

Supplementary information

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

In the format provided by the
authors and unedited

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:

$$g'_f = \mu_f \frac{1}{2} (1 + mg_{fm}) + (1 - \mu_f)g_f \quad (1)$$

$$g'_m = \mu_m \frac{1}{2} (1 + mg_{fm}) + (1 - \mu_m)g_m \quad (2)$$

$$\begin{aligned}
g'_{ff} &= \mu_f^2(1-d_f)^2 \frac{1}{4} \left(\left(\frac{1}{n_f} g_f + \frac{n_f-1}{n_f} g_{ff} \right) + 2m g_{fm} + m^2 \left(\frac{1}{n_m} g_m + \frac{n_m-1}{n_m} g_{mm} \right) \right) \\
&\quad + 2\mu_f(1-\mu_f)(1-d_f) \frac{1}{2} \left(\left(\frac{1}{n_f} g_f + \frac{n_f-1}{n_f} g_{ff} \right) + m g_{fm} \right) \\
&\quad + (1-\mu_f)^2 g_{ff}
\end{aligned} \tag{3}$$

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

$$\begin{aligned}
g'_{mm} &= \mu_m^2(1-d_m)^2 \frac{1}{4} \left(\left(\frac{1}{n_f} g_f + \frac{n_f-1}{n_f} g_{ff} \right) + 2m g_{fm} + m^2 \left(\frac{1}{n_m} g_m + \frac{n_m-1}{n_m} g_{mm} \right) \right) \\
&\quad + 2\mu_m(1-\mu_m)(1-d_m) \frac{1}{2} \left(m \left(\frac{1}{n_m} g_m + \frac{n_m-1}{n_m} g_{mm} \right) + g_{fm} \right) \\
&\quad + (1-\mu_m)^2 g_{mm}
\end{aligned} \tag{5}$$

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 equilibrium. We can then derive mean relatedness coefficients 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

$$r_{ff} = \frac{g_{ff}}{g_f}, r_{mf} = \frac{g_{fm}}{g_f}, r_{fm} = \frac{g_{fm}}{g_m}, r_{mm} = \frac{g_{mm}}{g_m} \quad (6)$$

(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 homologous 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

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

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

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

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

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

$1 - \mu_f$ 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

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

A note on methods of calculation

To facilitate calculation 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

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

where

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

and

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

where

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

This allows us to write

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

and

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

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 further 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

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

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}

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

(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).

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

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

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

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

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

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

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

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

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

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

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

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

Having derived expressions for the inclusive fitness impact of a helpful or harmful trait, we quantify 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 $n_m/(n_f + n_m - 1)$).

Supplementary 2: Study Systems

Banded Mongoose

Banded mongooses (*Mungos mungo*) are obligately social Carnivora distributed widely through sub-Saharan Africa¹. They inhabit stable multi-male multi-female groups, usually called packs¹. Each pack aggressively defends their territory from other packs². 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 males¹. Neither males nor females disperse from their natal group, with almost all mongooses remaining in their natal group for the whole life¹. 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 age¹⁰.

The banded mongoose data used here were collected as part of the Banded Mongoose Research Project (socialisresearch.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 1995¹. 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.

Acknowledgements

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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 maturity¹³. All adults have the potential to breed but there is some dominance-linked reproductive skew in males¹⁴. In the Tai Forest,

for example, the dominant male fathers, on average, 50% of offspring¹⁴. Extra-group mating is rare but can occur¹⁵.

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 1997¹⁶. Both groups are subject to detailed year-round behavioural observations¹⁷. Since the start of intensive observation of a group, births, deaths and dispersals in the groups have been reliably inferred from observation¹³. 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 behaviour¹³. Maternity is inferred from observations of parturient females and infant behaviour and confirmed by microsatellite analysis¹³. 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 group¹³. 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.

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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 year¹⁹. Territories usually contain a communal underground burrow, known as a sett, but may also contain additional, sometimes outlying setts within the territorial boundaries¹⁹. In this population, offspring of both sexes regularly disperse from their natal group²⁰⁻²², 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 population¹⁹. 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 year¹⁹. 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 location²⁵. Genotyping has been used to assign parents to cubs born since 1986^{24,26}.

