive success than females in
88   groups with low local relatedness, potentially as a result of increased cooperation and decreased
89   competition amongst females[25]. Where behaviours are contingent on local relatedness, a change in
90   local relatedness with age may lead to corresponding changes in behaviour. Further, while kinship
91   dynamics research thus far has focused on females, similar processes should lead to changes in male
92   local relatedness with age. Moreover, because kinship dynamics are driven by patterns of mating and
93   dispersal - and males and females of the same species often differ in their dispersal and mating
94   strategies - they are likely to differ between males and females in the same system. Sex differences in
95   kinship dynamics could lead to sex differences in behaviour, particularly in relation to the trajectories
96   of behavioural change with age. Despite the potential importance of kinship dynamics, its general role
97   in social evolution, and the conditions under which age-linked relatedness trajectories differ between
98   the sexes, remains largely overlooked.

99   In this study, we combine theoretical modelling with long term individual-based data from several
100 species of group-living mammals to investigate the predictability and consequences of sex differences
101 in kinship dynamics in animals. Specifically, we: (1) develop a theoretical model to predict male and
102 female kinship dynamics under different rates of dispersal and local mating; (2) compare these
103 predicted kinship dynamics with empirical data from seven mammal systems with contrasting social

104   and mating systems; (3) use a model to demonstrate that these patterns of kinship dynamics can select
105   for age-linked behavioural change and that these changes can differ by sex.

106   <u>Results and Discussion</u>

107   *Sex differences in kinship dynamics*

108   To explore and predict patterns of kinship dynamics in both sexes, we extended a previous model that
109   focused explicitly on female kinship dynamics[14], to also include the kinship dynamics of males
110   (supplementary 1). Our analytical model predicts the kinship dynamics of a population parameterised
111   by: the rates of male and female dispersal (d_m, d_f; proportion of each sex who permanently leave their
112   natal group at sexual maturity), rate of local mating (m; proportion of offspring fathered by in-group
113   males), group size (n, number of adults) and probability of mortality (μ). For simplicity here we focus
114   on the three dispersal and local mating scenarios most commonly exhibited in mammals (for all: $n =$
115   10, $\mu = 0.1$; see Supplementary Figure 2 for other combinations): (i) male-biased dispersal with
116   predominantly local mating ($d_f = 0.15$, $d_m = 0.85$, $m = 0.82$), (ii) female-biased dispersal with
117   predominantly local mating ($d_f = 0.85$, $d_m = 0.15$, $m = 0.82$) and (iii) bisexual philopatry with out-
118   group mating ($d_f = 0.15$, $d_m = 0.15$, $m = 0$). In each of these scenarios, our model predicts that the
119   sexes will differ in their patterns of kinship dynamics (figure 1). Under male-biased dispersal, male
120   local relatedness increases with age whereas female local relatedness decreases (figure 1). The
121   opposite pattern occurs under female-biased dispersal (figure 1). In both cases, these patterns occur
122   because a dispersing individual joins a group containing no relatives, but over time these non-kin are
123   replaced with that individual's offspring and grandoffspring of the opposite (philopatric) sex. For
124   example, under male-biased dispersal with local mating males join a group containing no relatives
125   and, over time, their own philopatric daughters and granddaughters replace the unrelated females in
126   the group, while their sons disperse. The philopatric sex, on the other hand, shows a decrease in local
127   relatedness with age as close kin of both sexes die and are only replaced by their philopatric-sex
128   offspring. Under bisexual philopatry with out-group mating female local relatedness increases
129   because offspring of both sexes join their group, replacing more distant relatives, but male local
130   relatedness decreases because their offspring are not recruited to their group and their close relatives
131   at birth are replaced by more distant relatives as they age.

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134

135   *Kinship dynamics in mammals*

136   We tested whether our simple model could predict patterns of kinship dynamics in real systems using
137   detailed empirical data from long-term individual-based studies of seven mammal systems with
138   differing dispersal and mating rates (table 1): banded mongooses (*Mungos mungo*), chimpanzees (*Pan*
139   *troglodytes*), European badgers (*Meles meles*), killer whales (resident-ecotype), rhesus macaques
140   (*Macaca mulatta*), spotted hyenas and yellow baboons (*Papio cynocephalus*). To generate predicted
141   kinship dynamics specific for each species, we first develop an agent-based formulation of our kinship
142   dynamic model (hereafter simulation model). This approach allowed us to more closely represent the
143   biology of our example species, particularly by including a non-breeding juvenile phase and a realistic
144   representation of time. We then compared these predicted patterns of kinship dynamics with observed
145   kinship dynamics derived from each study population.

146   Kinship dynamics in both the simulated and observed data are modelled in a Bayesian hierarchical
147   framework, which accounts for error in estimates of local relatedness. All results presented here
148   (simulated and observed) represent relatedness among adults (individuals older than the age of sexual
149   maturity; see Supplementary Figure 3 for an alternative approach including juveniles). We report
150   modelled change in local relatedness as the proportional change per year of adulthood: posterior mean
151   β [95% credible interval]. In examples where the 95% credible interval of slope-coefficient (β) did not
152   overlap 0, we also use the posterior mean to calculate Δr: the percentage expected change in local
153   relatedness between an individual of age-at-maturity and an individual reaching the sex-specific
154   expected adult lifespan. For example, if the average male in a population were predicted to double
155   their local relatedness from age-at-maturity to age of expected lifespan then Δr would equal +100%.

156   In six of our seven study species (exception: European badgers) at least one sex showed a change in
157   observed local relatedness with age (95% credible intervals of β slope parameter do not overlap 0;
158   figure 2H; Supplementary Table 1; see Supplementary Table 2 for a detailed breakdown of the β slope
159   parameter). In five of the seven species (exceptions: European badgers, yellow baboons) the observed
160   sexes show different local relatedness trajectories (95% credible intervals of β slope parameter do not
161   overlap; figure 2H; Supplementary Table 1). In addition, our simulation model correctly predicted the
162   direction of change (positive, negative, no change) in local relatedness with age in 10 of the 14
163   species-sexes (exceptions: female yellow baboons, male rhesus macaques, both sexes of European
164   badgers), and magnitude of change (95% credible intervals of β slope parameter overlap; complete
165   posterior overlap in Supplementary Table 2) in 9 of 14 species-sexes (figure 2; Supplementary Table
166   1; Supplementary Table 2; Supplementary Table 3; Supplementary Figure 4). The good match
167   between our simulated and observed kinship dynamics demonstrate that kinship dynamics are driven,
168   at least in part, by the parameters captured by our model, the most important of which are sex-
169   specific patterns of dispersal and rate of local mating.

170   Chimpanzees show strongly female-biased dispersal and rare extra-group mating[26–31] (table 1). This
171   female-biased dispersal is reflected in their kinship dynamics: females increase their local relatedness
172   as they age (β = 0.074 [0.051 – 0.098], Δr = +33%) while male relatedness does not change with age
173   (β = -0.009 [-0.067 – 0.049]). These observed results match our predictions in both sexes (figure 2B).

174   Rhesus macaques, spotted hyenas and yellow baboons all have strongly male-biased dispersal, very
175   rare female dispersal and high rates of local mating[32–38]. In both spotted hyenas and yellow baboons,
176   male local relatedness increased with age (spotted hyenas: β = 0.12 [0.105 – 0.135], Δr = +72%;
177   yellow baboons: β = 0.033 [0.009 – 0.058], Δr = +23%) as predicted by our simulation models
178   (figures 2F, 2G). In yellow baboons, this increase is more pronounced after age 14 when their own
179   adult offspring begin joining the reproductive pool of the group (β = 2.18 [1.398 – 2.96]). While our
180   modelling predicts that rhesus macaque males will show a modest increase in local relatedness with
181   age (figure 2E), this is not reflected in the observed data where male rhesus macaques showed an age-
182   linked decrease in local relatedness (β = -0.143 [-0.149 – -0.137], Δr = -40%). There is, however, a

183 positive relationship between the number of years a male has been in their group (their group-tenure)
184 and their local relatedness ($\beta = 0.85$ [0.79 – 0.92]). This suggests that the common secondary
185 dispersal in rhesus macaques[36,37] is nullifying age-linked kinship dynamics, but that local relatedness
186 is still dynamic in this species.

187 In female rhesus macaques, spotted hyenas and yellow baboons our simulations predict a slight
188 decrease in local relatedness with age (figures 2E, 2F 2G). In the observed data this decrease is found
189 in the rhesus macaques ($\beta = -0.034$ [-0.039 – -0.030], $\Delta r = -37\%$) and the spotted hyenas ($\beta = -0.021$
190 [-0.03 – -0.012], $\Delta r = -12\%$) but not in the yellow baboons. In the yellow baboons, observed female
191 local relatedness increases with age ($\beta = 0.011$ [0.005 – 0.016], $\Delta r = +10\%$), potentially as a result of
192 the occasional group-fissioning which occurs in this population[39].

193 In both the banded mongooses and killer whales, neither males nor females disperse from their natal
194 group at sexual maturity[40,41]. In both of these species female local relatedness increases with age as
195 more distant relatives are replaced by the female's own offspring (banded mongoose: $\beta = 0.025$
196 [0.008 – 0.043], $\Delta r = +7.5\%$; killer whales: $\beta = 0.011$ [0.000 – 0.023], $\Delta r = +42\%$). We predicted
197 that local relatedness of banded mongoose males would show no change with age because mating is
198 usually local, whereas male killer whale local relatedness would decrease because mating is non-local
199 [42,43]. Our predictions were matched in male killer whales but not in banded mongooses where male
200 local relatedness also decreased with age (killer whales: $\beta = -0.017$ [-0.037 – 0.000], $\Delta r = -14\%$;
201 banded mongooses $\beta = -0.033$ [-0.045 - -0.021], $\Delta r = -13\%$).

202 European badgers do not show strongly sex-biased dispersal, with 45% of males and 23% of females
203 dispersing at adulthood (table 1; Supplementary Table 6). In addition, 52% of offspring are fathered
204 by out-group males (table 1; Supplementary Table 6). This pattern of incomplete dispersal and local
205 mating results in a very shallow increase in local relatedness for both sexes in our simulations but no
206 detectable change in local relatedness in the observed data (figure 2C). The badgers represent an
207 interesting contrast to the other systems represented here because their groups are defined by shared
208 territory. Each group-territory contains at least one large breeding sett as well as multiple satellite
209 setts. Although we find no evidence of kinship dynamics at the group-territory level future work
210 investigating dynamics at a finer scale, within-sett or within-part-of-sett may find evidence of more
211 consistent changes in local relatedness. Supplementary Table

212 Supplementary Table

213   *The consequences of kinship dynamics*

214   Our models and empirical data demonstrate profound differences between the sexes in their changes
215   in local relatedness with age. Next, we explore the potential consequences of these sex differences in
216   kinship dynamics for behaviour and life history evolution. We extend our analytical model (see *Sex*
217   *differences in kinship dynamics* section) by using an inclusive fitness approach to determine the
218   strength of selection on helping and harming given age[6,7], under different rates of male and female
219   dispersal and local mating[14]. In this model, individuals can incur a cost (*c*) to their own fitness to
220   change the fitness of their group mates (*b*). The effect on group mates can be positive (*b* > 0; hereafter
221   help) – increasing their group-mates fitness – or negative decreasing their group-mates fitness (*b* < 0;
222   hereafter harm). We consider fitness in terms of survival and fecundity. In terms of survival,
223   individuals incur a decrease in their own survival to increase or decrease the survival of their group
224   mates. Similarly, females incur a cost to their own fecundity to increase or decrease the number of
225   offspring produced by their group mates. In both scenarios, while the cost is incurred by the
226   individual, the help or harm is undirected, applying to all their group mates (see Supplementary
227   Figures 5 & 6 for sex-directed behaviours).

228   Selection on helping and harming changes with age, differs with demographic pattern and is different
229   for males and females (figure 3). As in the *Sex differences in kinship dynamics* section (above), while
230   our model makes general predictions, we focus here on three demographic scenarios as examples -
231   male-biased dispersal with local mating, female-biased dispersal with local mating and bisexual
232   philopatry with non-local mating - which span the diversity of social systems in mammals.

233   The magnitude and direction of selection are determined primarily by the inclusive fitness outcomes
234   of the behaviours, while changes with age are driven by kinship dynamics (figure 3). Under selection
235   for survival (figure 3A), for example, harming decreases the survival probability of group mates,
236   decreasing within-group competition. Individuals will harm when, overall, reduced within-group
237   competition allows the recruitment of a more closely related individual than their current group mates.
238   Conversely, they will help when any newly recruited individuals are likely to be less closely related
239   than their current group mates. For example, under female-biased dispersal, females are always
240   predicted to harm because they are decreasing the survival of, mostly, non-relatives who will
241   potentially be replaced in the group by their own sons (figure 3Aii). On the other hand, under male-
242   biased dispersal, females will always help because by doing so they increase the survival of their
243   mother, father and daughters while any replacement has only a $1/n_f$ probability (ignoring fitness
244   differences) of being their offspring (figure 3Ai). However, as individuals age, the magnitude of
245   selection for helping or harming changes in line with changes in kinship dynamics: less harm or more
246   help is selected for with increasing relatedness, and more harm or less help with decreasing
247   relatedness. These changes can be dramatic, for example, under bisexual philopatry females are under
248   strong selection to harm the survival of group mates when young, but by the time their grandchildren
249   are born (generation 2) there is almost no selection for harming (figure 3Aiii). In contrast, males in the
250   same bisexual philopatry system are strongly selected to help when young, but by the time their
251   grandoffspring are born (in other groups) there is much lower selection to help (figure 3Avi). Similar
252   sex differences in helping and harming trajectories are found under other demographic scenarios.

253   In our model, as in most mammals, groups are characterised by female demographic dominance:
254   females compete for the number of offspring they produce, males compete to father those
255   offspring[46,47]. This has important implications for selection on fecundity behaviours (figure 3B).
256   Under female demographic dominance, males can increase their fitness both by increasing the
257   fecundity of in-group females and by increasing the fecundity of their male and female relatives
258   (figures 3Biv, 3Bv & 3Bvi). When mating is local, males can increase their direct fitness by
259   increasing the fecundity of within-group females. Therefore, in situations with local mating, males
260   have a strong selection for helping their group because that help is averaged over both sexes (figures

261 3Biv & 3Bv; see figure S5B for selection on sex-specific helping and harming). Males can
262 additionally increase their indirect fitness if the females or males they are helping are close relatives,
263 and it is these indirect benefits that are affected by kinship dynamics. For example, older males under
264 male-biased dispersal (figure 3Biv) or younger males under female-biased dispersal and bisexual
265 philopatry (figures 3Bv & 3Bvi) tend to inhabit groups with their close relatives and can therefore
266 increase the inclusive fitness by increasing their relatives' fecundity, whereas males of other ages in
267 these systems are less related to their group and therefore under weaker selection to help. These
268 indirect fitness benefits are particularly highlighted under bisexual philopatry where mating is outside
269 the group so males cannot gain direct benefits by helping or harming other group members, so all
270 changes are due to the indirect fitness benefits of helping relatives (figure 3Bvi).

271 In contrast to males, under female-demographic dominance, females are in direct reproductive
272 competition with other females in their group. In general, females are selected to help when their
273 female group mates are close kin - for example, all females under male-biased dispersal (figure 3Bi)
274 and older females under female-biased dispersal and bisexual philopatry (figures 3Bii & Biii)– and
275 are selected to harm when they are unrelated (e.g. young females under female-biased dispersal) or
276 under particularly intense reproductive competition (e.g. young females under bisexual philopatry).
277 Kinship dynamics play an important role in female fecundity because the change with local
278 relatedness changes the relative importance of kin cooperation and kin competition with age. This is
279 particularly highlighted for females under female-biased dispersal and bisexual philopatry where
280 selection switches from harm to help at around the age of generation one when females begin sharing
281 the group with their own adult offspring (figures 3Bii and 3Biii).

282

283

284 *General Discussion*

285 We have shown that kinship dynamics are widespread, can show meaningful differences between the
286 sexes and can be predicted from simple demographic parameters. Further, our modelling predicts that
287 kinship dynamics can drive sex differences in selection in age-related patterns of helping and harming
288 in social species, which will have profound implications for the evolution of social behaviours and life
289 history.

290 In both the modelled and real populations, we found strong sex differences in kinship dynamics under
291 male-biased dispersal with local mating, female-biased dispersal with local mating and bisexual
292 philopatry with out-group mating. The modelling results demonstrate that the patterns of kinship
293 dynamics are driven, at least in part, by dispersal and mating patterns. Under male and female-biased
294 dispersal, the dispersing sex shows an increase in local relatedness with age (after maturity), as
295 unrelated group members are replaced with their own philopatric offspring. The philopatric sex, under
296 these scenarios, shows less pronounced changes in relatedness with age because offspring are
297 replacing close kin. If neither sex disperses, female relatedness increases with age, while male local
298 relatedness can increase or decrease depending on mating patterns. Our models of kinship dynamics
299 are relatively simple and yet can accurately reproduce patterns of age-linked changes in local
300 relatedness observed in complex biological systems. This is particularly striking given the number of
301 important biological processes that can affect individual reproductive success not represented in the
302 model such as dominance, senescence and social support. Notably, although secondary dispersal did
303 affect the observed kinship dynamics of male rhesus macaques, in other species exhibiting this
304 behaviour -such as spotted hyenas and yellow baboons[34,38]- our model was still able to predict changes
305 in local relatedness with age. Dispersal as a driver of kinship dynamics is supported by recent cross-
306 cultural ethnographic comparisons of human societies which have shown that, in general, the local
307 relatedness of dispersing individuals increases with age, while that of philopatric individuals does not
308 change[17]. More generally, our results support previous results highlighting an important role of
309 dispersal rates in determining within-group local relatedness[48–50].

310 Kinship dynamics provide a framework to understand age-linked changes in social behaviours which
311 have been found in a variety of species and contexts (Table 2). As well as selection on helping and
312 harming *per se* predictable changes in local relatedness have the potential to contribute to other age-
313 linked changes in behaviour such as social selectivity, extra-group mating and intergroup conflict
314 (Table 2). In addition to behavioural effects, kinship dynamics can also have life history
315 consequences. This is clearly illustrated by research in humans and killer whales demonstrating that
316 kinship dynamics and their resultant relatedness asymmetries can lead to selection for prolonged
317 female post-reproductive lifespans[14,21,51]. By creating relatedness asymmetries and by influencing life
318 history trade-offs, kinship dynamics are likely to be an important influence on selection for other life
319 history traits such as reproductive schedules, age at maturity and rates of senescence. The influence of
320 kinship dynamics on life history traits is an exciting area for future research.