Acknowledgements

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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 salmon²⁷⁻²⁹. 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 months³⁰. 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 matriline consisting of females, their adult offspring of both sexes and their matrilineal grand-offspring³⁰. Southern-resident matriline in turn preferentially associate into three pods³⁰. While within pod associations matriline 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 lives³⁰. Mating occurs both within and between pods, but rarely within matriline³².

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 patch³⁰. Adult killer whales have sexually dimorphic dorsal fin shapes, and immature whales are sexed based on opportunistic sightings of their ventral markings³⁰. 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 observed³⁰. Maternity is inferred based on observations of mother-calf behaviour conducted by the Center for Whale Research³⁰. 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; see³⁰). 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 belongs³³. 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

Data were collected by the Center for Whale Research under federal permits (Marine Mammal Protection Act permit 532-1822 and/or Department of Fisheries and Oceans licence 200-08/SRA-34) in both Canada and the USA. All applicable international, national and institutional guidelines for the use of animals were followed. We would also like to acknowledge the contributions of many volunteers over the years of data collection.

Rhesus macaque

Rhesus macaques (*Macaca mulatta*) are generalist *Cercopithecine* primates inhabiting a range of habitats throughout southern, south-eastern and eastern Asia³⁴. Rhesus macaques form stable, mixed-sex, closed social groups throughout their range³⁵. Individuals of both sexes all show a variety of affiliative interactions resulting in complex within-group social networks³⁶. 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-fission³⁹. 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 females⁴². 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 subcontinent⁴⁵. 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 identification⁴⁵. 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 1992⁴⁶. Some macaques die before the end of their first year when they would be captured so have unknown paternity.

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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 life⁵⁰ whereas most males disperse to another clan after reaching sexual maturity^{51,52}. Clan social structure is characterised by a linear dominance hierarchy⁵³. The dominance relationships and clan hierarchy emerge from asymmetries in the number of recruitable social allies between clan members⁵⁴. Social alliances are strongest among close kin and stronger among philopatric hyenas than between philopatric and immigrant individuals and among immigrants⁵⁵. As a result, social dominance fluctuates depending on the kin and demographic structure of the clan⁵⁴. 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 season⁵⁶. Females have control over copulation owing to the unusual anatomy of their genitals⁵⁷ and exercise mate choice^{52,56}. Females almost always mate with males of their clan; immigrant and philopatric males are similarly successful⁵¹. 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 brothers⁵². 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 rare⁶⁰. Female investment in cubs is high: the gestation period is 110 days⁶¹ and cubs are nursed for an average of 13 months with highly nutritious milk⁶². Males do not provide care for their young⁵⁶.

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 notches⁵⁹. 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 dispersal⁵². The age of individuals born in Crater clans is estimated based on pelage and ear characteristics, body size, behaviour, and locomotory abilities⁵⁹. 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 glans⁶³. Parentages are assigned using amplification of nine polymorphic spotted hyena microsatellites^{51,52,64} and maximum likelihood methods as implemented in CERVUS 3.0⁶⁵; 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 (\pm SD) increased from 24.3 (\pm 13.4) to 42.9 (\pm 14.4) during the study period.

Acknowledgements

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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 Africa⁶⁶.

Yellow and olive baboons exhibit the same social system: populations are subdivided into stable social groups consisting of multiple adults and juveniles of both sexes⁶⁶. 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 age⁶⁷.

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 years⁷⁰. Both sexes have strong linear dominance hierarchies determining priority of access to resources⁶⁶. 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 interactions⁷¹. In contrast, male dominance rank is not affected by maternal dominance rank⁷². 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 lines⁷⁵.

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 characteristics⁷⁴. 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}.

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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 $1 / \text{age of maturity}$ 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 patterns 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

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

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

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

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 within 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 (β), with separate random intercepts for individual id (\bar{a}), sex specific intercepts (s) and a group size parameter (γ). 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	\bar{a}	σ_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).

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

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

<i>Parameter</i>	<i>Definition and discussion</i>	<i>Equivalent parameter in Johnstone and Cant (2010)</i>
<i>Dispersal rate (male and female)</i>	<p>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.</p> <p>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.</p>	d_f, d_m
<i>Adult Group size</i>	<p>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.</p> <p>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.</p>	$n_f + n_m$
<i>Juvenile group size</i>	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.	<i>n/a</i>
<i>Local mating rate</i>	<p>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.</p> <p>Local mating rate for a given species will result from that species mating system⁸³ and the proportion of offspring fathered by extra-group males^{84,85}.</p>	m
<i>Expected adult lifespan (male and female)</i>	<p>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.</p> <p>We use expected adult lifespan to calculate sex-specific mortality rates (equation 1).</p> <p>Equation 1: $\mu = 0.5/e_{L\alpha} - \alpha$</p> <p>Where μ is adult mortality rate, α is age at maturity at $e_{L\alpha}$ is the expected lifespan at maturity.</p> <p>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 in⁸⁷.</p>	μ_f, μ_m
<i>Age at maturity</i>	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.	<i>n/a</i>

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

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.

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

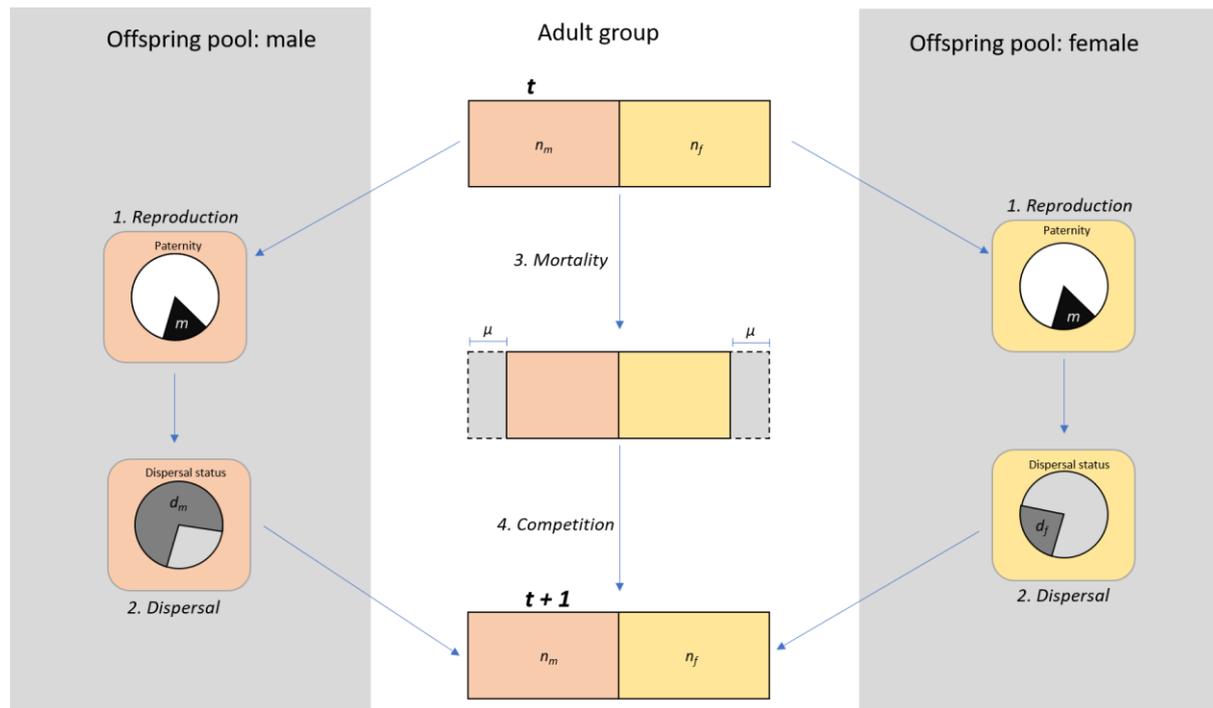
Supplementary Table 7. Description of the variables used in the statistical models. See equations 2, S1 and S2.