321 We have also shown here that kinship dynamics can and do differ between the sexes. Although they
322 are not widely studied, sex differences in the age-linked trajectories of social behaviours have been
323 documented in some systems. For example, in Hadza hunter-gatherer societies, females increase their
324 time spent foraging for shared resources as they age, whereas male foraging activity peaks in late
325 adolescence and declines thereafter[52]. However, age-linked changes in behaviour have rarely been
326 linked to changes in local relatedness. The results from the Hadza study, for example, would fit the
327 predictions of investment in helping behaviours under kinship dynamics of increasing female
328 relatedness and decreasing male relatedness with age. This pattern would result from female-biased
329 dispersal which is the norm in chimpanzees[27,29,31] and bonobos (*Pan paniscus*)[53,54]. However, there
330 remains considerable debate over ancestral human dispersal patterns[55–61], and female-biased dispersal
331 is not the case for all contemporary hunter-gatherer groups[17,50,62,63] or the Hadza in particular[64,65].

332 Kinship dynamics represent a framework under which to investigate and evaluate these sex
333 differences in trajectories of social behaviour.

334 Kinship dynamics represent a step forward in the development of a theory of social life history.
335 Classical life history theory describes how selection acts on fecundity and mortality over an
336 individual's lifespan[66–69]. Because it deals with events across the lifespan, life history theory is
337 explicitly dynamic. However, classic life history theory is also asocial, with models usually
338 optimising population-level fitness traits without a social component[67]. Kin selection theory in
339 contrast is explicitly social but static, with demographic change across the lifespan rarely included in
340 the framework[1,70 but see16,71–73]. Moreover, kin selection based 'social ageing' theories remain largely
341 distinct from life history theories of ageing[74]. Kinship dynamics represent an important bridge
342 between these traditions. This bridging is important because recent work has begun to explore the
343 links between group-living and life history evolution, particularly the role of sociality in the evolution
344 of senescence[75–77].

345 Here we have shown that in real animal systems relatedness – the r in Hamilton's rule – can change
346 systematically with age, changing selection on patterns of helping and harming across the lifespan.
347 However, it is not just relatedness that is likely to change with age. Both the benefits and costs –
348 Hamilton's b and c – of a behaviour may also change systematically with age. Theoretical work has
349 shown that the state of the actor can dynamically influence the payoff of (in terms of b and c) and
350 subsequent selection for behaviours[78]. As an individual's state can vary systematically with age, the
351 payoffs from behaviour will also vary with age[e.g. 79]. Further, both reproductive value and knowledge
352 can change systematically with age which will also feed into the costs and benefits of a behaviour. For
353 example, older and more experienced individuals may be important as repositories of ecological
354 knowledge- and therefore more able to benefit their relatives in times of ecological hardship[e.g. 80,81]. A
355 greater understanding of how payoffs change with age and integrating these findings with the kinship
356 dynamics results presented here would represent an important next step towards understanding the
357 social dimensions of life history evolution.

358 Although in this study we focus on age-linked kinship dynamics, other axes of kinship dynamics
359 could also have important implications for social evolution. We show that tenure – the length of time
360 an individual has been present in a group – can be an important driver of kinship dynamics. We found
361 that for male rhesus macaques group tenure, but not age, predicted local relatedness change.
362 Similarly, the amount of social support received by immigrant male spotted hyenas during intragroup
363 agonistic interactions is positively correlated with their group tenure[24]. In many systems, tenure and
364 age are likely to be closely correlated but in some systems, notably those where animals may disperse
365 multiple times over their lifetime, they may not be. The action of selection on tenure-length, and the
366 interaction between tenure length and changes in local relatedness are exciting areas for further
367 research.

368 Our examples in this study demonstrate the impact of kinship dynamics in group-living species with
369 pluralistic or partly pluralistic breeding, where all mature individuals have the potential to reproduce.
370 However, in many species, including some mammals, breeding is monopolised by one or a few
371 individuals within the group[82]. While the mechanisms of kinship dynamics presented here may not
372 apply to non-pluralistic breeders, age-related changes in relatedness have been found in several
373 cooperatively breeding vertebrates. In African wild dogs (*Lycaon pictus*), dwarf mongooses (*Helogale*
374 *parvula*) and Lake Tanganyika cichlids (*Neolamprologus pulcher*) the relatedness of helpers to the
375 dominant breeders is higher in younger than in older helpers[83–85]. These patterns are driven by turn-
376 over of the dominant individuals in the philopatric sex and dispersal by groups, rather than by
377 individuals, in the dispersing sex[84]. Interestingly, male banded mongooses also have a strict
378 reproductive dominance hierarchy[41], and rather than showing no change in local relatedness with age
379 as our pluralistic breeding model predicted, male banded mongoose local relatedness decreased with

380   age. Dominance may be playing a role in modulating male banded mongoose kinship dynamics.
381   Overall, these reproductive-dominance linked patterns demonstrate that kinship dynamics, perhaps
382   achieved by different mechanisms, are likely to be widespread beyond the examples of group-living
383   pluralistic breeding mammals presented here.

384   In conclusion, predictable age-linked changes in local relatedness can and do occur in social species,
385   and have the potential to profoundly affect behaviour and life history evolution. Kinship dynamics
386   have the potential to be an important but underappreciated force in social evolution.

387 **Methods**

388 *Analytical kinship dynamics model*

389 This model explores a sexually reproducing diploid population with an arbitrarily large number of
390 discrete groups. Each group contains a fixed number of males and females (n_m, n_f). At each discrete
391 time step, individuals: reproduce, disperse, experience mortality and compete for reproduction (in
392 order). During *reproduction,* females produce an arbitrarily large number of offspring with an even
393 sex ratio creating an offspring pool for the group. A proportion *m* of these offspring are fathered by
394 the males in the group, the rest are fathered by males randomly chosen from other groups. Male and
395 female offspring *disperse* from the pool at rate d_m and d_f respectively and immigrate into other groups
396 in the population at random. In turn, offspring dispersing from other groups will disperse into the
397 offspring pool of the focal group. After dispersal, each adult male and female have a probability of
398 *mortality* μ_m and μ_f. Offspring in the offspring pool then *compete* equally to fill the empty male and
399 female slots and restore sex-specific group sizes to n_m and n_f respectively. The remaining offspring in
400 the group then die. More details about the implementation and derivation of this model can be found
401 in the supplementary material (supplementary 1; Supplementary Figure 1).

402 Throughout the manuscript we focus on three illustrative scenarios (but see Supplementary Figure 2
403 for other dispersal scenarios): male-biased dispersal with local mating ($d_f = 0.15$, $d_m = 0.85$, $m =$
404 0.82), female-biased dispersal with local mating ($d_f = 0.85$, $d_m = 0.15$, $m = 0.82$) and bisexual
405 philopatry with out-group mating ($d_f = 0.15$, $d_m = 0.15$, $m = 0$). Male-biased dispersal is the most
406 common dispersal pattern in mammals[98–100]. Female-biased dispersal is relatively rare in mammals but
407 is common in the great apes[57]. Bisexual philopatry is also relatively rare in mammals and is illustrated
408 here with reference to the dispersal pattern found at the matriline level in the multi-level society of
409 resident killer whales[40]. Dispersal rates are chosen to match those illustrated in Johnstone and Cant's
410 (2010)[14] study, representing high but not complete dispersal or philopatry. For the case studies with
411 local mating, we model $m = 0.82$ because this is the mean local mating rate reported for 26 species of
412 group-living mammal[101]. Group size ($n_m + n_f = n$) determines the absolute local relatedness values but
413 does not affect patterns of kinship dynamics while $n_m \approx n_f$. For these case studies we set $n_m = n_f = 5$.

414 We use this model to predict selection on helping and harming given age under different patterns of
415 male and female dispersal. An actor can choose to pay a cost *c* to change the fitness by *b* of their
416 group members. *b* is undirected and applies to all group members at once, or (to put it another way) a
417 randomly chosen group member. We explore the cost-benefit ratio (*c/b*) of actions selected for under
418 different patterns of male and female dispersal. If *b>0* individuals are considered to be helping their
419 group by sacrificing their own fitness to increase the fitness of group members. If *b<0* actors are
420 harming group members, paying a cost to decrease the fitness of group mates. We then use an
421 inclusive fitness approach[6,7] to determine the strength of selection for helping and harming at different
422 ages given rates of male and female dispersal. We explore two measures of fitness: survival and
423 fecundity. Both *c* and *b* are considered in terms of the same measure of fitness.

424 Two other approaches have recently been used to model age-linked changes in local relatedness.
425 Caswell (2019)[15] takes a demographic approach to model the number of various classes of kin a focal
426 individual is likely to have given their age and the demographic parameters of the population. This
427 approach considers the population as a whole, rather than social groups, so is less suited to
428 understanding the role of kinship dynamics in social evolution, as we aim to do here. Rodrigues
429 (2018)[16] uses an inclusive fitness approach, like that used here, to investigate patterns of helping and
430 harming across the lifespan under different patterns of survival and mortality, while dispersal is
431 allowed to evolve independently. This approach gives valuable insights into the coevolution of
432 demography, life history and age-dependent behaviour. However, because the modelled populations
433 are asexually reproducing and haploid, and because dispersal is an evolving rather than imposed trait,
434 it is not suited to predicting patterns of kinship dynamics in real animal populations.

435 *Kinship dynamics in mammals*

436 We calculated patterns of change in relatedness with age in seven mammal populations. Each
437 population has been the subject of a long-term research project, from which the data for this study are
438 derived. The populations are: banded mongooses in Queen Elizabeth National Park, Uganda;
439 chimpanzees in Taï National Park, Ivory Coast; European badgers in Woodchester Park, UK; southern
440 resident-ecotype killer whales in the north-east Pacific ocean; rhesus macaques on Cayo Santiago
441 Island, Puerto Rico, USA; spotted hyenas in the Ngorongoro crater, Tanzania; and yellow baboons in
442 Amboseli National Park, Kenya (further details including data collection and maternity and paternity
443 assignment in each system are in supplementary 2; for sample sizes see Supplementary Table 4).

444 In each system, we calculated the pairwise relatedness of all adults of known age to all adult members
445 of their group in a given year. We focus on adults and consider offspring to be extensions of their
446 parents' fecundity until they reach adulthood and begin reproducing (see Supplementary Figure 3 for
447 relatedness including juveniles). The analysis is annual, with ages and group composition considered
448 to be stable for one calendar year. In all populations, the ages of most individuals are derived from
449 known birth years. For some individuals of unknown age, researchers have been able to infer age
450 based on biological characteristics (see supplementary 2). Pairwise relatedness was calculated by
451 creating pedigrees based on known parents (supplementary 2; see *Calculating relatedness* section). To
452 be consistent with the other systems, for female resident killer whales we only calculate kinship
453 dynamics over their reproductive lifespan (i.e. we do not calculate kinship dynamics for females
454 during their long post-reproductive lifespan) but females of all ages are included in calculations of
455 local relatedness.

456 Local relatedness is defined between group members. We consider a social group to be a set of
457 individuals who mostly interact with each other and rarely with other similar sets of individuals[102,103].
458 With the exception of killer whales, all the species studied here inhabit closed groups and defining
459 group boundaries is relatively straightforward (supplementary 2). Resident killer whales, on the other
460 hand, inhabit a multi-level society with pronounced fission-fusion dynamics[40]. We used binomial
461 mixture modelling to define an individual's local social environment based on their patterns of
462 association[104]. We used the mixture models and 40 years of association data to categorise every
463 pairwise social association in the population into four components[104] (supplementary 2). We consider
464 an individual's local social environment to be the partners with whom they share the strongest
465 category of social bond. These local social environments approximately correspond to matrilines as
466 defined in other studies of this population[40]. For the purposes of this study, these local social
467 environments are equivalent to the groups in the other study populations because they represent the
468 partners who are the main recipients of helping or harming behaviour performed by the focal whale.

469 *Kinship dynamics simulation model*

470 To facilitate comparison with the empirical data, we reformulated our analytical model (see *analytical*
471 *kinship dynamics* model section) as an agent-based simulation model. For each of the seven mammal
472 examples, we used the simulation model to predict the expected pattern of kinship dynamics. The
473 simulation model requires 6 input parameters: male and female dispersal rates, adult group size,
474 juvenile group size, local mating rate, expected adult female lifespan, expected adult male lifespan
475 and age at maturity (see Supplementary Table 5 for detailed definitions). For each species, we defined
476 these six parameters based on the published literature and by deriving them directly from the
477 empirical data (Supplementary Table 6).

478 The agents in the model are adult individuals. Each model iteration is considered to be a year, and
479 agents increase their age each iteration. The agents inhabit groups of fixed size and even sex ratio. At
480 each time step, the agents have a fixed probability of mortality, determined by sex-specific expected
481 lifespan. Dead agents are replaced by either a philopatric or immigrant of the same sex. All agents

482   join a group at a fixed age input as 'age at maturity'. The probability that individuals are philopatric or
483   immigrants is determined by the sex-specific rates of dispersal. Philopatric individuals have a mother
484   chosen from within the group, and the rate of in-group mating determines the probability that the
485   father is also from within the group. Immigrants are unrelated to the other members of their group.
486   The model is run until 2000 individuals have lived in the group- for some species due to
487   computational limitations the target of 2000 was reached by running the model 4 times to 500
488   individuals. Patterns of kinship dynamics from the simulation model are robust and qualitatively
489   identical for 500 and 2000 individuals. If juveniles are being included in the analysis, after the model
490   of adults has run, non-breeding juveniles are added to each group-year *post-hoc*. Juvenile group size is
491   an inputted model parameter and is filled by maturing philopatric individuals and other offspring who
492   are considered to die or disperse before reaching maturity. More details about the formulation of the
493   simulation model can be found in supplementary 3. The model outputs the age and pedigree of all
494   individuals in the group in each model-year. We use this information to calculate kinship dynamics
495   (see *calculating relatedness* and *statistically modelling* sections).

496   *Calculating relatedness*

497   We calculate the pairwise relatedness of an individual to all other members of their group in both the
498   simulated and real data from pedigrees. We developed and applied a novel method to calculate
499   relatedness from pedigrees to overcome two problems that would preclude accurate assessment of
500   relatedness and comparison between species and between real and simulated populations: (1)
501   pedigrees are of different depth (i.e. number of known ancestral generations), (2) pedigrees are
502   sometimes incomplete. More classes of relative can be distinguished in deeper pedigrees which will
503   increase observed local relatedness. Incomplete pedigrees - pedigrees where some individuals have
504   missing parents – can result in an underestimation of local relatedness. For example, if two
505   individuals have no known common ancestors but one has an unknown parent, they could be siblings.
506   Distinguishing individuals of unknown relatedness from true non-relatives is important to properly
507   estimate relatedness in the empirical data where unknown pairwise relatedness is common. For this
508   study, we developed a methodological pipeline in R to (1) limit all pedigrees in all species and
509   simulations to a depth of 2 and (2) identify individuals of unknown pairwise relatedness. This pipeline
510   was developed in R using the igraph and kinship2 packages[105,106] and is incorporated into a new
511   package: comparekin (github.com/samellisq/comparekin).

512   Local relatedness is the mean pairwise relatedness between an individual and other members of the
513   group. In the simulations, this can be calculated directly because all pedigrees are complete. However,
514   logistical limitations in real data mean that pedigrees are often incomplete, and taking a mean of an
515   individual's known pairwise relatedness's $\bar{r}$ will misrepresent the true local relatedness (r). We,
516   therefore, calculate an estimated local relatedness ($\hat{r}$) – and the error around that estimate (σ_r) - for
517   each individual, given the number of other group members to whom their relatedness is unknown (u).

518   The estimated local relatedness is calculated as a weighted mean of the potential local relatednesses
519   (R). R_j is the conditional true local relatedness if j of the u unknown pairwise relatednesses are kin
520   (equation 1).

521   equation 1.

522 $$R_j = \frac{\Sigma\bar{r} + (j)(\bar{r}_{>0}) + (u - j)(0)}{g - 1}$$

523   Where $\bar{r}_{>0}$ is the mean of all pairwise relatedness's in the population that are known and not 0, $\Sigma\bar{r}$ is
524   the total known local relatedness, and g is the number of individuals in the group. Weights are
525   calculated by using binomial theorem to determine (given $p = 0.2$) the probability that j of the n
526   unknown relatednesses are kin (equation 2).

527   equation 2

528
$$w_j = \binom{u}{j} \cdot 0.2^j \cdot 0.8^{u-j}$$

535

529   p=0.2 is likely to overestimate the number of relatives, and therefore lead to an overestimate of local
530   relatedness because it is likely that most unknown relatedness pairs are non-relatives. However, in the
531   absence of any information, we use $p = 0.2$ as a simple assumption. Changing this assumption
532   rescales local relatedness but does not change the observed patterns of kinship dynamics. We use the
533   true value of local relatedness and weights to calculate the estimated local relatedness as a weighted
534   mean (equation 3).

536   equation 3.

538
$$\hat{r} = \frac{\sum_{j=0}^{u} w_j R_j}{\sum_{j=0}^{u} w_j}$$

537

539

540   We also calculate the weighted standard deviation σ_r using the same inputs implemented in the Hmsic
541   package in R[107]. We use this pipeline to calculate an estimated local relatedness ($\hat{r}$) and the error
542   around that estimate (σ_r) for every individual in each year. If all relatednesses are known to all of an
543   individuals group mates $\sigma_r = 0$, however, to facilitate statistical modelling this error is assumed to be
544   an arbitrarily small non-zero number. Individuals who have no known pairwise relatednesses (i.e. all
545   their pairwise relatedness' are unknown) are not included in the analysis.

546   *Statistical modelling*

547   We use a hierarchical Bayesian framework to model change in local relatedness with age in both the
548   real and simulated data. For the real data, because the error is generated by an additive process we
549   model the estimated local relatedness ($\hat{r}$) as a sample from a normally distributed function centred on
550   the true local relatedness (r) with standard deviation of σ_r. The true local relatedness (r) is considered
551   to be drawn from a beta distribution with a mean of $\bar{p}$ and variance θ. Mean local relatedness at
552   datapoint i ($\bar{p}_i$) is modelled as a function group size (G_i) and sex-specific age (A_i), with an intercept
553   for sex ($s_{sid[i]}$) and an individual-level intercept for individual id ($\alpha_{id[i]}$; equation 4; supplementary 4).
554   All parameters have weakly informative priors (supplementary 4). The same framework is used to
555   model the simulated data but without the estimated relatedness step or the group size term because
556   pedigrees are complete and the group size is constant (supplementary 4).

557   equation 4

564
$$\hat{r} \sim Normal(r, \sigma_r)$$
565
$$r \sim Beta(\bar{p}, \theta)$$
566
$$logit(\bar{p}_i) = \alpha_{id[i]} + s_{sid[i]} + \beta_{sid[i]}A_i + \gamma G_i$$
558
$$\alpha_j \sim Normal(\bar{\alpha}, \sigma_a) \; for \; j = 1..n$$

559

560   Where n is the number of individuals (id), $\bar{\alpha}$ is a shared population-level intercept for individual and
561   *sid* is a numeric index for sex. We fit models using Hamiltonian Monte Carlo with 4 chains
562   implemented in R via the RStan package with additional functionality from the rethinking
563   package[108,109].Supplementary Figure

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Author contributions

SE, RAJ, MAC, DWF, MNW and DPC conceived and designed the study programme. SE designed and implemented the analysis, made the figures and wrote the first draft of the manuscript with input from RAJ, MAC, DWF, MNW and DPC. RAJ designed and implemented the analytical model with MAC and with input from SE, DWF, MNW and DPC. Data from long-term research projects were contributed, collected and managed by: MAC, MM, HJN, FJT (banded mongoose data); CC, LV, RMW (chimpanzee data); CHB, RJD, RAM (European badger data); KCB, DKE, MNW (killer whale data); LJNB (rhesus macaque data); ED, OPH (spotted hyena data) and SCA (yellow baboon data). All authors contributed to later drafts of the manuscript and approved the manuscript for publication.

Data availability

Data to reproduce these analyses are available at: osf.io/pzfex. Anonymised data to derive kinship dynamics are included for: banded mongooses, chimpanzees, killer whales and spotted hyena. Data sharing agreements mean that for the remaining species, anonymised data to reproduce the analysis needs to be requested from the corresponding author, all other forms of data request should be addressed to the manager of the system in question.

Code availability

Code to reproduce these analyses are available at: osf.io/pzfex. The repository includes: a Mathematica file to run and reproduce the mathematical model; R code to implement the kinship dynamics simulation model; and R code to analyse both the simulation and observed kinship dynamics data. A simplified version of the simulation model can be explored at samellisq.shinyapps.io/kinship_dynamics_shinyapp_basic/ or downloaded from github.com/samellisq/kinship_dynamics_shinyapp. In addition, an R package, comparekin, created as part of this study, can be accessed at github.com/samellisq/comparekin.

612   **Competing interests**

613   The authors declare no competing interests.

614

615

616 **Tables**

617 Table 1. Species-specific dispersal and local mating input parameters for the simulation model and used to
618 generate predicted kinship dynamics. References and other input parameters can be found in Supplementary
619 Table 6.

Species	Female dispersal rate	Male dispersal rate	Local mating rate
Banded mongoose	0.12	0.12	0.64
Chimpanzee	0.89	0	0.93
European badger	0.23	0.45	0.52
Killer whale	0	0	0.02
Rhesus macaques	0.05	0.79	0.13
Spotted hyena	0	0.91	0.96
Yellow baboon	0	0.8	1

620

621 Table 2. Examples of behaviours that could be affected by kinship dynamics. The 'examples of age-linked change in the behaviour' highlights empirical
622 examples of these types of behaviour changing with age. These empirical examples demonstrate that the behaviour example in question can change with age-
623 further work is required to establish if the changes fit the patterns expected under kinship dynamics. Only in two studies (†) have the changes been explicitly
624 linked to kinship dynamics.

BEHAVIOUR EXAMPLES	POTENTIAL ROLE OF KINSHIP DYNAMICS	EXAMPLES OF AGE-LINKED CHANGE IN THE BEHAVIOUR
COOPERATION/HELPING	The maintenance of cooperation depends on the costs and benefits of the behaviour and the relatedness between the partners[1]. Helping can involve both directed cooperation with a particular partner or undirected help, such as investment in common goods. Kinship dynamics allow selection for investment in helping to change with age.	- In Hadza hunter-gatherers, females increase time spent foraging with age whereas male foraging activity peaks in late adolescence[52]. - Younger male meerkats (*Suricata suricatta*) spend more time mobbing potential predators than older male meerkats[86]. - Banded mongooses, of both sexes, in good condition, decrease their probability of providing cooperative offspring care with increasing age[87]. - Older female killer whales are more likely to share food than younger female killer whales[88]. - Male spotted hyenas with longer group tenures have higher local relatedness and receive more social support during intragroup conflict[24].
AGGRESSION/HARMING	The payoff of aggression towards or harm inflicted on social partners depends in part on the relatedness between the partners[1]. Kinship dynamics change the payoff from aggression with age and allows selection for systematic change with age.	- Prime-aged female Columbian ground squirrels (*Urocitellus columbianus*) show more aggression to more partners than younger females (some evidence of a decreased aggression in older females relative to prime-age)[89]. - Older meerkats have higher pairwise rates of aggressive interactions than younger meerkats[90].
REPRODUCTION	Reproduction is a form of generalised harm. By reproducing into a group, an individual increases competition for group resources at the expense of other group members[6,7]. Kinship dynamics allow for selection on the payoff of inflicting this generalised harm with age.	- In humans and killer whales, females reproducing at the same time as their daughters suffer increased infant mortality risk[21†, 51†].
KIN DISCRIMINATION/ BEHAVIOURAL SPECIFICITY	Exhibited social behaviours are linked to within-group relatedness[11,13]. Specifically, high local relatedness is linked to generalised helping behaviours, while low local relatedness is linked to increased kin discrimination in social partners[11]. Kinship dynamics allows selection for behavioural specificity to change systematically with age.	- Male chimpanzees become more socially selective (spend time with a smaller circle of social partners) as they become older[91]. - Barbary macaques (*Macaca sylvanus*), of both sexes, decrease their rate of social affiliation as they age[92].
EVICTION & SECONDARY DISPERSAL	Inbreeding risk[93] and competition with relatives[11,13] can be resolved by dispersing ('voluntarily' leaving a group) or eviction (being ejected from a group). Kinship dynamics change the payoff from dispersing predictably with age or group tenure.	- Male secondary dispersal in black-tailed prairie dogs (*Cynomys ludovicianus*) and yellow baboons coincides with their philopatric daughters reaching reproductive maturity[34,94]. - Eviction probability in banded mongooses of both sexes peaks at age 2-3 before declining. For males, there is an increased eviction risk in very old males[41].
EXTRA-GROUP MATING	Inclusive fitness gains can be an important part of the payoff from extra-group mating. For example, when local relatedness is high the risks of inbreeding will be high. Kinship dynamics can change the risk of inbreeding predictably with age. The payoff from extra-group mating may, therefore, also change with age selecting for different mating decisions in animals of different ages.	- Female banded mongooses demonstrate an increased probability of mating outside their group as they age[95].
INTERGROUP CONFLICT	Local relatedness can regulate the costs and benefits of engaging in risky intergroup aggressive interactions[96]. Kinship dynamics will modulate this payoff from engaging in intergroup conflict with age.	- The probability of male grey wolves (*Canis lupus*) engaging in aggressive chases during intergroup encounters increases with age[97].

625

626 **Figure legends**

627 Figure 1. Modelled sex differences in kinship dynamics under three scenarios: male-biased dispersal with local
628 mating ($d_f = 0.15$, $d_m = 0.85$, $m = 0.82$, $n = 10$, $\mu = 0.1$), female-biased dispersal with local mating ($d_f = 0.85$, d_m
629 $= 0.15$, $m = 0.82$, $n = 10$, $\mu = 0.1$) and bisexual philopatry with out-group mating ($d_f = 0.15$, $d_m = 0.15$, $m = 0$, n
630 $= 10$, $\mu = 0.1$). Local relatedness is the mean relatedness of an individual of that sex-age to all other individuals
631 in their group (of both sexes). Age is scaled relative to mean generation time, where age 0 is the age of maturity
632 and dispersal. Only patterns up to the third generation are plotted. The model assumes an arbitrarily large
633 population (and therefore with no population-size effects) of social groups of size n with an even sex ratio. The
634 model iterates through fixed times steps. At each time step, individuals have a fixed probability of mortality (μ),
635 and vacated slots are filled by a new individual of the same sex. Replacements have a *1-d* probability of being
636 offspring of group females and have a *m* probability of being fathered by in-group males (see methods;
637 Supplementary Figure 1).

638

639   Figure 2. Predicted (left-hand panels, orange outline) and observed (right-hand panels, black outline) kinship
640   dynamics for males (green) and females (purple) in 7 species of group-living mammal: banded mongooses (A),
641   chimpanzees (B), European badgers (C), killer whales (D), rhesus macaques (E), spotted hyenas (F) and yellow
642   baboons (G). In all panels, line and ribbon show mean changes in local relatedness with age generated as the
643   posterior mean (+/- 95% credible interval) from a linear model, incorporating error around local relatedness
644   estimation.   Predictions are generated from a simulation model calculating local relatedness change with age,
645   parametrised by rates of male and female dispersal and local mating. Plotted relationships result from a linear
646   model applied to the output of the simulation model. Observed data are derived from long term studies of the
647   species. In both the predicted and observed panels local relatedness is calculated as the mean pairwise
648   relatedness from an individual to all other members of their group. Accounting for unknown relatedness' results
649   in an estimated local relatedness with error (points and error) in the observed data. Different relatedness scales
650   in the simulated and observed axis are consequences of group size and relatedness assumptions, changing these
651   assumptions changes the y axis scales but does not change the patterns of kinship dynamics. For male
652   chimpanzees and male killer whales, maximum age represents an absence of older individuals in the data rather
653   than their maximum lifespan. For female killer whales, we only calculate female kinship dynamics over the
654   reproductive lifespan and not over their post-reproductive lifespan (see methods). For the rhesus macaque
655   observed data a number of outliers with relatedness above 0.06 are not included in the plot. Panel H compares
656   species and sexes and shows the expected percentage change in local relatedness for an adult from age at
657   maturity to the expected adult lifespan in the species-sex calculated from the distribution of β slope parameters
658   Bayesian hierarchical model fitted to the observed data. Distribution widths are scaled within species-sex for
659   visibility. All silhouette images except the killer whale are taken from PhyloPic[44] and are in the public domain,
660   the killer whale image is original.

661

662

663   Figure 3. Selection on group directed behaviours given kinship dynamics under three dispersal scenarios for a)
664   survival and, b) fecundity. Age is scaled relative to mean generation time, where age 0 is the age of maturity and
665   dispersal. In both a and b, the selective landscape for females is shown on the upper row (blue lines and areas)
666   and males are on the lower row (green lines and areas). The lines and areas on each panel show the absolute cost
667   (c) to benefit (b) ratio under which an outcome will be favoured by selection. c is borne by the individual while
668   b applies to the whole group. In panel A, c and b are in terms of survival (a cost to an individuals' own survival
669   to increase or decrease the survival of group mates), and in panel B c and b are considered in terms of fecundity
670   (a cost to an individuals' own fecundity to increase or decrease the fecundity of their group mates). c always
671   has a positive value, whereas b can be either positive – the behaviour helps their group mates – or negative – the
672   behaviour harms their group mates. Therefore, areas above 0 c/b ratio indicate selection for helping behaviours,
673   areas below 0 for harm. In each panel, behaviours with a cost/benefit outcome between the line and c/b=0 (filled
674   areas) are selected. Lines distant from c/b=0 indicate that behaviours resulting in a relatively smaller b for a
675   larger c will be selected. While lines close to c/b=0 indicate that behaviours will require either a relatively small
676   c or a large b to be selected. The direction a line trends, therefore, indicates how selection for behaviours will
677   change with age. Model parameters in all dispersal scenarios are the same as those used in figure 1.

678

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915

Figure 1

Figure 2

A: Survival

Male-biased dispersal | Female-biased dispersal | Bisexual philopatry

B: Fecundity

Male-biased dispersal | Female-biased dispersal | Bisexual philopatry

Age (relative to mean generation time)

Figure 3

Patterns and consequences of age-linked change in local relatedness in animal societies
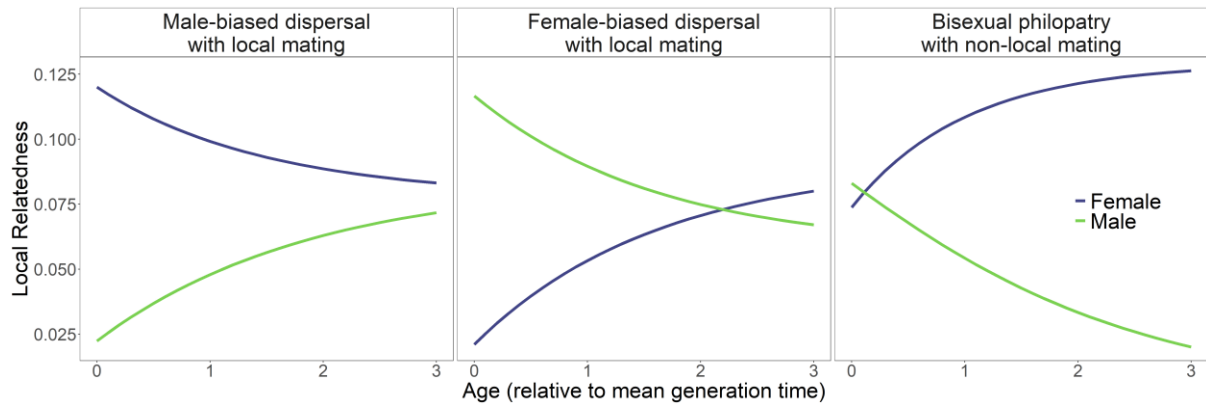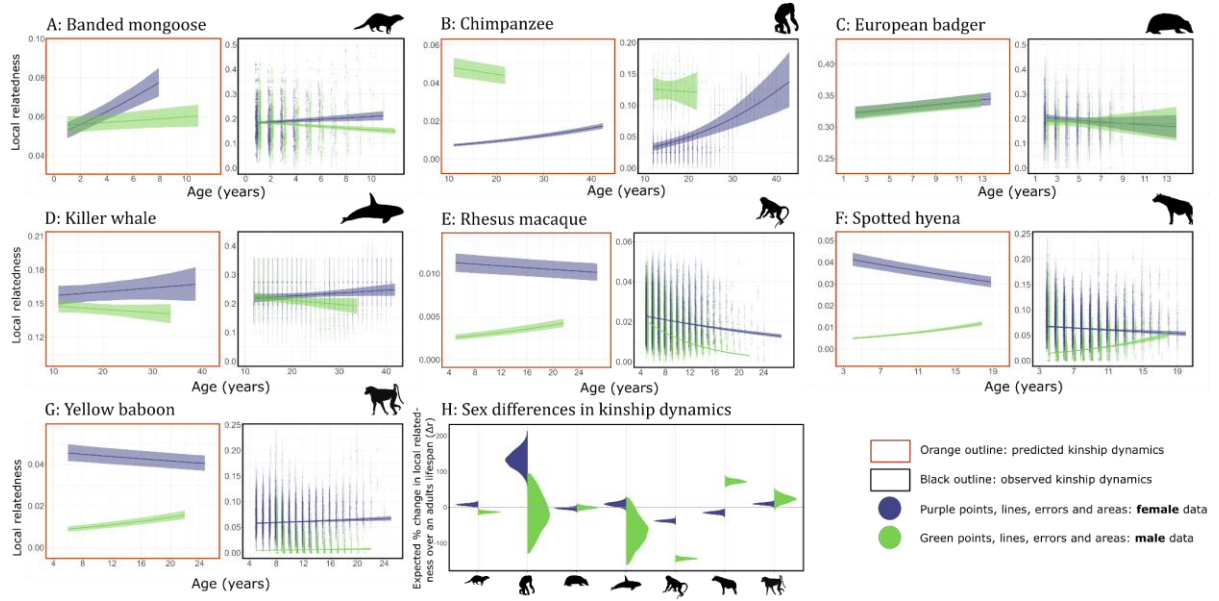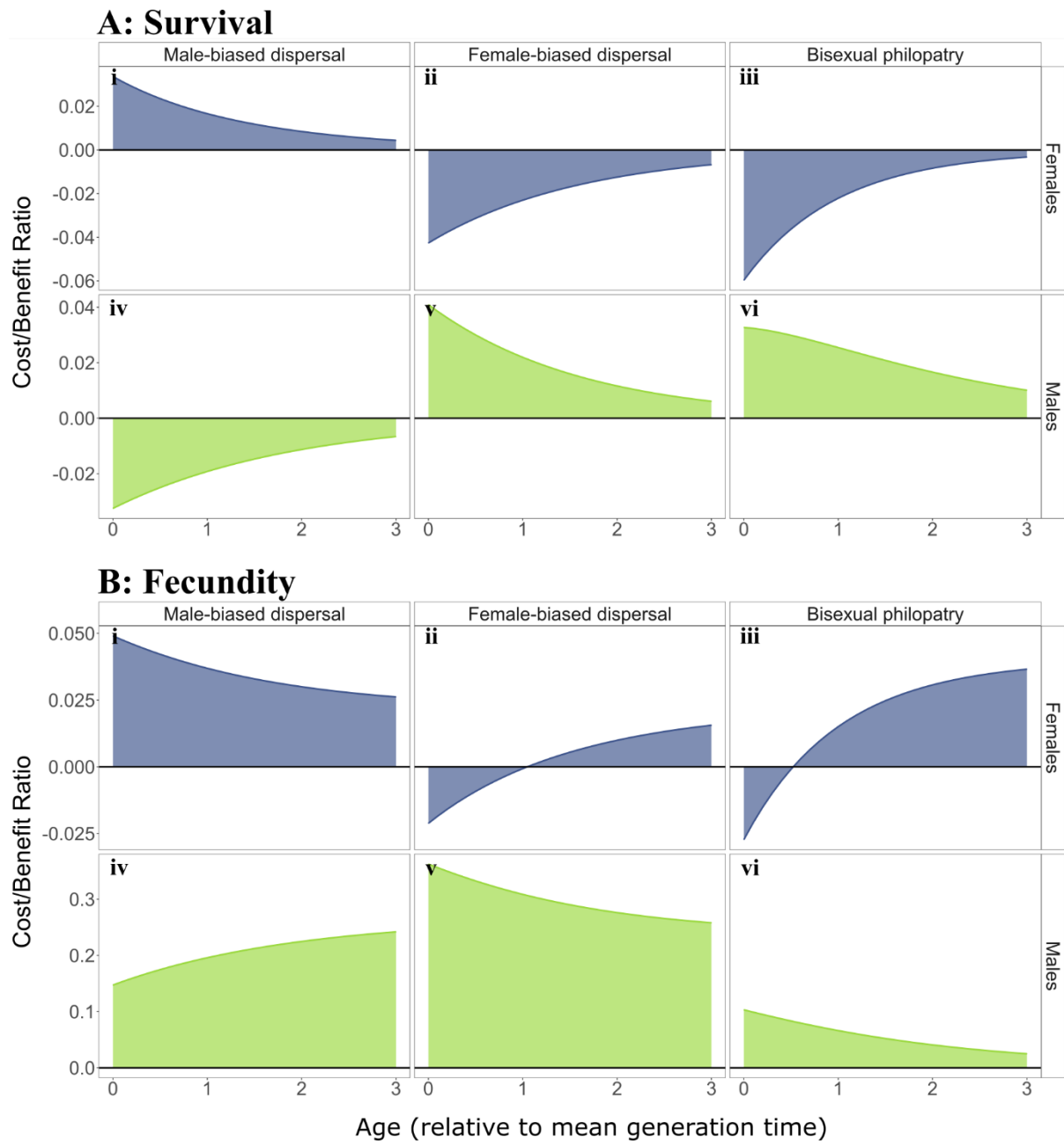
Supplementary 1: Mathematical Model

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Patterns and consequences of age-linked change in local relatedness in animal societies - Appendix

We focus on an infinite, diploid, sexual population, divided into discrete groups, each of which contains n_f established female and n_m established male breeders. Time proceeds in discrete steps. In each such time-step, every female breeder produces a large number of offspring, of which a fraction m are each fathered by a local male breeder chosen at random from the same group as their mother, and the remaining fraction $1-m$ are each fathered by a non-local male breeder chosen at random from some other group. We suppose that there is a fixed primary sex-ratio, but the precise value of this ratio does not affect our calculations. After offspring are produced, a fraction d_f of female offspring each disperse to another group, chosen at random from the population at large, while the remaining fraction $1 - d_f$ remain in their natal group. Likewise, a fraction d_m of male offspring each disperse to another group, chosen at random from the population at large, while the remaining fraction $1 - d_m$ remain in their natal group. Following offspring dispersal, established breeders each die with a probability of μ_f for females and μ_m for males. Offspring in a group, both native-born and immigrant, then compete (in a fair lottery) for the breeding vacancies created by the death of established adults in the group. Those offspring that fail to obtain a breeding vacancy die, and the cycle then repeats.