Model variables	Description
\hat{r}	Estimated local relatedness. See main text section <i>calculating relatedness</i> 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 <i>calculating relatedness</i> 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 $\theta = 2$ probability is equal between 0 and 1, if $\theta < 2$ probabilities near 0 and 1 are more common and if $\theta > 2$ 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 .

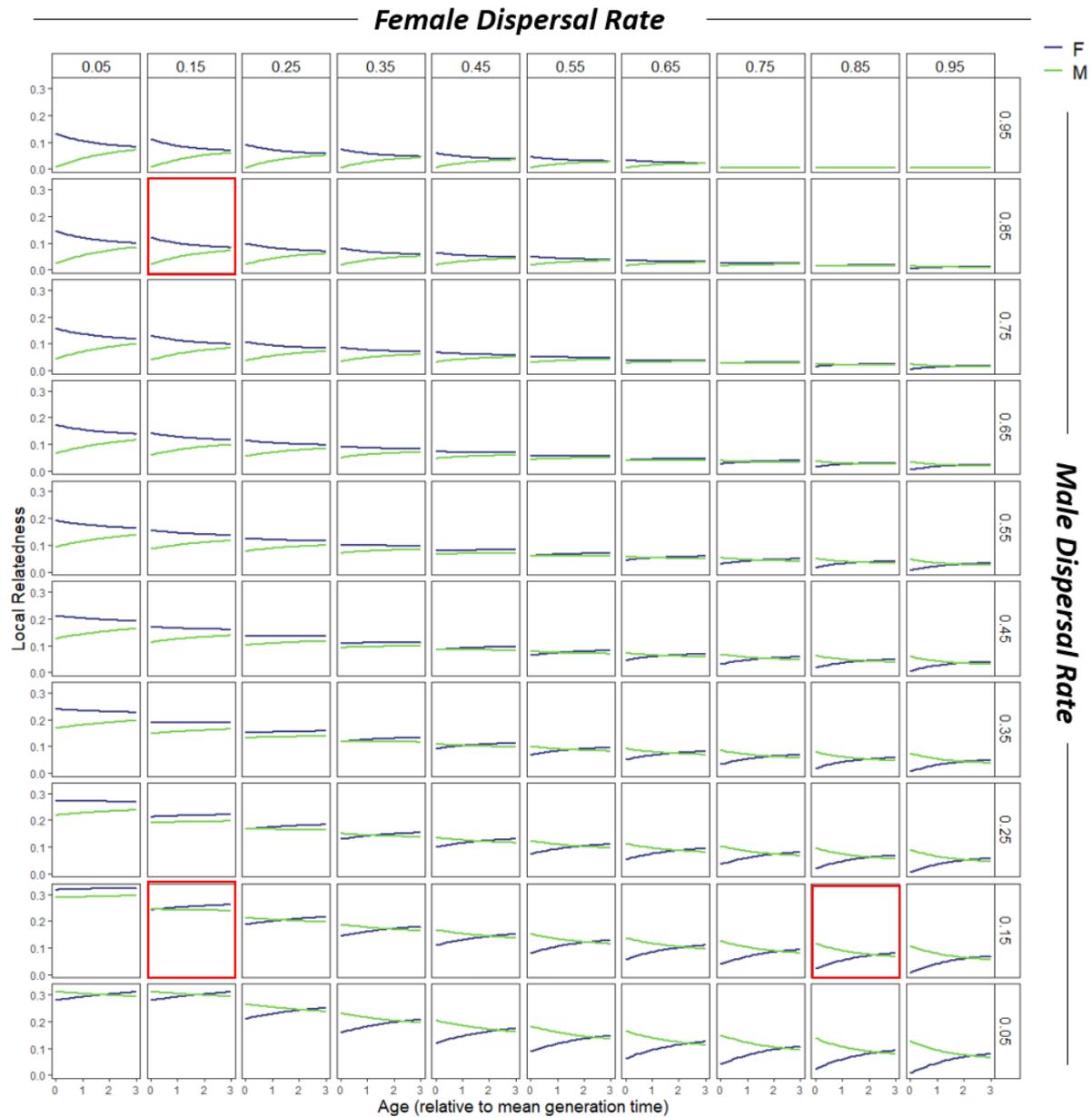
Supplementary Table 8. Prior parameters on the sex intercept s used in each model. Intercept priors are a normal distribution with mean x and standard deviation y . Note all priors are defined in the logit scale.