Mean relatedness among breeders

Let g_f and g_m denote the probability of identity by descent of two homologous gene copies sampled randomly (with replacement) from the same individual female or male, respectively (chosen at random from among their sex within a group). Similarly let g_{ff} denote the probability of identity by descent for gene copies chosen one from each of two distinct females in the same group (sampled randomly without replacement), g_{mm} for gene copies chosen one from each of two distinct males in the same group (sampled randomly without replacement), and g_{fm} for gene copies chosen one from a female and one from a male in the same group (each sampled randomly from among their sex).

The above probabilities then change from one time step to the next according to the following equations:

$$g'_f = \mu_f \frac{1}{2} \left(1 + m g_{fm} \right) + (1 - \mu_f) g_f \tag{1}$$

$$g'_m = \mu_m \frac{1}{2} \left(1 + m g_{fm} \right) + (1 - \mu_m) g_m \tag{2}$$

$$g'_{ff} = \mu_f^2(1-d_f)^2\frac{1}{4}\left(\left(\frac{1}{n_f}g_f + \frac{n_f-1}{n_f}g_{ff}\right) + 2mg_{fm} + m^2\left(\frac{1}{n_m}g_m + \frac{n_m-1}{n_m}g_{mm}\right)\right)$$
$$+ 2\mu_f(1-\mu_f)(1-d_f)\frac{1}{2}\left(\left(\frac{1}{n_f}g_f + \frac{n_f-1}{n_f}g_{ff}\right) + mg_{fm}\right)$$
$$+ (1-\mu_f)^2 g_{ff}$$

$$(3)$$

$$g'_{fm} = \mu_f\mu_m(1-d_f)(1-d_m)\frac{1}{4}\left(\left(\frac{1}{n_f}g_f + \frac{n_f-1}{n_f}g_{ff}\right) + 2mg_{fm} + m^2\left(\frac{1}{n_m}g_m + \frac{n_m-1}{n_m}g_{mm}\right)\right)$$
$$+ \mu_f(1-\mu_m)(1-d_f)\frac{1}{2}\left(m\left(\frac{1}{n_m}g_m + \frac{n_m-1}{n_m}g_{mm}\right) + g_{fm}\right)$$
$$+ (1-\mu_f)\mu_m(1-d_m)\frac{1}{2}\left(\left(\frac{1}{n_f}g_f + \frac{n_f-1}{n_f}g_{ff}\right) + mg_{fm}\right)$$
$$+ (1-\mu_f)(1-\mu_m)g_{fm}$$

$$(4)$$

$$g'_{mm} = \mu_m^2(1-d_m)^2\frac{1}{4}\left(\left(\frac{1}{n_f}g_f + \frac{n_f-1}{n_f}g_{ff}\right) + 2mg_{fm} + m^2\left(\frac{1}{n_m}g_m + \frac{n_m-1}{n_m}g_{mm}\right)\right)$$
$$+ 2\mu_m(1-\mu_m)(1-d_m)\frac{1}{2}\left(m\left(\frac{1}{n_m}g_m + \frac{n_m-1}{n_m}g_{mm}\right) + g_{fm}\right)$$
$$+ (1-\mu_m)^2 g_{mm}$$

$$(5)$$

To illustrate the derivation of these equations, consider (3). If gene copies are sampled from two distinct adult females, then there are three cases to consider: (i) with probability μ_f^2 both females are newly born in the current time-step, (ii) with probability $2\mu_f(1-\mu_f)$, one female is newly born and the other a survivor from the previous time-step, (iii) with probability $(1-\mu_f)^2$ both are survivors. In case (i), the two gene copies may prove identical by descent (IBD) only if both newly-born females are of local origin, with probability $(1-d_f)^2$. Assuming both females are local, then there are three sub-cases to consider: (a) With probability $\frac{1}{4}$ both derived their sampled gene copy from their mother; in this case, with probability $\frac{1}{n_f}$ they share the same mother, and the probability that the two gene copies are IBD is g_f, while with probability $\frac{n_f-1}{n_f}$ they have distinct mothers, and the probability that the two gene copies are IBD is g_{ff}. (b) With probability $\frac{1}{2}$, one female derived her gene copy from her mother, and the other from her father. In this case the probability that both are IBD is equal to the probability of local mating m, multiplied by g_{fm}. (c) With probability $\frac{1}{4}$, both females derived their sampled gene copy from their father; in this case, the two gene copies may prove IBD only if both fathers were local, with probability

m^2, in which case with probability $\frac{1}{n_m}$ the two females share the same (local) father, and the probability that the two gene copies are IBD is g_m, while with probability $\frac{n_m-1}{n_m}$ they have distinct (local) fathers, and the probability that the two gene copies are IBD is g_{mm}. Turning to case (ii), if one female is a survivor and the other newly-born, then the gene copies may prove IBD only if the latter is of local origin, with probability $(1-d_f)$. If she is local, then there are two sub-cases to consider: (a) With probability $\frac{1}{2}$ she derived her sampled gene copy from her mother; in this case, with probability $\frac{1}{n_f}$ her mother was the surviving female, and the probability that both gene copies are IBD is g_f, while with probability $\frac{n_f-1}{n_f}$ her mother was distinct from the surviving female, and the probability that both gene copies are IBD is g_{ff}. (b) With probability $\frac{1}{2}$ the newly-born female derived her sampled gene copy from her father; in this case, the probability that both gene copies are IBD is equal to the probability of local mating m, multiplied by g_{fm}. Finally, in case (iii), if both females are survivors, then the probability that their sampled gene copies are IBD is simply g_{ff}.

Setting $g'_f = g_f$, $g'_m = g_m$, $g'_{ff} = g_{ff}$ and so on, we can solve for the values of the various probabilities at demographic equilibrum. We can then derive mean relatedness coefficents for a randomly chosen individual of sex $i(\in f, m)$ to a distinct, randomly-chosen individual of sex $j(\in f, m)$ in the same group, denoted r_{ij}, which are given by

$$r_{ff} = \frac{g_{ff}}{g_f}, r_{mf} = \frac{g_{fm}}{g_f}, r_{fm} = \frac{g_{fm}}{g_m}, r_{mm} = \frac{g_{mm}}{m} \tag{6}$$

(note that, given our assumptions, $g_f = g_m$ and consequently $r_{mf} = r_{fm}$).

Age-specific breeder relatedness

Now, in a population at demographic equilibrium, let g_{ff}^a denote the probability that two homologus gene copies sampled randomly from two different females in the same group are identical by descent, given that one of the females is of age a, and g_{mm}^a the equivalent probability for gene copies from two different males, given that one of them is of age a. Similarly, let g_{mf}^a denote the probability for gene copies sampled one from a random male (of whatever age) and one from a female of age a, and g_{fm}^a denote the probability for gene copies sampled one from a random female (of whatever age) and one from a male of age a. Then, for newly established individuals of age $a = 0$, we have

$$g_{ff}^0 = \mu_f(1-d_f)^2 \frac{1}{4}\left((\frac{1}{n_f}g_f + \frac{n_f-1}{n_f}g_{ff}) + 2mg_{fm} + m^2(\frac{1}{n_m}g_m + \frac{n_m-1}{n_m}g_{mm})\right)$$
$$+ (1-\mu_f)(1-d_f)\frac{1}{2}\left((\frac{1}{n_f}g_f + \frac{n_f-1}{n_f}g_{ff}) + mg_{fm}\right) \tag{7}$$

3

$$g_{mf}^0 = \mu_m(1-d_f)(1-d_m)\frac{1}{4}\left(\left(\frac{1}{n_f}g_f + \frac{n_f-1}{n_f}g_{ff}\right) + 2mg_{fm} + m^2\left(\frac{1}{n_m}g_m + \frac{n_m-1}{n_m}g_{mm}\right)\right)$$
$$+ (1-\mu_m)(1-d_f)\frac{1}{2}\left(m\left(\frac{1}{n_m}g_m + \frac{n_m-1}{n_m}g_{mm}\right) + g_{fm}\right) \tag{8}$$

$$g_{fm}^0 = \mu_f(1-d_f)(1-d_m)\frac{1}{4}\left(\left(\frac{1}{n_f}g_f + \frac{n_f-1}{n_f}g_{ff}\right) + 2mg_{fm} + m^2\left(\frac{1}{n_m}g_m + \frac{n_m-1}{n_m}g_{mm}\right)\right)$$
$$+ (1-\mu_f)(1-d_m)\frac{1}{2}\left(\left(\frac{1}{n_f}g_f + \frac{n_f-1}{n_f}g_{ff}\right) + mg_{fm}\right) \tag{9}$$

$$g_{mm}^0 = \mu_m(1-d_m)^2\frac{1}{4}\left(\left(\frac{1}{n_f}g_f + \frac{n_f-1}{n_f}g_{ff}\right) + 2mg_{fm} + m^2\left(\frac{1}{n_m}g_m + \frac{n_m-1}{n_m}g_{mm}\right)\right)$$
$$+ (1-\mu_m)(1-d_m)\frac{1}{2}\left(m\left(\frac{1}{n_m}g_m + \frac{n_m-1}{n_m}g_{mm}\right) + g_{fm}\right) \tag{10}$$

For individuals of older ages

$$g_{ff}^a = \mu_f(1-d_f)\frac{1}{2}\left(\left(\frac{1}{n_f}g_f + \frac{n_f-1}{n_f}g_{ff}^{a-1}\right) + mg_{mf}^{a-1}\right) + (1-\mu_f)g_{ff}^{a-1} \tag{11}$$

$$g_{mf}^a = \mu_m(1-d_m)\frac{1}{2}\left(\left(\frac{1}{n_f}g_f + \frac{n_f-1}{n_f}g_{ff}^{a-1}\right) + mg_{mf}^{a-1}\right) + (1-\mu_m)g_{mf}^{a-1} \tag{12}$$

$$g_{fm}^a = \mu_f(1-d_f)\frac{1}{2}\left(m\left(\frac{1}{n_m}g_m + \frac{n_m-1}{n_m}g_{mm}^{a-1}\right) + g_{fm}^{a-1}\right) + (1-\mu_f)g_{fm}^{a-1} \tag{13}$$

$$g_{mm}^a = \mu_m(1-d_m)\frac{1}{2}\left(m\left(\frac{1}{n_m}g_m + \frac{n_m-1}{n_m}g_{mm}^{a-1}\right) + g_{fm}^{a-1}\right) + (1-\mu_m)g_{mm}^{a-1} \tag{14}$$

To illustrate the derivation of these equations consider (11). Here, one gene copy is sampled from a focal female of age $a(>0)$ and another from a randomly chosen other female in the same group. There are two cases to consider: (i) With probability μ_f the other female is newly born, while (ii) with probability

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$1 - \mu_f$ she is a survivor from the previous time step. In case (i), the two gene copies may prove IBD only if the newly born female is of local origin, with probability $(1 - d_f)$. If she is local, then there are two sub-cases to consider: (a) With probability $\frac{1}{2}$ her gene copy was derived from her mother; in this case, with probability $\frac{1}{n_f}$ her mother was the focal female of age a, and the gene copies are IBD with probability g_f, while with probability $\frac{n_f - 1}{n_f}$ her mother was a distinct local female, and the gene copies are IBD with probability g_{ff}^{a-1} (the probability of identity between gene copies sampled from the focal female and another local female in the previous time step, when the focal female was of age $a - 1$). (b) With probability $\frac{1}{2}$ the newly born female's gene copy was derived from her father; in this case, the probability that both gene copies are IBD is equal to the probability of local mating m, multiplied by g_{mf}^{a-1} (the probability of identity between gene copies sampled from the focal female and a local male in the previous time step, when the focal female was of age $a - 1$). Lastly, in case (ii), if the other female is a survivor from the previous time step, then the probability that the two gene copies are IBD is equal to g_{ff}^{a-1} (the probability of identity between gene copies sampled from the focal female and another local female in the previous time step, when the focal female was of age $a - 1$).

Through iterative application of the above one can determine probabilities of allele sharing for any given age a. Finally, one can then derive relatedness coefficients conditional on age

$$r_{ff}^a = \frac{g_{ff}^a}{g_f}, r_{mf}^a = \frac{g_{mf}^a}{g_f}, r_{fm}^a = \frac{g_{fm}^a}{g_m}, r_{mm}^a = \frac{g_{mm}^a}{g_m} \tag{15}$$

A note on methods of calculation

To facilitate calcuation of age-specific relatedness values, we express the above equations specifying probabilities of identity by descent for gene copies sampled from older individuals in the form

$$\begin{pmatrix} g_{ff}^a \\ g_{mf}^a \\ 1 \end{pmatrix} = F \begin{pmatrix} g_{ff}^{a-1} \\ g_{mf}^{a-1} \\ 1 \end{pmatrix} \tag{16}$$

where

$$F = \begin{pmatrix} \mu_f(1-d_f)\frac{1}{2}\frac{n_f-1}{n_f} + (1-\mu_f) & \mu_f(1-d_f)\frac{1}{2}m & \frac{\mu_f(1-d_f)g_f}{2n_f} \\ \frac{\mu_m(1-d_m)(n_f-1)}{2n_f} & 1 - \mu_f + \mu_f(1-d_f)m\frac{1}{2} & \frac{mu_m(1-d_m)g_m}{2n_f} \\ 0 & 0 & 1 \end{pmatrix} \tag{17}$$

and

$$\begin{pmatrix} g_{mm}^a \\ g_{fm}^a \\ 1 \end{pmatrix} = M \begin{pmatrix} g_{mm}^{a-1} \\ g_{fm}^{a-1} \\ 1 \end{pmatrix} \tag{18}$$

where

$$M = \begin{pmatrix} \mu_m(1-d_m)\frac{1}{2}m\frac{n_m-1}{n_m} + (1-\mu_m) & \mu_m(1-d_m)\frac{1}{2} & \frac{\mu_m(1-d_m)mg_m}{2n_m} \\ \frac{\mu_f(1-d_f)m(n_m-1)}{2n_m} & 1-\mu_f+\mu_f(1-d_f)\frac{1}{2} & \frac{mu_f(1-d_f)mg_f}{2n_m} \\ 0 & 0 & 1 \end{pmatrix} \tag{19}$$

This allows us to write

$$\begin{pmatrix} g_{ff}^a \\ g_{mf}^a \\ 1 \end{pmatrix} = F^a \begin{pmatrix} g_{ff}^0 \\ g_{mf}^0 \\ 1 \end{pmatrix} \tag{20}$$

and

$$\begin{pmatrix} g_{mm}^a \\ g_{fm}^a \\ 1 \end{pmatrix} = M^a \begin{pmatrix} g_{mm}^0 \\ g_{fm}^0 \\ 1 \end{pmatrix} \tag{21}$$

from which we obtain closed-form expressions for g_{ff}^a, g_{mf}^a etc.

Helping and harming

Having determined patterns of age-linked change in local relatedness, we now turn to consider how these influence selection for helping and harming. To this end, we focus on a mutant allele expressed by females or by males of a given age, the average effect of which is to inflict some small cost on the focal actor, and to impose a cost or benefit on the recipients of its actions (we assume additive allelic effects). These costs and benefits (to both actor and recipients) might take the form of changes in mortality or fecundity; specifically, we focus on either (i) an allele that incurs a small increase of c in the actor's mortality risk during the time-step in which it is expressed, and induces a reduction of b in the mortality risk of a recipient of specified sex (other than the actor) in the local group, or (ii) an allele that incurs a small decrease c in the actor's fecundity (relative to its baseline value), and induces an increase of b in the fecundity of a recipient of the specified sex (other than the actor) in the local group (again relative to the baseline fecundity value). In either case, a positive value of b

denotes a 'helpful' act, and a negative value of b a 'harmful' act. We quantify the strength of selection for helping or harming as the critical ratio of c relative to the absolute magnitude of b below which the allele is favoured by selection.

The above summary requires some futher explanation of what we mean by male 'fecundity'. We assume female demographic dominance, such that males merely compete for paternity of offspring produced by females. The probability that an offspring is sired by any given male is then proportional to his 'mating output', multiplied by a factor m for local males and $1 - m$ for non-local males (so that m, as defined above, specifies the probability that an offspring is the product of a local mating). Consequently, while fecundity costs and benefits incurred by or imposed upon females alter the number of young produced within a group, fecundity costs and benefits incurred by or imposed upon males merely affect their mating output, and thereby influence their expected paternity.

To determine the strength of selection for helping or harming we adopt an inclusive fitness approach (see Lehmann & Rousset 2020 for a very general justification of the application of inclusive fitness methods to evolution in a group-structured population such as we consider here). Below, we (i) derive the reproductive values of females and males, (ii) use these to construct expressions for the fitness of a focal female or male as a function of its own fecundity and mortality, and the fecundities and mortalities of others in its focal group, and (iii) use these expressions to determine the inclusive fitness impact of a mutant allele with helpful or harmful effects (on either fecundity or mortality) expressed by females or males of a given age and directed at either female or male recipients. This allows us to determine the strength of selection for helping or harming (as defined above), and how this changes with age for females and males.

Reproductive values

Let w_{ff} and w_{mf} denote the expected number of gene copies in females and males in the next time step derived (via survival or reproduction) from a gene copy in a female in the current timestep; likewise let w_{fm} and w_{mm} denote the expected number of gene copies in females and males in the next time step derived (via survival or reproduction) from a gene copy in a male in the current timestep. These values may be written in the form of a matrix

$$\mathbf{W} = \begin{pmatrix} w_{ff} & w_{fm} \\ w_{mf} & w_{mm} \end{pmatrix} = \begin{pmatrix} 1 - \frac{\mu_f}{2} & \frac{n_m \mu_m}{2 n_f} \\ \frac{n_f \mu_f}{2 n_m} & 1 - \frac{\mu_m}{2} \end{pmatrix} \qquad (22)$$

The vector $\mathbf{v} = (v_f, v_m)^{\top}$ of female and male individual reproductive values can then be derived as the dominant left eigenvector of the matrix $\mathbf{W}$

$$\begin{pmatrix} v_f \\ v_m \end{pmatrix} = \begin{pmatrix} \frac{\mu_m (n_f + n_m)}{(\mu_f + \mu_m) n_f} \\ \frac{\mu_f (n_f + n_m)}{(\mu_f + \mu_m) n_m} \end{pmatrix} \tag{23}$$

(which we have scaled such that mean reproductive value across the population is equal to 1).

Fitness

Having derived reproductive values, we can write expressions for the fitness of a gene copy carried by a focal female (w_f) or male (w_m), as a function of the focal individual's own fecundity and mortality (denoted p_{fi} and μ_{fi} for a female, or p_{mi} and μ_{mi} for a male), the mean fecundity and mortality of females or males other than the focal in the local group (denoted p_{fg} and μ_{fg} for local females, or p_{mg} and μ_{mg} for local males), and the mean fecundity and mortality of females and males across the population (denoted p_f and μ_f for females, or p_m and μ_m for males).

$$
\begin{aligned}
w_f = v_f &\left[(1 - \mu_{fi}) + \frac{(1-d_f)(\mu_{fi} + (n_f - 1)\mu_{fg})p_{fi}}{2((1-d_f)p_{fi} + (1-d_f)(n_f-1)p_{fg} + d_f n_f p_f)} + \frac{d_f \mu_f p_{fi}}{2 p_f} \right] \\
&+ v_m \left[\frac{(1-d_m)\mu_{mg} n_m p_{fi}}{2((1-d_m)p_{fi} + (1-d_m)(n_f-1)p_{fg} + d_m n_f p_f)} + \frac{d_m \mu_m n_m p_{fi}}{2 n_f p_f} \right]
\end{aligned}
\tag{24}
$$

$$
\begin{aligned}
w_m = v_f &\left[\left(\frac{(1-d_f)\mu_{fg} n_f p_{fg}}{2((1-d_f)p_{fg} + d_f p_f)} + \frac{d_f \mu_f n_f p_{fg}}{2 p_f} \right) \frac{m p_{mi}}{m p_{mi} + m(n_m - 1)p_{mg} + (1-m)n_m p_m} \right. \\
&\left. + \frac{\mu_f n_f (1-m)p_{mi}}{2 n_m p_m} \right] \\
&+ v_m \left[(1 - \mu_{mi}) \right. \\
&+ \left(\frac{(1-d_m)(\mu_{mi} + (n_m - 1)\mu_{mg})p_{fg}}{2((1-d_m)p_{fg} + d_m p_f)} + \frac{d_m \mu_m n_m p_{fg}}{2 p_f} \right) \frac{m p_{mi}}{m p_{mi} + m(n_m - 1)p_{mg} + (1-m)n_m p_m} \\
&\left. + \frac{\mu_m (1-m)p_{mi}}{2 p_m} \right]
\end{aligned}
\tag{25}
$$

In each of the above equations, fitness is obtained by summing male and female components, weighted by reproductive value. To illustrate, the first square-bracketed term in the expression for w_f represents the female component of fitness for a focal female, and features three terms that reflect the contribution from (i) the survival of the focal individual herself, (ii) the production of surviving local daughters and (iii) the production of surviving non-local daughters. The

second of these terms (production of surviving local daughters) is equal to the expected number of local female breeding vacancies created through local deaths, multiplied by the number of local daughters born to the focal individual, relative to the expected total number of female offspring competing for breeding vacancies in the local group. This number of locally competing female offspring is in turn obtained by summing contributions from the focal female, from the $(n_f - 1)$ other females in the local group, and from non-local females.

Inclusive fitness effects

To determine whether or not a mutant allele will be favoured by selection we determine its inclusive fitness effect, by summing its impact on the fitness of a focal individual that expresses it, and of females and males (other than the focal individual) in the local group, the latter weighted by their relatedness to the focal. For an allele expressed in females of age a that affects the fecundity of female recipients, this inclusive fitness effect is given by

$$
\begin{aligned}
I_{ff}^{\text{fec}} = & \left(-c \frac{\partial w_f}{\partial p_{fi}} + \frac{b}{n_f - 1} \frac{\partial w_f}{\partial p_{fg}} \right) \\
& + (n_f - 1) r_{ff}^a \left(\frac{b}{n_f - 1} \frac{\partial w_f}{\partial p_{fi}} + \left(\frac{n_f - 2}{n_f - 1} \frac{b}{n_f - 1} - \frac{c}{n_f - 1} \right) \frac{\partial w_f}{\partial p_{fg}} \right) \\
& + n_m r_{mf}^a \left(\frac{b - c}{n_f} \frac{\partial w_m}{\partial p_{fg}} \right)
\end{aligned}
\tag{26}
$$

where all derivatives are evaluated at $p_{fi} = p_{fg} = p_f = 1$.

Considering each of the three terms in the above equation, the first term represents the impact of the allele expressed by the focal individual on the fitness of the focal herself, which is the result of a decrease of c in her own fecundity, and an increase of $b/(n_f - 1)$ in the mean fecundity of the other females in her local group; the second term represents the impact of the allele expressed by the focal on the fitness of the $n_f - 1$ other local females, each of which experiences a mean increase of $b/(n_f - 1)$ in her own fecundity, and a mean change in the fecundity of other females in her group equal to the bracketed expression preceding the second partial derivative (this expression is complex, because, from the perspective of a non-focal female, the mean fecundity of local females other than herself changes due to the costs incurred by the focal actor, and due to the benefits conferred on her recipient, who might or might not be the female in question); finally, the third term represents the impact of the allele expressed by the focal on the fitness of local males, each of which experiences a mean change of $(b - c)/n_f$ in the fecundity of local females.

In a similar way, we can derive the inclusive fitness impact of alleles expressed by either females and males of a given age, directed at either female or male

recipients, with impacts on either fecundity or mortality

$$I_{mf}^{\text{fec}} = \left(-c\frac{\partial w_f}{\partial p_{fi}}\right)$$
$$+ (n_f - 1)r_{ff}^a\left(-\frac{c}{n_f - 1}\frac{\partial w_f}{\partial p_{fg}}\right)$$
$$+ n_m r_{mf}^a\left(\frac{b}{n_m}\frac{\partial w_m}{\partial p_{mi}} + \frac{b}{n_m}\frac{\partial w_m}{\partial p_{mg}} - \frac{c}{n_f}\frac{\partial w_m}{\partial p_{fg}}\right) \tag{27}$$

$$I_{fm}^{\text{fec}} = \left(-c\frac{\partial w_m}{\partial p_{mi}} + \frac{b}{n_f}\frac{\partial w_m}{\partial p_{fg}}\right)$$
$$+ n_f r_{fm}^a\left(\frac{b}{n_f}\frac{\partial w_f}{\partial p_{fi}} + \frac{b}{n_f}\frac{\partial w_f}{\partial p_{fg}}\right)$$
$$+ (n_m - 1)r_{mm}^a\left(\frac{-c}{n_m - 1}\frac{\partial w_m}{\partial p_{mg}} + \frac{b}{n_f}\frac{\partial w_m}{\partial p_{fg}}\right) \tag{28}$$

$$I_{mm}^{\text{fec}} = \left(-c\frac{\partial w_m}{\partial p_{mi}} + \frac{b}{n_m - 1}\frac{\partial w_m}{\partial p_{mg}}\right)$$
$$+ (n_m - 1)r_{mm}^a\left(\frac{b}{n_m - 1}\frac{\partial w_m}{\partial p_{mi}} + (\frac{n_m - 2}{n_m - 1}\frac{b}{n_m - 1} - \frac{c}{n_m - 1})\frac{\partial w_m}{\partial p_{mg}}\right) \tag{29}$$

$$I_{ff}^{\text{mort}} = \left(c\frac{\partial w_f}{\partial \mu_{fi}} - \frac{b}{n_f - 1}\frac{\partial w_f}{\partial \mu_{fg}}\right)$$
$$+ (n_f - 1)r_{ff}^a\left(-\frac{b}{n_f - 1}\frac{\partial w_f}{\partial \mu_{fi}} - \left(\frac{n_f - 2}{n_f - 1}\frac{b}{n_f - 1} - \frac{c}{n_f - 1}\right)\frac{\partial w_f}{\partial \mu_{fg}}\right)$$
$$+ n_m r_{mf}^a\left(\frac{-(b - c)}{n_f}\frac{\partial w_m}{\partial \mu_{fg}}\right) \tag{30}$$

$$I_{mf}^{\text{mort}} = \left(c\frac{\partial w_f}{\partial \mu_{fi}} - \frac{b}{n_m}\frac{\partial w_f}{\partial \mu_{mg}}\right)$$
$$+ (n_f - 1)r_{ff}^a\left(\frac{c}{n_f - 1}\frac{\partial w_f}{\partial \mu_{fg}} - \frac{b}{n_m}\frac{\partial w_f}{\partial \mu_{mg}}\right)$$
$$+ n_m r_{mf}^a\left(-\frac{b}{n_m}\frac{\partial w_m}{\partial \mu_{mi}} - \frac{b}{n_m}\frac{\partial w_m}{\partial \mu_{mg}} + \frac{c}{n_f}\frac{\partial w_m}{\partial \mu_{fg}}\right) \tag{31}$$

$$I_{fm}^{\mathrm{mort}} = \left(c\frac{\partial w_m}{\partial \mu_{mi}} - \frac{b}{n_f}\frac{\partial w_m}{\partial \mu_{fg}} \right)$$
$$+ n_f r_{fm}^a \left(-\frac{b}{n_f}\frac{\partial w_f}{\partial \mu_{fi}} - \frac{b}{n_f}\frac{\partial w_f}{\partial \mu_{fg}} + \frac{c}{n_m}\frac{\partial w_f}{\partial \mu_{mg}} \right) \qquad (32)$$
$$+ (n_m - 1)r_{mm}^a \left(\frac{c}{n_m - 1}\frac{\partial w_m}{\partial \mu_{mg}} - \frac{b}{n_f}\frac{\partial w_m}{\partial \mu_{fg}} \right)$$

$$I_{mm}^{\mathrm{mort}} = \left(c\frac{\partial w_m}{\partial \mu_{mi}} - \frac{b}{n_m - 1}\frac{\partial w_m}{\partial \mu_{mg}} \right)$$
$$+ n_f r_{fm}^a \left(-\frac{b - c}{n_m}\frac{\partial w_f}{\partial \mu_{mg}} \right)$$
$$+ (n_m - 1)r_{mm}^a \left(-\frac{b}{n_m - 1}\frac{\partial w_m}{\partial \mu_{mi}} - (\frac{n_m - 2}{n_m - 1}\frac{b}{n_m - 1} - \frac{c}{n_m - 1})\frac{\partial w_m}{\partial \mu_{mg}} \right)$$
$$(33)$$

Having derived expressions for the inclusive fitness impact of a helpful or harmful trait, we quanitfy the strength of selection for helping or harming by determining the critical ratio of c to the absolute magnitude of b below which this impact is positive.

Note that, in the main text, we plot the strength of selection for helping and harming by females and males as a function of age, without specifying whether the help or harm is directed at female or male recipients. For these results, we have assumed that help or harm is directed at a randomly chosen member of the group (other than the focal), who might be of either sex (so that, for instance, the probability of a female helping or harming a female recipient is equal to $(n_f - 1)/(n_f + n_m - 1)$, and a male recipient $n_m/(n_f + n_m - 1)$).

Patterns and consequences of age-linked change in local relatedness in animal societies

Supplementary 2: Study Systems

Banded Mongoose

Banded mongooses (*Mungos mungo*) are obligately social Carnivora distributed widely through sub-Saharan Africa[1]. They inhabit stable multi-male multi-female groups, usually called packs[1]. Each pack aggressively defends their territory from other packs[2]. Banded mongooses undertake a form of communal breeding; female reproduction is highly synchronised with reproduction into a common litter[1,3]. Pups in this litter are raised communally with help provided by all pack members of both sexes[1,4]. All adult females can reproduce into this litter, with some, but not complete, reproductive skew introduced by variation in fetal size and abortion frequency[1,5,6]. Males reproduce based on an age-linked dominance hierarchy with reproduction monopolised by the oldest males[1]. Neither males nor females disperse from their natal group, with almost all mongooses remaining in their natal group for the whole life [1]. Temporary and permanent eviction of females and (less commonly) males does occasionally occur, as well as low rates of dispersal by groups of younger males to join all-female groups[1,7]. However, these dispersal and permanent eviction events are uncommon. The majority of mating is local, which can result in a high degree of inbreeding and inbreeding depression[8,9]. The risk of inbreeding increases with female age and group age[10].

The banded mongoose data used here were collected as part of the Banded Mongoose Research Project (socialsresearch.org/about-the-banded-mongoose-project/). The Banded Mongoose Research Project has been collecting detailed social and demographic data on a population of mongooses inhabiting the area on and around the Mweya peninsula in western Uganda since 1995[1]. The population consists of 197-326 (mean 255.2) mongooses in 6 -13 packs (mean 9.65) in any given year (2000-2019). All mongooses in the population are individually marked and since 2000 each group has been under close observation every 1-4 days. Therefore, since the beginning of the study, the dates of birth and death of all individuals and group membership of all mongooses in the population are known. We use this information to calculate the annual group composition and age of all mongooses in this population. In addition, genotyping has been used to accurately identify the maternity and paternity of almost all mongooses present in the population since 2000[11,12]. While most juvenile births, deaths, maternity and paternities are known some juvenile mortality occurs before the emergence of pups from the natal den before genotyping.

Chimpanzee

Chimpanzees (*Pan troglodytes*) are group-living apes inhabiting forest habitats across central Africa. Chimpanzees live in stable mixed-sex social groups with high within-group fission-fusion dynamics. Groups (sometimes called communities) defend spatially defined territories from members of other groups. Males are philopatric whereas females disperse at sexual maturity[13]. All adults have the potential to breed but there is some dominance-linked reproductive skew in males[14]. In the Taï Forest,

for example, the dominant male fathers, on average, 50% of offspring[14]. Extra-group mating is rare but can occur[15].

Data used in this study are from the North and South community chimpanzees studied intensively as part of the Taï Forest chimpanzee research project (www.taichimps.org). These chimpanzees inhabit primary rainforest in the Taï National Park, Côte d'Ivoire. The study began in 1979, with full census and behavioural data available for north group beginning in 1985 and south group in 1997[16]. Both groups are subject to detailed year-round behavioural observations[17]. Since the start of intensive observation of a group, births, deaths and dispersals in the groups have been reliably inferred from observation[13]. Ages of individuals born since the start of the study can be calculated from their date of birth, while for chimpanzees born before the start of the study age is inferred based on appearance and behaviour [13]. Maternity is inferred from observations of parturient females and infant behaviour and confirmed by microsatellite analysis[13]. Paternity is inferred from the pool of potential fathers using genetic methods[15,18]. As no females have been observed emigrating to groups with close kin we assume that females are unrelated to all other chimpanzees when they join a group[13]. We combine the long-term observational and demographic data to infer annual group membership. Group sizes ranged from 10-42 (mean, 20.5) and 15-34 (mean, 25.8) adult chimpanzees in North and South groups respectively.

European Badger

European badgers (*Meles meles*; hereafter badgers) are mustelid carnivorans. Badger social structure varies considerably across their range. We used data from a well-studied population at Woodchester Park, Gloucestershire, UK. At Woodchester Park, the badgers live in mixed-sex groups with each group defending a territory, the precise area of which can vary from year to year[19]. Territories usually contain a communal underground burrow, known as a sett, but may also contain additional, sometimes outlying setts within the territorial boundaries[19]. In this population, offspring of both sexes regularly disperse from their natal group[20–22], and approximately half of mating occurs within the group with the other half from extra-group males, often from neighbouring groups[23,24].

The Woodchester Park Study began in 1976, with the primary aim of studying the epidemiology of bovine tuberculosis in a wild badger population[19]. The population consists of approximately 100-400 badgers living in 23 to 35 social groups. Trapping occurs at each group four times per year, and most badgers are captured at least once per year[19]. Upon their first capture, badgers are tattooed with a unique identification number, sexed and assigned to an age class. 81% of badgers born since 1976 were captured in their first year of life so can be aged accurately. The remaining 19% of badgers are likely to represent immigrants from outside the core population. Captures occur within known group territories (the boundaries of which are mapped by bait marking) so badgers can be assigned to a social group based on capture location[25]. Genotyping has been used to assign parents to cubs born since 1986[24,26].

Patterns and consequences of age-linked change in local relatedness in animal societies

Killer Whale

Killer whales (*Orcinus orca*) are highly social odontocete cetaceans inhabiting oceans worldwide. They are obligate carnivores and top predators. We use killer whale data from the southern resident killer whale population inhabiting the northeast Pacific Ocean. Resident-ecotypes are specialists salmon feeders, and the northeast pacific population feed almost exclusively on chinook salmon[27–29]. The southern-resident population are a genetically distinct resident-ecotype killer whale population regularly observed around the San Juan Islands, Washington State, USA during the summer months[30]. In a given year the population consist of 73-98 whales (1976-2018). Southern resident killer whales have a multilevel sociality with pronounced fission-fusion dynamics[30,31]. The basic unit in the society are matrilines consisting of females, their adult offspring of both sexes and their matrilineal grand-offspring [30]. Southern-resident matrilines in turn preferentially associate into three pods[30]. While within pod associations matrilines are more common, between pod associations do also occur as well as (rarely) the whole population being observed together at once. Neither male nor female killer whales disperse from their natal matriline, and both sexes are regularly found in very close spatial association with their mother for their whole lives[30]. Mating occurs both within and between pods, but rarely within matrilines[32].

The Center for Whale Research (www.whaleresearch.com/) has performed an annual census of the southern-resident killer whale population since 1976. We use data collected by the Center for Whale Research covering the years 1976 to 2018 (inclusive). Whales can be accurately individually identified based on their shape of their dorsal fin and the unique patterns of their saddle patch[30]. Adult killer whales have sexually dimorphic dorsal fin shapes, and immature whales are sexed based on opportunistic sightings of their ventral markings[30]. All living whales are observed every year. Photographs taken of the whales are compared to identification catalogues to accurately ascertain their identities. Deaths are declared by the Center for Whale Research after repeated sightings of a matriline without the missing individual. The very high social and spatial fidelity of whales and the absence of emigration out of the population means that years of death are known with high confidence. Over the 40 years of the study, no whale declared dead has subsequently been resighted. Similarly, the year of birth of whales born since 1976 are inferred from the date of their first sighting as a calf. For whales observed born before 1976 ages have been inferred based on developmental and reproductive status when first observed[30]. Maternity is inferred based on observations of mother-calf behaviour conducted by the Center for Whale Research[30]. Ford et al (2018)[32] used 68 microsatellites to assign paternities in this population, and it is these paternities we use in this study.