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

Supplementary figures

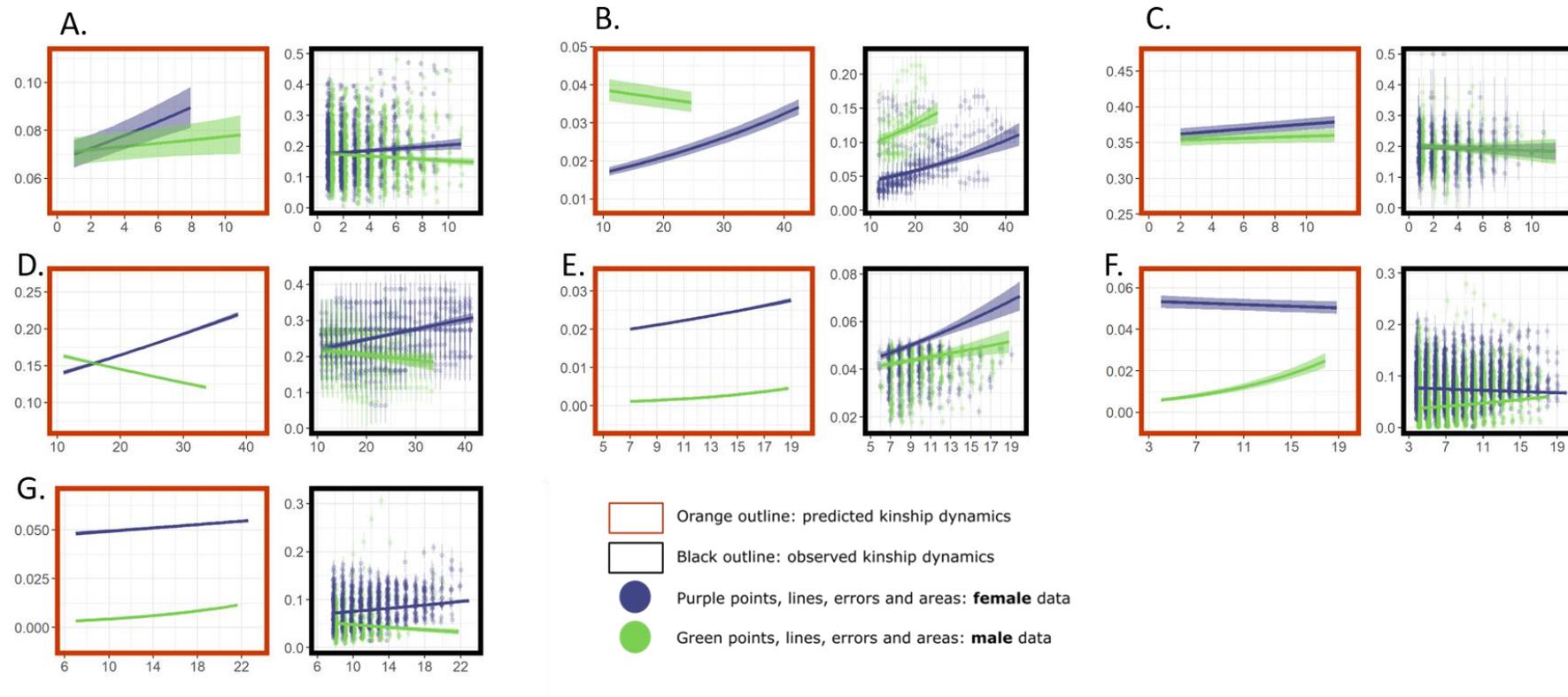


Supplementary Figure 1. Schematic of the analytical model. Moving from time t to time $t+1$ a series of discrete events occur: (1) reproduction, (2) dispersal, (3) mortality and (4) competition. Offspring pools are represented separately here but all actions occur concurrently to both sexes. Adult groups 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 $1-\mu$. Offspring from the offspring pool then compete equally to replace same-sex group spots.