Unlike the other systems we consider in this study, resident killer whales do not inhabit closed social groups. We therefore use a 'bottom-up' approach to define the local social environment in resident killer whales to select the social units over which helping and harming behaviour in the animals can be expected to act. We use a social network approach – based on patterns of association within the fission-fusion society – to define social groups within the population. We consider whales to be associating if they are observed within 10km (approximately whales within acoustic range; see[30]). Combining data over all years of the study we calculate for each pair of whales in the population we calculate the number of times they are observed association (given that they are both alive) and the number of times each member of the pair is observed separately (given that they are both alive). This corresponds to the simple ratio index commonly used in animal social network studies. We then use binomial mixture models to estimate the number of types of association present in the population, and

which 'type' of association to which each pairwise social association belongs[33]. We found that the four-component mixture model is the most parsimonious. We consider pairs of whales sharing the strongest k4 component social association to part of each other's local social environment. These local social environments are conceptually equivalent to the groups in other systems and are referred to as such hereafter. The average size of these groups is 3.2 ± 2.4 (mean $\pm$ std dev.), and their composition corresponds well to 'matrilines' often used in this population. An interesting feature of this method is that group membership is not transitive, and that if A and B are in the same group, and A and C are in the same group it does not necessarily mean that B and C are also in the same group. Using this method, we have derived functional groups from a society with strong fission-fusion based on whale social behaviour. These groups necessarily correspond to the group of individuals a whale will be associating with most commonly, and will therefore affect with their helping and harming decisions.

Acknowledgements

Rhesus macaque

Rhesus macaques (*Macaca mulatta*) are generalist *Cercopithecine* primates inhabiting a range of habitats throughout southern, south-eastern and eastern Asia[34]. Rhesus macaques form stable, mixed-sex, closed social groups throughout their range[35]. Individuals of both sexes all show a variety of affiliative interactions resulting in complex within-group social networks[36]. Dispersal is strongly male-biased with most males moving groups multiple times over their adult lifetime[37,38]. Females almost always remain in their natal group for their entire life except in rare cases of group-fission[39]. Within groups rhesus macaques have linear dominance hierarchies with all males dominant to all females[40,41]. While these dominance hierarchies result in moderate reproductive skew for males there is limited reproductive skew in females [42]. Overall rates of extra group paternity but there is some variation in rates linked to traits including group size, group sex ratio and female rank[43,44].

We use data from a free-ranging population of rhesus macaques on Cayo Santiago, Puerto Rico, USA. The population are non-native and are the descendants of 409 rhesus macaques introduced to the island in 1938 from the Indian subcontinent[45]. The Cayo Santiago macaques are managed and studied by the Caribbean Primate Research Center and the University of Puerto Rico, USA (cprc.rcm.upr.edu/). The macaques on Cayo Santiago are free-ranging and do not have regular veterinary intervention, but are provisioned daily. As an introduced population, they have no predators on the island. The Cayo Santiago macaque population consists of 654 and 1042 adult macaques on any given year living in 5-9 social groups (2010-2020). All animals are captured and released around the age of 1, at which time they are marked with a tattoo, which is used for individual identification[45]. The population is under continual observation and are censused weekly at minimum, resulting in a monthly census report. Dates of birth and death, as well as maternity and group membership, are inferred from these census data. Paternities have been systematically calculated using microsatellite genetic markers derived from blood drawn at the annual capture-releases since 1992[46]. Some macaques die before the end of their first year when they would be captured so have unknown paternity.

Acknowledgements

Spotted Hyena

Spotted hyenas (*Crocuta crocuta*) are large, long-lived, highly social carnivores of the family Hyaenidae. They live in mixed-sex groups (usually called 'clans') in a wide range of habitats throughout sub-Saharan Africa. Within clans there are some fission-fusion dynamics with members often spending time alone or in subgroups of varying size and composition[47,48]. Each clan defends a territory, but individuals frequently intrude into territories of other clans to hunt and scavenge[49,50]. Dispersal is strongly male-biased: females typically remain in their birth clan throughout life[50] whereas most males disperse to another clan after reaching sexual maturity[51,52]. Clan social structure is characterised by a linear dominance hierarchy[53]. The dominance relationships and clan hierarchy emerge from asymmetries in the number of recruitable social allies between clan members[54]. Social alliances are strongest among close kin and stronger among philopatric hyenas than between philopatric and immigrant individuals and among immigrants[55]. As a result, social dominance fluctuates depending on the kin and demographic structure of the clan[54]. Intersexual dominance is usually female-biased because, in contrast to most males, females remain in their natal clan and retain their network of social allies.

The mating system is polygynandrous. All females reproduce and there is no distinct breeding season[56]. Females have control over copulation owing to the unusual anatomy of their genitals[57] and exercise mate choice[52,56]. Females almost always mate with males of their clan; immigrant and philopatric males are similarly successful[51]. There is a considerable degree of reproductive overlap between generations but breeding between close relatives is rare because females apply simple, tenure-based mate-choice rules that effectively prevent breeding between daughters and fathers and sisters and older brothers[52]. Survival and reproductive success are strongly and positively linked to social rank in both sexes[51,58,59]. The females of a clan rear their cubs at a communal den but they typically only nurse their own cubs and adoptions are rare[60]. Female investment in cubs is high: the gestation period is 110 days[61] and cubs are nursed for an average of 13 months with highly nutritious milk[62]. Males do not provide care for their young[56].

We use data from the eight clans of spotted hyenas inhabiting the floor of the Ngorongoro Crater (3°11´S, 35°34´E) in northern Tanzania. This population has been subject to intensive study since 1996 as part of the Ngorongoro Hyena Project (hyena-project.com). All spotted hyenas of the population are individually known by their unique spot pattern and other cues such as ear notches[59]. Demographic and life-history data are collected routinely during near-daily visits of the clans. Observations are made from a vehicle to which all study animals are well habituated. Most males disperse to one of the other Crater clans but each year, a small number of males disperses to and immigrates from, populations outside the Crater[51,52]. Approximately 17% of males undertake secondary dispersal[52]. The age of individuals born in Crater clans is estimated based on pelage and ear characteristics, body size, behaviour, and locomotory abilities[59]. The age of immigrant males from other populations is estimated based on pelage characteristics and other cues such as the presence of scars. Individuals are considered to have died or disappeared when their dead body was found or when they were not sighted for at least 1 year. Individuals are sexed based on the shape of their phallic glans[63]. Parentages are assigned using amplification of nine polymorphic spotted hyena microsatellites[51,52,64] and maximum likelihood methods as implemented in CERVUS 3.0[65]; maternities of cubs who died before a genetic sample was collected are assigned based on observations of suckling behaviour. Genetic samples have been collected from almost all adults and a large proportion

of cubs of the population. Mean clan size (± SD) increased from 24.3 (± 13.4) to 42.9 (± 14.4) during the study period.

Acknowledgements

Yellow Baboon

We use long-term demographic and behavioural data collected by the Amboseli Baboon Research Project (amboselibaboons.nd.edu/) to understand the kinship dynamics of baboons. The Amboseli Baboon Research Project has been collecting data on the baboons inhabiting Amboseli National Park, Kenya since 1971, although for this study we use data collected since 1988. The Amboseli baboons primarily exhibit yellow baboon phenotypes and ancestry (*Papio cynocephalus*), but they also experience natural admixture with neighbouring populations of olive baboons (*P. anubis*). The most recent wave of such genetic admixture in Amboseli, during the past four decades, appears to have been preceded by repeated episodes of admixture during the evolutionary history of this population. Both yellow and olive baboons (*Papio cynocephalus* and *P. anubis*) are largely terrestrial cercopithecine primates found widely throughout eastern Africa[66].

Yellow and olive baboons exhibit the same social system: populations are subdivided into stable social groups consisting of multiple adults and juveniles of both sexes[66]. Males are approximately twice the size of females. Females remain in their natal group throughout life, while males typically disperse to other social groups, first in the late sub-adult or early adult period and then several more times throughout life. Females mate with multiple males, typically in the context of mate-guarding episodes that occur when females are in the ovulatory phase of their sexual cycle. Female baboons produce a single offspring with each birth; offspring are born relatively helpless and depend upon mother's milk for nutrition until approximately 70 weeks of age[67].

Females remain in their natal group throughout their life, but males usually disperse before beginning to reproduce[68,69]. Females reach menarche at a median age of 4.5 years, and first birth at a median age of 6 years; males reach testicular enlargement at a median age of 5.4 years and achieve first mate-guarding at a median age of 7.5 years[70]. Both sexes have strong linear dominance hierarchies determining priority of access to resources[66]. Female dominance rank experiences familial influences: daughters (but not sons) strongly resemble their mothers in the dominance rank they attain as an adult, largely as a consequence of familial intervention in agonistic interactions[71]. In contrast, male dominance rank is not affected by maternal dominance rank[72]. Higher ranking males produce more offspring than lower-ranking males, but monopolisation of reproduction by the highest-ranking males is incomplete[73,74]. Although groups are generally stable, group fission occasionally occurs, often along matrilineal lines[75].

This study focuses on fission descendants of 2 original study groups; a mean of 5 groups per year was studied. Groups consist of between 14 and 130 baboons (mean 60) in any given year. Behavioural and

demographic data are collected on a near-daily basis during regular observations of the baboons within the study groups. We derive annual group membership, years of birth and maternal identity from these long-term data. For individuals born into the study population, birthdates are generally known to within a few days. For males that immigrate into the study population from the surrounding area, birthdates are estimated based on body size and physical characteristics[74]. Group membership is defined annually, and therefore due to fission and dispersal, a given baboon can occasionally be members of multiple groups in a given year. Unless known otherwise, males dispersing into a group are considered to be unrelated to baboons in their new group.

Maternities were identified from long-term records of births; both maternities and paternities were verified with genetic parentage analysis. Specifically, microsatellite genotypes were obtained from DNA derived from faecal samples or, in some cases, blood samples. For samples extracted from faeces, all apparent homozygous genotypes were reamplified at least four and up to seven additional times to guard against allelic dropout. All microsatellite genotype data were produced on either an ABI 3700 Sequence Analyzer or an ABI 3730xl Sequence Analyzer. Parentage was assigned using the *Cervus* software, most recently version 3.0[65,76]. Parentage analysis has been routinely conducted for the study population for over two decades, with the result that paternity has been assigned to many infants born into the population between approximately 1988 and 2015[69,73,74,77].

Supplementary 3: Kinship dynamics simulation model

In the simulation model each agent is an individual. Groups consist of a fixed number of adults. During each model cycle (hereafter 'year') there are two phases: mortality and replacement. During the mortality phase every adult has a fixed probability of mortality (death) based on their expected average lifespan (table 1). Mortality risk does not vary with age but each sex can have its own mortality risk. Mortality phase corresponds to the 'adult mortality' event in Johnstone and Cant's (2010) analytical model. In the replacement phase the group members lost to mortality are replaced. Replacement is sex-specific. Each sex-specific group space is replaced by either a philopatric or immigrant individual. All replacements are of 'age of maturity'. The probability of a group-space being replaced by an immigrant is determined by that sex's dispersal rate. So in a sex with a 0.85 dispersal rate, each sex-space in that group has an 85% chance of being filled by an immigrant (and a 15% chance of being filled by a philopatric individual). Immigrants have unknown mothers and fathers. Philopatric individuals however have mothers chosen from the group. The mother of a given philopatric individual is chosen at random from the adult females present when the individual would have been born (year - age of maturity). The rate of local mating determines the probability that an individual's father is chosen from the group - by the same process as the mother – or is from outside the group, and therefore unknown. The replacement phase corresponds to the dispersal, reproduction and competition phases of Johnstone and Cant's (2010) analytical model.

After the model has run, juveniles are retrospectively added to the groups following two principles: (1) individuals must be present for 'age at maturity' years before joining the group; and (2) juvenile group size should (where possible) be maintained at the specified juvenile group size. We also make the simplifying assumption that every individual who immigrates into the group is matched by an equivalent juvenile in the group who dispersed at maturity. Without this simplifying assumption emergent patterns of kinship dynamics remain similar to those reported but the group size in the population can sometimes fall to 0- we therefore do not include this functionality in the model presented here. This results in two populations of juveniles whose fates are known *a priori*: individuals who will survive to maturity and either join the group or disperse (hereafter, the Elect) and those who will not survive to maturity (hereafter, the Damned). The Elect are retroactively added to the years in which they were immature before joining the group or dispersing. Individuals immigrating into the group are considered to 'replace' a juvenile of the same sex present in the group for age at maturity years before their immigration. Philopatric Elect have the parents chosen for them in the original model (above). Emigrating Elect have a mother chosen from within the adult females present in the group when they are age 0, and a father chosen from within the group with probability *local mating rate*, otherwise a father from outside the group.

After the Elect are applied to the groups, the number of juveniles present in the group in a given year is raised to the 'juvenile group size' by adding 'Damned' individuals who will not reach maturity. Damned juveniles stay in the group from time *t-1* to time *t* but have three sources of mortality, applied in order: (1) if the spaces *s* for damned individuals is lower in *t* than *t-1* (caused by an increase in the number of Elect juveniles) then *s* Damned juveniles are selected at random from the Damned population at *t-1*; (2) Damned juveniles reaching 'age at maturity' at time *t* are removed; and (3) each Damned juvenile (less than the age at maturity) at *t-1* has a fixed probability (the juvenile mortality rate) of surviving to *t*. The juvenile mortality rate is *1 / age of maturity* which results in, on average, no Damned individuals surviving to maturity. Any individuals who do, by chance, survive to the 'age of maturity' they are considered to have a mortality rate of 1 (see phase 2 above). After mortality is applied, juvenile group spaces *s* (the difference between the juvenile group size and the number of juveniles at time *t*) are filled with *s* new juveniles of age 0. Spaces are sex-specific to maintain an even juvenile sex ratio. Each new juvenile has a mother chosen from within the group and a father chosen from within the group with a local mating rate probability, or else an extra-group father. All juveniles age by one year between time *t* and time *t+1*. Occasionally the number of Elect required is

greater than the juvenile group size, this is allowed within the model framework resulting in a temporary increase in the juvenile group (and therefore overall group) size.

The model repeats after a burn-in (discarded iterations to remove the effect of the starting conditions) period until 2000 individuals have lived in the group. 2000 was chosen as a conservative sample size, and visual exploration of the model output demonstrates that observed patters of kinship dynamics are very robust and emerge under much smaller sample sizes. Patterns at 500 individuals are qualitatively identical to those from 2000 individuals. In each group-year the relatedness between group members is calculated from the pedigrees of individuals (see below). Relatedness is calculated for both adults and juveniles to all adults and juveniles but we only report changes in adult local relatedness. The model was developed in R v3.6.1 [78], and the dplyr package [79]. Model R code can be found at REPOSITORY and a basic web app implementation can be viewed at: samellisq.shinyapps.io/kinship_dynamics_shinyapp_basic/.

Supplementary 4: Statistical modelling

Kinship dynamics in both the simulated (from the simulation model) and real data were modelled using in a hierarchical Bayesian framework. The variables and parameters used in these statistical models are described in Supplementary Table 7.

Equation S1 is an expanded version of main text equation 2 including the priors used to model the real data.

equation S1

$$
\begin{aligned}
\hat{r} &\sim Normal(r, \sigma_r) \\
r &\sim Beta(d_1, d_2) \\
d_1 &= \bar{p} * \theta \\
d_2 &= (1 - \bar{p}) * \theta \\
logit(\bar{p}_i) &= \alpha_{id[i]} + s_{sid[i]} + \beta_{sid[i]}A_{[i]} + \gamma G_{[i]} \\
\alpha_j &\sim Normal(\bar{\alpha}, \sigma_a) \; for \; j = 1..n \\
\sigma_a &\sim Exponential(1) \\
\bar{\alpha} &\sim Normal(0, 1.5) \\
s_k &\sim Normal(x, y) \; for \; k = 1..2 \\
\beta_k &\sim Normal(0, 1.5) \\
\gamma &\sim Normal(0, 1.5) \\
\theta &= \phi + 2 \\
\phi &= Exponential(1)
\end{aligned}
$$

For data simulated from the simulation model, pedigrees are complete so it is unnecessary to calculate or model an estimated local relatedness. We therefore directly model the observed local relatedness as r. Group size is held constant through the model so the group size parameter will be uninformative and is not included. Complete simulated data model shown in equation S2.

equation S2

$$
\begin{aligned}
r &\sim Beta(d_1, d_2) \\
d_1 &= \bar{p} * \theta \\
d_2 &= (1 - \bar{p}) * \theta \\
logit(\bar{p}_i) &= \alpha_{id[i]} + s_{sid[i]} + \beta_{sid[i]}A_{[i]} \\
\alpha_j &\sim Normal(\bar{\alpha}, \sigma_a) \; for \; j = 1..n \\
\sigma_a &\sim Exponential(1) \\
\bar{\alpha} &\sim Normal(0, 1.5) \\
s_k &\sim Normal(x, y) \; for \; k = 1..2 \\
\beta_k &\sim Normal(0, 1.5) \\
\theta &= \phi + 2 \\
\phi &= Exponential(1)
\end{aligned}
$$

Supplementary Tables

Supplementary Table 1. Model coefficients from the observed kinship dynamics of seven mammal species. Models describe the relationship between age and local relatedness (beta), with separate random intercepts for individual id (abar), sex specific intercepts (s) and a group size parameter (gamma). See text and Supplementary 3 for a full description of the model. All coefficients are rescaled to represent the relationship with real age rather than normalised age.

species	abar	sigma_a	s.F	s.M	beta.F	beta.M	gamma
Banded Mongoose	-0.1 (-0.108--0.093)	0.057 (0.055-0.06)	0.051 (0.046-0.058)	0.052 (0.046-0.06)	0.025 (0.008-0.043)	-0.033 (-0.045--0.021)	0.002 (0.001-0.004)
Chimpanzee	-0.036 (-0.052--0.019)	0.066 (0.047-0.087)	0.017 (0.016-0.019)	0.018 (0.016-0.019)	0.074 (0.051-0.098)	-0.009 (-0.067-0.049)	-0.005 (-0.01-0)
European Badger	-0.08 (-0.09--0.068)	0.058 (0.049-0.068)	0.048 (0.044-0.052)	0.047 (0.043-0.051)	-0.031 (-0.08-0.016)	-0.01 (-0.079-0.057)	-0.013 (-0.02--0.006)
Killer Whale	-0.027 (-0.031--0.023)	0.007 (0.005-0.011)	0.02 (0.018-0.021)	0.02 (0.018-0.022)	0.011 (-0.001-0.023)	-0.017 (-0.037-0.003)	-0.01 (-0.013--0.007)
Rhesus macaque	-0.162 (-0.163--0.161)	0.02 (0.019-0.021)	0.024 (0.023-0.025)	0.023 (0.023-0.024)	-0.034 (-0.039--0.03)	-0.143 (-0.149--0.137)	-0.008 (-0.009--0.008)
Spotted Hyena	-0.2 (-0.205--0.195)	0.077 (0.073-0.081)	0.044 (0.042-0.046)	0.032 (0.031-0.032)	-0.021 (-0.03--0.012)	0.12 (0.105-0.135)	0.005 (0.004-0.007)
Yellow Baboon	-0.178 (-0.185--0.17)	0.103 (0.096-0.11)	0.029 (0.026-0.031)	0.025 (0.025-0.026)	0.011 (0.005-0.016)	0.033 (0.009-0.058)	-0.005 (-0.006--0.004)

Supplementary Table 2: Descriptive breakdown of the posterior (post.) of the slope (β) parameter for each species-sex. *Post. Mean* and *post. sd* describe the sex-specific beta posterior distribution. *Post. >0 & Post. <0* describe the proportion of the beta posterior distribution greater than and less than 0 respectively. *Sex diff. mean* and *Sex diff. sd* describe the posterior distribution of the difference between the sexes. Difference is calculated as female posterior mean – male posterior mean in each sample from the posterior. *Sex diff. > 0* and *Sex diff. less 0* show the proportion of the sex difference posterior distribution greater than and less than 0 respectively. *Obs. vs Sim. post. overlap* describes the proportion of the joint posterior beta distribution from the simulation model and the observed data model which is contained with the area bounded by the area in which the distributions overlap.

species	sex	Post. mean	Post. sd	Post >0	Post <0	Post. sex diff. mean	Post. sex diff. sd	Post. sex diff. >0	Post. sex diff. <0	Obs. vs Sim. post. overlap
Banded Mongoose	F	0.28	0.12	0.99	0.01	0.64	0.15	1.00	0.00	0.42
Banded Mongoose	M	-0.36	0.08	0.00	1.00	0.64	0.15	1.00	0.00	0.01
Chimpanzee	F	2.30	0.45	1.00	0.00	2.58	1.20	0.99	0.01	0.40
Chimpanzee	M	-0.28	1.12	0.40	0.60	2.58	1.20	0.99	0.01	0.26
European Badger	F	-0.38	0.37	0.14	0.86	-0.26	0.57	0.32	0.68	0.27
European Badger	M	-0.12	0.50	0.42	0.58	-0.26	0.57	0.32	0.68	0.40
Killer Whale	F	0.32	0.22	0.92	0.08	0.84	0.37	0.99	0.01	0.87
Killer Whale	M	-0.52	0.37	0.08	0.92	0.84	0.37	0.99	0.01	0.52
Rhesus macaques	F	-0.76	0.06	0.00	1.00	2.39	0.09	1.00	0.00	0.00
Rhesus macaques	M	-3.15	0.08	0.00	1.00	2.39	0.09	1.00	0.00	0.00
Spotted Hyena	F	-0.34	0.09	0.00	1.00	-2.26	0.17	0.00	1.00	0.88
Spotted Hyena	M	1.92	0.15	1.00	0.00	-2.26	0.17	0.00	1.00	0.00
Yellow Baboon	F	0.21	0.07	1.00	0.00	-0.45	0.32	0.08	0.92	0.00
Yellow Baboon	M	0.66	0.30	0.98	0.02	-0.45	0.32	0.08	0.92	0.60

Supplementary Table 3. Model coefficients from the predicted kinship dynamics of seven mammal species derived from an agent-based simulation model. Models describe the relationship between age and local relatedness (beta), with separate random intercepts for individual id (abar), sex specific intercepts (s) and a group size parameter (gamma). See text and Supplementary 3 for a full description of the model and Supplementary 2 for a full description of the agent-based simulation. All coefficients are rescaled to represent the relationship with real age rather than normalised age.

species	abar	sigma_a	s.F	s.M	beta.F	beta.M
Banded Mongoose	-0.236 (-0.243--0.228)	0.09 (0.084-0.096)	0.047 (0.046-0.049)	0.048 (0.046-0.049)	0.063 (0.045-0.08)	0.009 (-0.002-0.018)
Chimpanzee	-0.151 (-0.154--0.148)	0.019 (0.017-0.021)	0.016 (0.016-0.017)	0.016 (0.016-0.017)	0.066 (0.064-0.069)	-0.02 (-0.022--0.018)
European Badger	0 (-0.007-0.006)	0.074 (0.07-0.079)	0.051 (0.047-0.054)	0.049 (0.045-0.053)	0.019 (0.013-0.026)	0.02 (0.012-0.028)
Killer Whale	-0.036 (-0.042--0.029)	0.031 (0.026-0.037)	0.018 (0.017-0.019)	0.018 (0.017-0.019)	0.004 (-0.003-0.011)	-0.004 (-0.01-0.002)
Rhesus macaque	-0.202 (-0.207--0.196)	0.034 (0.03-0.038)	0.023 (0.023-0.023)	0.023 (0.023-0.023)	-0.006 (-0.01--0.002)	0.048 (0.044-0.052)
Spotted Hyena	-0.196 (-0.203--0.189)	0.058 (0.053-0.063)	0.032 (0.031-0.032)	0.032 (0.031-0.032)	-0.006 (-0.014-0.002)	0.091 (0.074-0.108)
Yellow Baboon	-0.141 (-0.146--0.136)	0.033 (0.029-0.036)	0.025 (0.025-0.025)	0.025 (0.025-0.025)	-0.013 (-0.017--0.009)	0.062 (0.054-0.069)

Supplementary Table 4. Sample sizes of data used to fit the kinship dynamics model (see text and Supplementary 2) for the seven study species. N individuals describes the number of unique ids present in the dataset, id-years is the number of individual-years in the data (because one individual can be present in the data for multiple years) and included id-years are the number of years included in the final model. Id-years are included based on various factors such as having a known age, a known sex and having a known local relatedness to more than 20% of group mates (see methods and Supplementary 1 for complete details). Note: because group definitions in killer whales are defined at an individual level, and are not transitive, study groups per year is not a meaningful concept (supplementary 1).

Species	N study groups per year	Adults			All		
		n individuals	id-years	Included id-years	n individuals	id-years	Included id-years
Banded mongoose	6-13	1322	3297	2263	2330	5073	2262
Chimpanzee	2	137	1314	265	316	2772	957
Eurasian badger	23-35	1412	4067	384	2843	8163	1066
Killer whale	-	136	2394	329	205	3678	1069
Rhesus macaque	5-9	1882	9676	6619	4179	19590	2736
Spotted hyena	8	1011	5717	5223	2071	10171	5057
Yellow baboon	4-10	739	4686	3167	1509	9857	4947

Supplementary Table 5. Description of the input parameters for kinship dynamics simulation model.

Parameter	Definition and discussion	Equivalent parameter in Johnstone and Cant (2010)
Dispersal rate (male and female)	In common with other studies in animal behaviour, we define dispersal as the permanent movement of individuals out of their native range or group [80,81]. Philopatry, in contrast, is defined as the continued presence of individuals within their native range or group [80,81]. Other definitions, such as those based on dispersal distances or movement out of the natal population/deme are less relevant to the current study which is interested in the dynamics and behaviours of social groups. The dispersal rate for each sex is the proportion of that sex dispersing from the natal group, where 1 reflects all of that sex disperse and 0 all of that sex are philopatric.	d_f, d_m
Adult Group size	We consider a social group (hereafter group) to be a set of individuals who mostly interact with each other and rarely with members of other such sets [82,83]. This is a deliberately general definition to allow comparisons between taxonomically and behaviourally diverse species. Adult group size is the number of adults (that is individuals greater than the age of maturity) in the social group. In the model, the group is considered to have an equal adult sex ratio.	$n_f + n_m$
Juvenile group size	The number of juveniles – individuals before the age of sexual maturity – present in the group. The model assumes that juveniles have an even juvenile sex ratio and a fixed rate of mortality.	*n/a*
Local mating rate	Local mating rate is the proportion of mating's occurring within a group – between group members – compared to mating with members of other groups. In the model, mating rate corresponds to the proportion of offspring fathered. Local mating rate is therefore synonymous with the proportion of offspring sired by the males of a group. Local mating rate for a given species will result from that species mating system [83] and the proportion of offspring fathered by extra-group males [84,85].	*m*
Expected adult lifespan (male and female)	Expected adult lifespan is given as the number of years an adult of a given sex can expect to live if they reach the age of maturity. Expected adult lifespan allows comparison of life-history between species (e.g. [86]) without the confounding effects of differing juvenile mortality rates. We focus on the relationship between individuals of reproductive age when considering kinship dynamics. We use expected adult lifespan to calculate sex-specific mortality rates (equation 1). Equation 1: $$\mu = {0.5}/{e_{L\alpha - \alpha}}$$ Where μ is adult mortality rate, α is age at maturity at $e_{L\alpha}$ is the expected lifespan at maturity. To prevent individuals living for a biologically unrealistic length of time individuals living for longer than 2.39 times the expected adult lifespan have mortality set to 1. 2.39 is used as it is the average ratio of expected lifespan to the maximum observed lifespan in the 52 mammal species studied in [87].	μ_f, μ_m
Age at maturity	Age at maturity is the age at which an individual becomes sexually mature and enters the breeding population. It is also the age at which individuals disperse from (and immigrate into) groups. In the base model age at maturity effectively acts only to scale age values and makes no difference to observed patterns relative to Cant and Johnstone's (2010)[88] model. It is important to note that in real populations it is not always the case that these three events occur at the same age, and that the age is the same for males and females.	*n/a*

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Supplementary Table 6. Parameter values input into the simulation model for the 7 mammal species studied. When appropriate we chose the value for each parameter preferentially from the published literature on the population. If no published value were available (or our definitions differ from those in the published literature), we calculated it directly from data used to calculate the populations' kinship dynamics (denoted with *italics*). Adult group size, juvenile group size, adult lifespans and age at maturity are rounded to the nearest integer.

Species	Dispersal rate (female)	Dispersal rate (male)	Adult group size	Juvenile group size	Local mating rate	Expected adult lifespan (female)	Expected adult lifespan (male)	Age at maturity	References
Banded mongoose	0.12	0.12	*16.25*	*12*	0.64	3	4	1	[1]
Chimpanzee	0.89	0	23	25	0.93	*30*	*28*	12	[13,15]
European badger	*0.23*	*0.45*	*4*	*5*	0.52	*3*	*3*	*2*	[24]
Killer whale	0	0	4	3	*0.02*	19	50	12	[30,33,87,89]
Rhesus macaque	*0.05*	*0.79*	*112*	*151*	0.13	*15*	*14*	5	[38,41,44]
Spotted hyena	*0*	*0.91*	*23*	*28*	*0.96*	*10*	*9*	4	[50–52]
Yellow baboon	*0*	*0.8*	*24*	*36*	*1*	16	14	6	[68,90–92]

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Supplementary Table 7. Description of the variables used in the statistical models. See equations 2, S1 and S2.

| Model variables	Description
$\hat{r}$	Estimated local relatedness. See main text section *calculating relatedness* for a description of how this is estimated. As local relatedness is, in practice, limited to between 0 and 0.5 (0.5 representing a group of all full-siblings for example) to simplify parameter estimation the model is fit to 2* $\hat{r}$. All reported parameters have been rescaled to remove the effect of this multiplication. Beta distributions cover the range 0<x<1. Values cannot, therefore, be either 0 or 1. In line with usual practice (e.g. [93]) values of 0 and 1 were replaced with values an arbitrarily small distance within the range (0 to $1e^{-6}$, 1 to $1 – 1e^{-6}$). This will not affect model interpretation.
r	'True' local relatedness parameter. This parameter is limited to be between 0 and 1 (see rescaling explanation in $\hat{r}$).
σ_r	Standard deviation around $\hat{r}$. See main text section *calculating relatedness* for a description of how this is calculated. For model fitting, this standard deviation has been rescaled as described for $\hat{r}$.
d_1 , d_2	Beta distribution shape parameters. We use established practice to rearrange these parameters in terms of average probability ($\bar{p}$) and a dispersion parameter θ.
$\bar{p}$	Average probability (in this case local relatedness)
θ	Dispersion parameter describing the distribution of probability around $\bar{p}$. Where θ = 2 probability is equal between 0 and 1, if θ < 2 probabilities near 0 and 1 are more common and if θ > 2 probability is more concentrated around $\bar{p}$. In practice calculated as a transformed parameter of φ.
α_{id}	Individual intercept parameter, where id is indexed from 1 to *n*.
n	Number of individuals
s_{sid}	Sex-specific intercept parameter, where sid is indexed from 1 to 2 (1 = female, 2 = male).
x,y	Mean (x) and standard deviation (y) of normally distributed prior for sex-specific intercept. The different distributions of local relatedness in each data set required a different x and y value to produce a meaningfully uninformative prior distribution for the model. x and y were chosen to encompass the full range of possible local relatedness values for the dataset. See Supplementary Table 8 for x and y values by model.
β_{sid}	Sex-specific kinship dynamics coefficient parameter describing the slope of the relationship between local relatedness and age.
A	Age. To aid model fitting and prior choice this is standardised to between 0 and 1 for every dataset using the function: $(A_i – min(A)) / max(A – min(A))$. Where min(A) will correspond to the 'age at maturity' because we only model the kinship dynamics of adults.
γ	Parameter describing the relationship between group size and local relatedness. This is to control for the fact that individuals in the larger group will have the potential to have a lower local relatedness simply by virtue of the number of available partners.
G	Group size
$\bar{\alpha}$	Average individual intercept parameter. All individuals are considered to be drawn from a distribution centred on $\bar{\alpha}$.
σ_a	Standard deviation parameter describing the distribution of individuals around the average individual.
φ	Model fitting parameter, transformed to *θ*.

Supplementary Table 8. Prior parameters on the sex intercept *s* used in each model. Intercept priors are a normal distribution with mean *x* and standard deviation *y*. Note all priors are defined in the logit scale.

| Species	Model	x	y
Banded mongoose	observed	0.53	0.12
	simulated	0.523	0.015
Chimpanzee	observed	0.54	0.03
	simulated	0.51	0.005
European badger	observed	0.575	0.03
	simulated	0.6	0.03
Killer whale	observed	0.6	0.03
	simulated	0.535	0.02
Rhesus macaque	observed	0.515	0.02
	simulated	0.502	0.001
Spotted Hyena	observed	0.54	0.03
	simulated	0.51	0.005
Yellow baboon	observed	0.525	0.03
	simulated	0.505	0.002

Supplementary figures
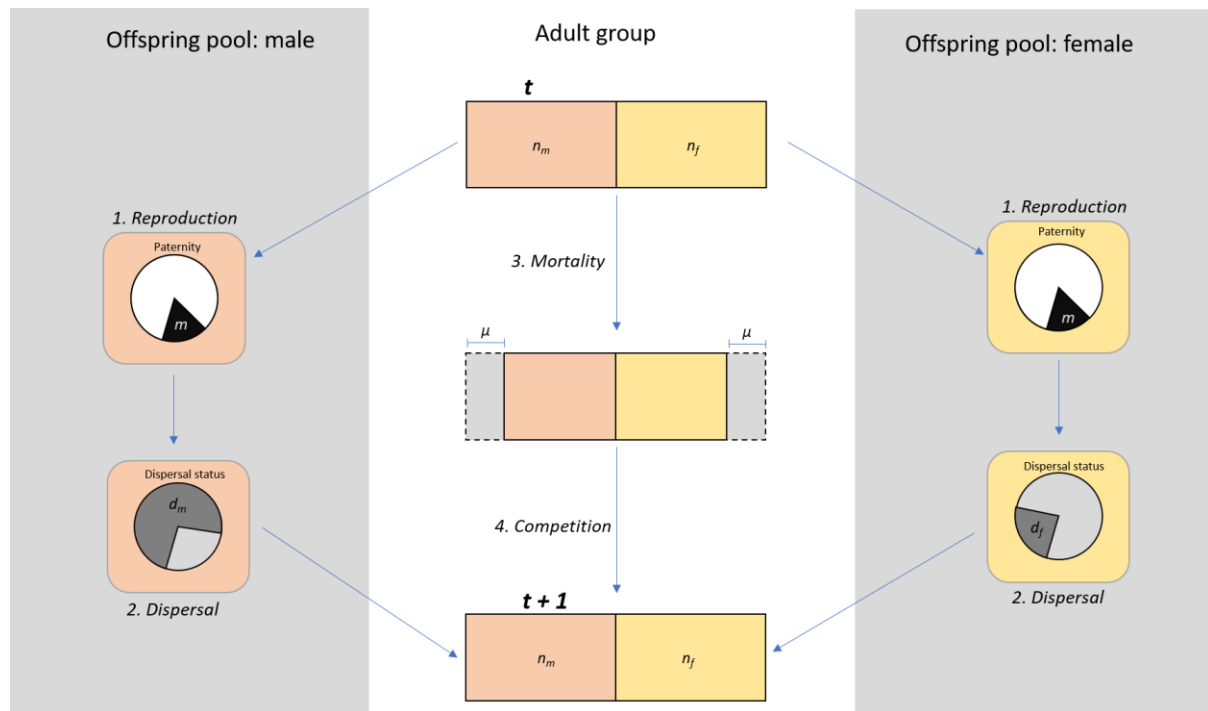
Supplementary Figure 1. Schematic of the analytical model. Moving from time *t* to time *t+1* a series of discrete events occur: (1) reproduction, (2) dispersal, (3) mortality and (4) competition. Offspring pools are represented separately here but all actions occur concurrently to both sexes. Adult groups consist of a fixed number of males (n_m, pale orange) and females (n_f, pale yellow). An arbitrarily large number of offspring of each sex are produced by in-group females. Proportion *m* of offspring are fathered by out-group males (black slice) and the rest are produced by in-group males (white slice). Dispersal then occurs; dispersing offspring join a new group at random. Males and females have separate dispersal rates d_m and d_f respectively. After dispersal, the offspring pool consists of philopatric offspring (light grey slice) and immigrants from other groups (dark grey slice). In the adult group, each individual survives with probability 1-μ. Offspring from the offspring pool then compete equally to replace same-sex group spots.
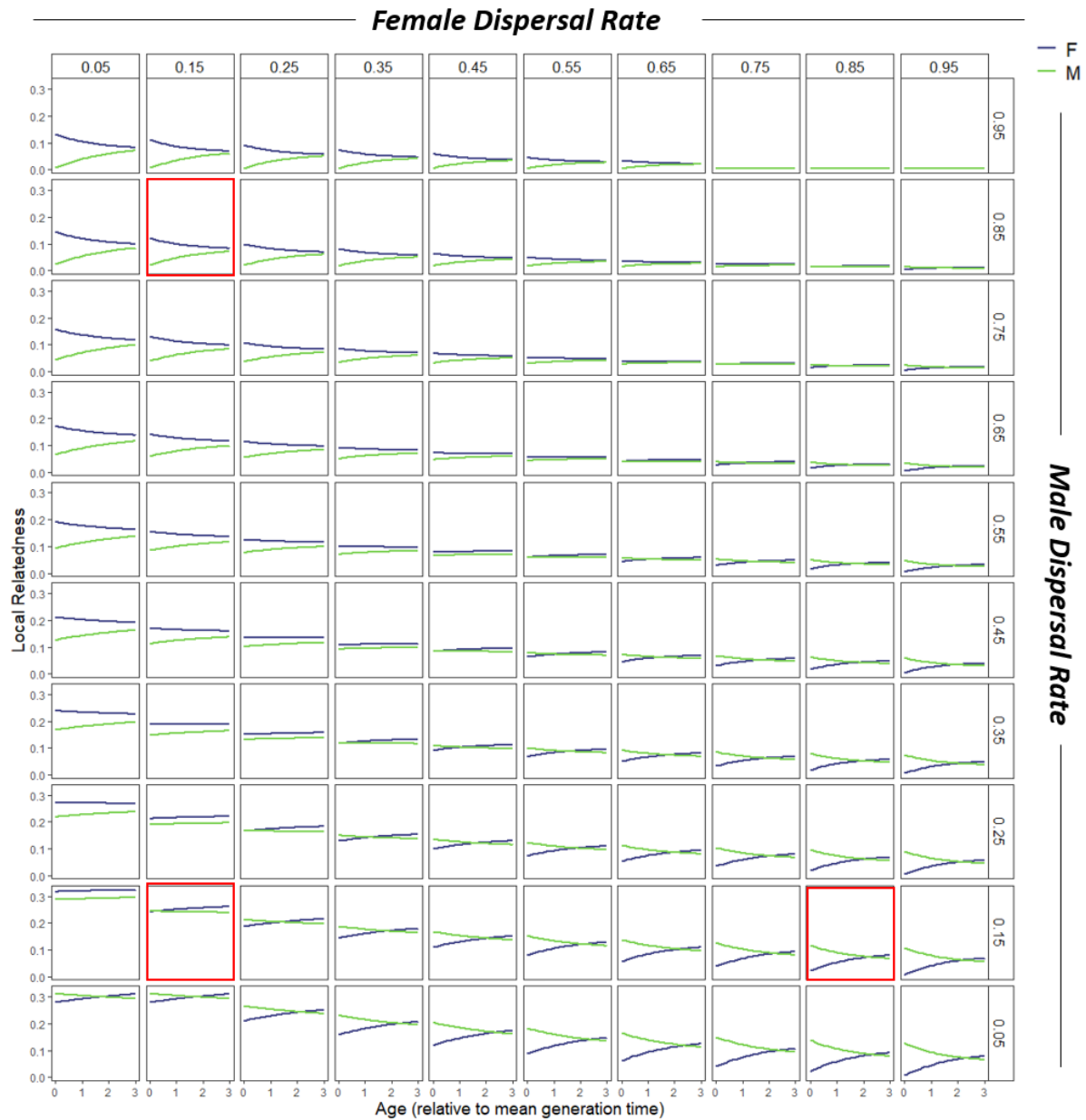
Supplementary Figure 2. Expected kinship dynamics under different rates of female (left to right) and male dispersal (down to up) rate. Predictions are generated from the analytical model with male and female dispersal rates as individuated in the panel and other variables set to $m = 0.82$, $n = 10$, $\mu = 0.1$. In each panel, purple lines show predicted female kinship dynamics and green predicted male kinship dynamics. The structure of the panels means that the bottom left panels represent low dispersal by both sexes, upper right panels show high dispersal by both sexes, top left show low female but high male dispersal and the lower right panels show high female but low male dispersal. Red outlined panels are the (clockwise from top right), male-biased dispersal, female-biased dispersal and bisexual philopatry examples (note here $m = 0.82$ but bisexual philopatry throughout actually has $m = 0$) used throughout the manuscript.

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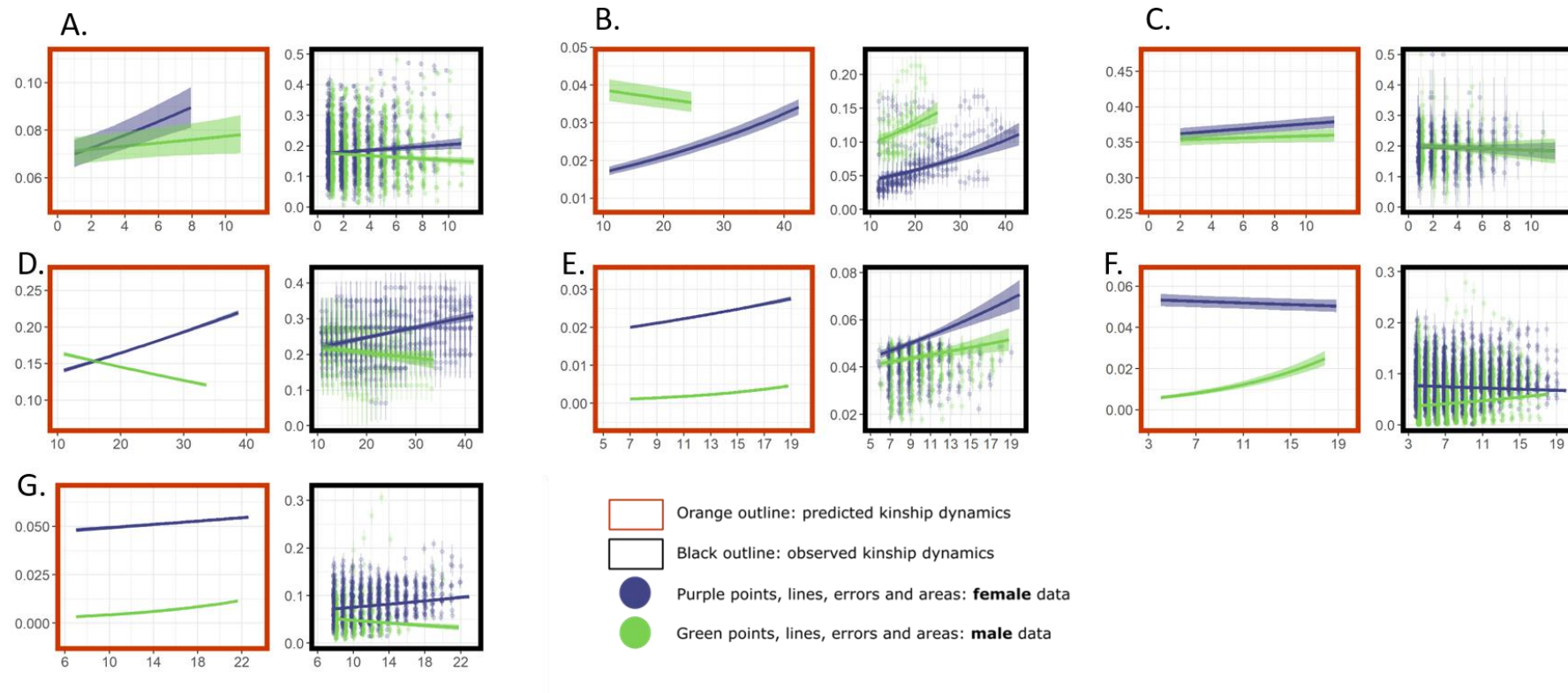

Supplementary Figure 3 Predicted (orange outline panels; i) and observed (black outlined panel; ii) kinship dynamics for males (green) and females (purple) in 7 species of mammal: banded mongooses (A), chimpanzees (B), European badgers (C), killer whales (D), rhesus macaques (E), spotted hyena (F) and yellow baboons (G). Here, local relatedness is calculated to all group members including juveniles. This contrasts with the results presented in the main text where relatedness is only calculated between adults. For model and simulation. As for main text figure 2, in both the predicted and observed plots lines and error represent the mean and 95% credible interval respectively from Bayesian linear models. In the observed plots, points are the mean estimated relatedness with error around the mean estimated relatedness as bars. For further model and simulation, details see main text and the legend to figure 2.

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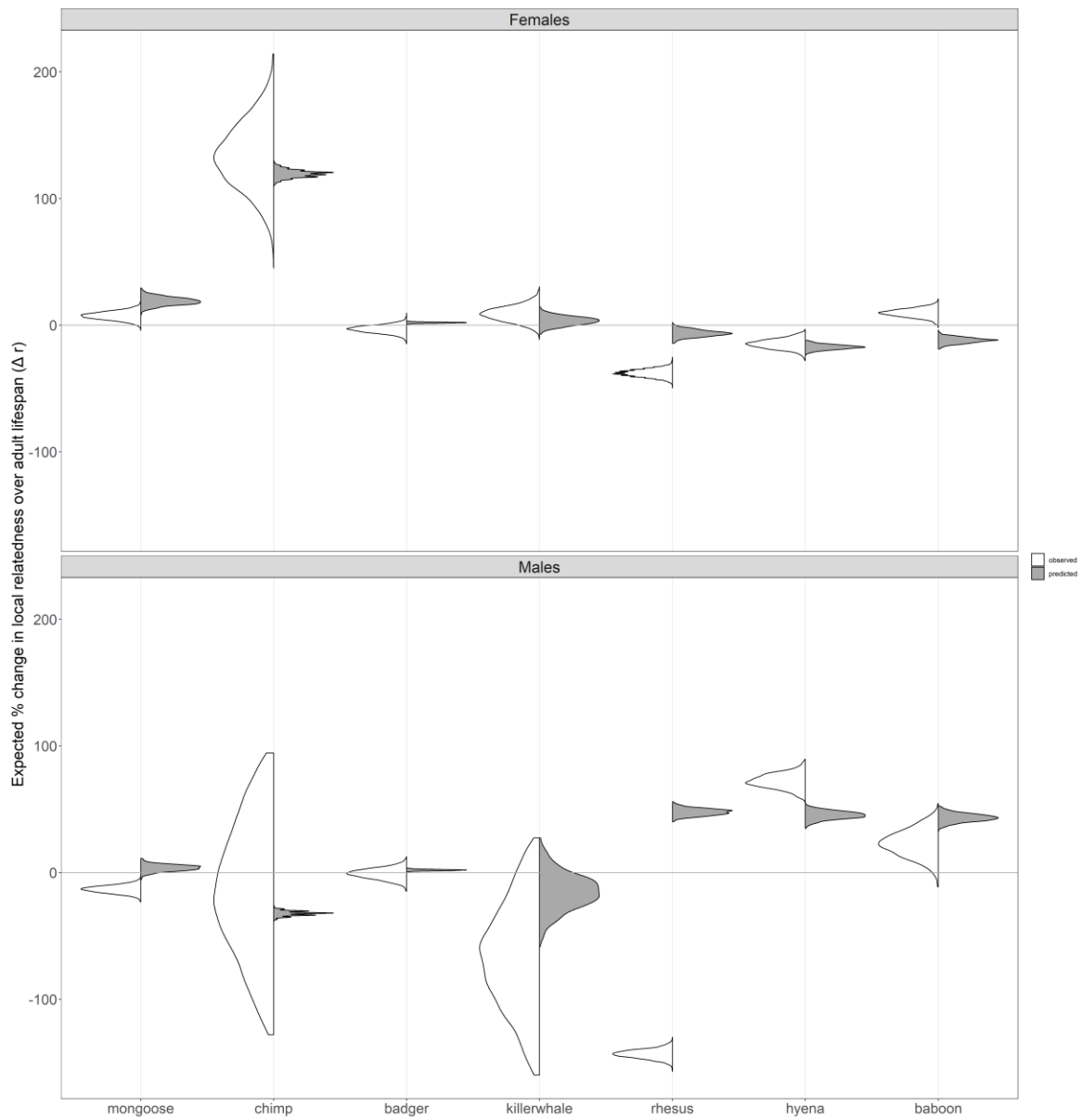

Supplementary Figure 4. Predicted (white) and observed (grey) expected percentage change in local relatedness over adult lifespan for males and females of seven species of mammal. Each area shows the distribution of potential changes from the distribution of beta slope parameters in Bayesian hierarchical models fitted to the predicted and observed data. The observed (grey) areas match those in figure 2 panel H. Overlapping areas show examples where the predicted and observed kinship dynamics are in agreement.

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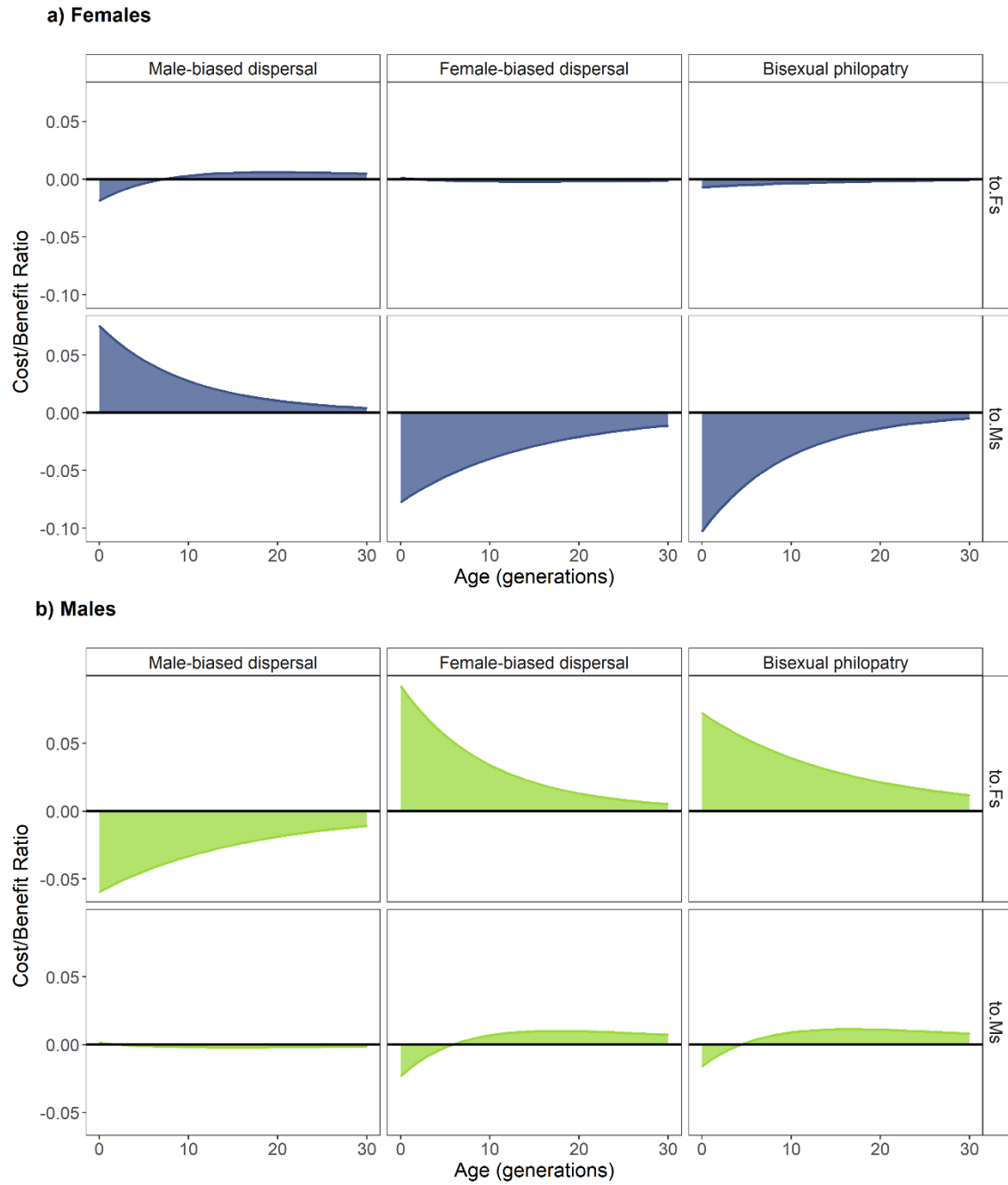
Supplementary Figure 5. Sex-specific selection for survival. a) selection on females interacting with females (top row) and males (bottom row). And b) selection for males interacting with females (top row) and males to help males (bottom row). See main text figure 3 legend for further details.
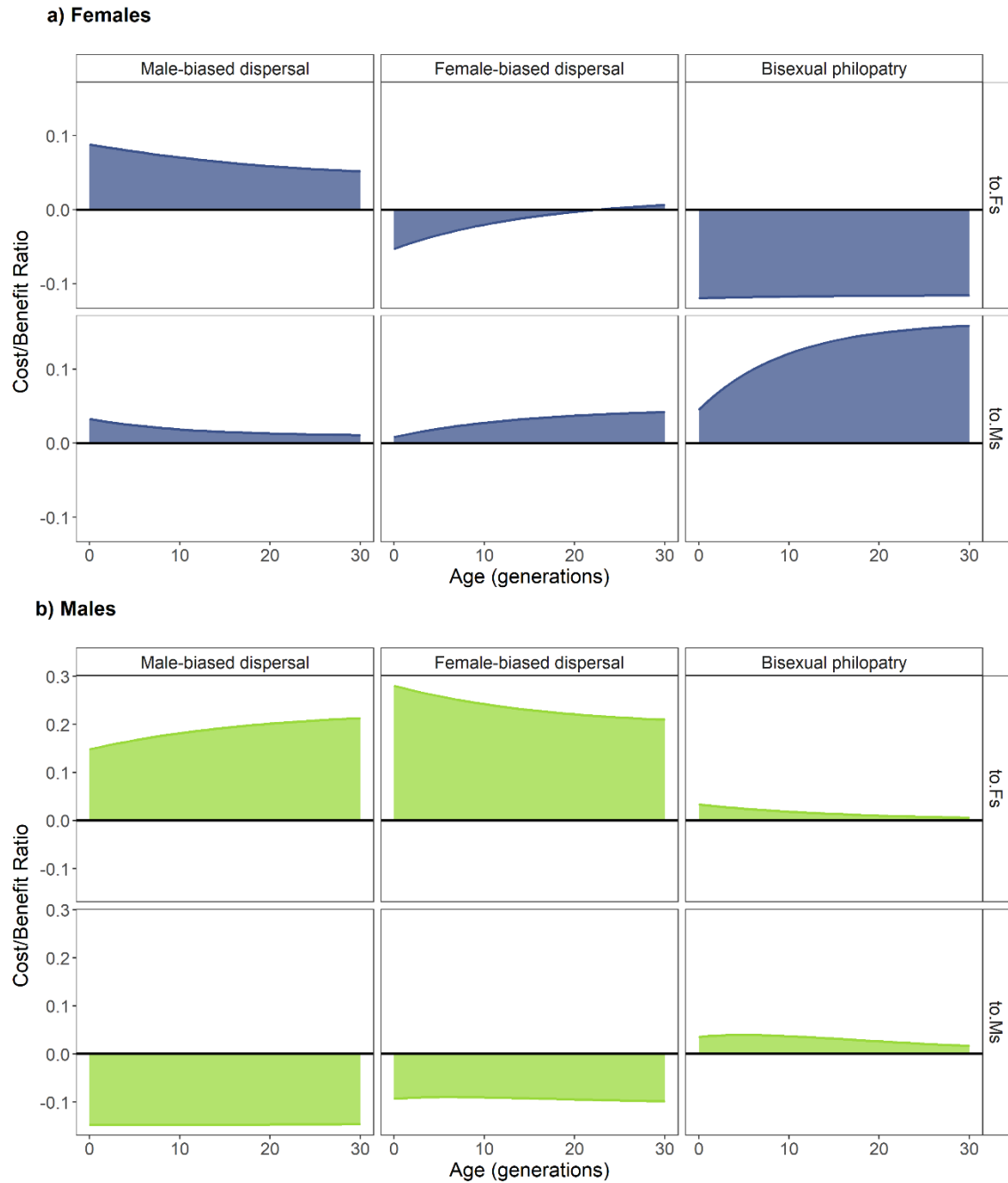
Supplementary Figure 6. Sex-specific selection for fecundity. a) selection for females to interact with females (top row) and males (bottom row). And b) selection on males interacting with females (top row) and males (bottom row). See main text figure 3 legend for further details.

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