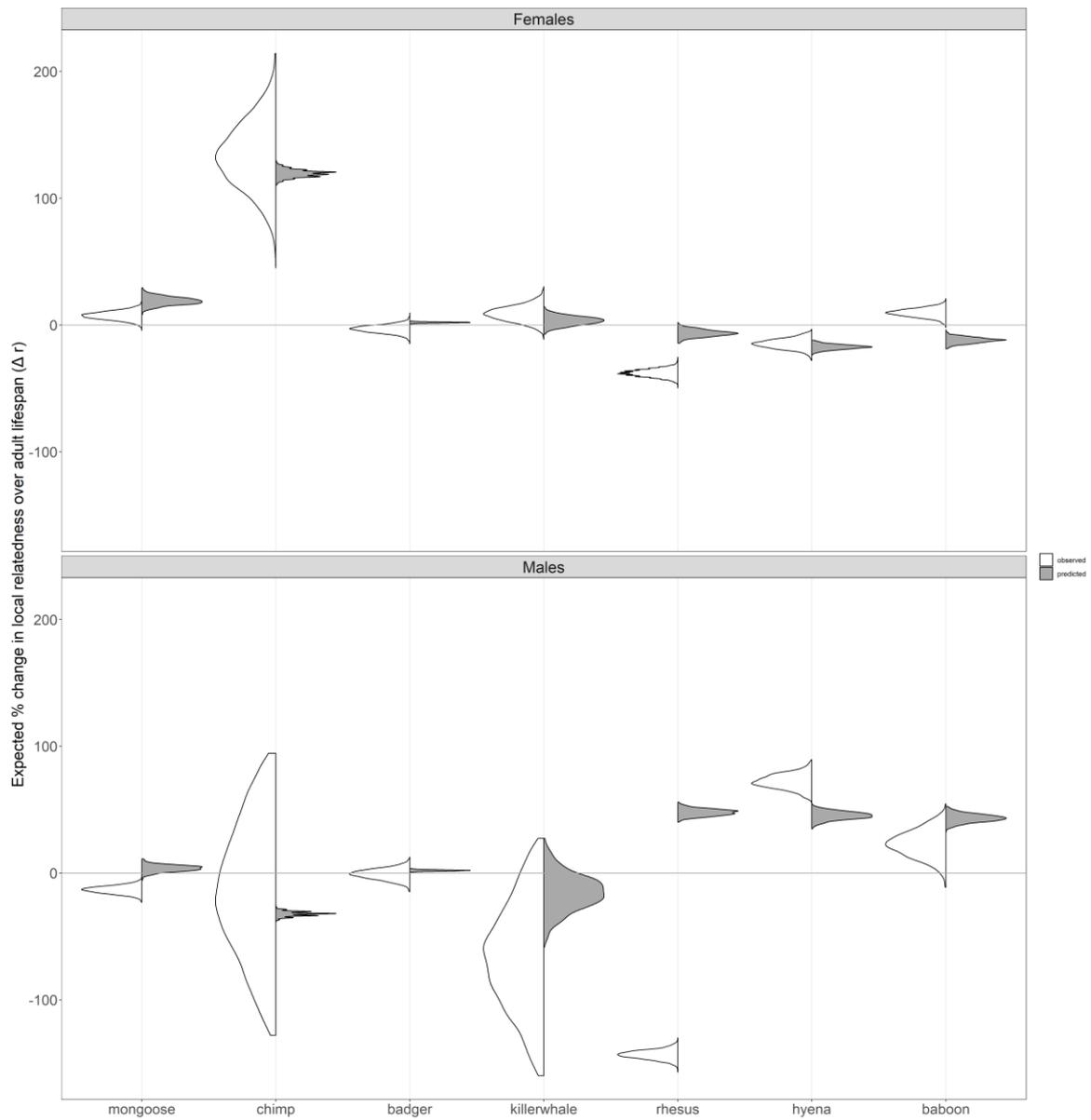


Supplementary Figure 2. Expected kinship dynamics under different rates of female (left to right) and male dispersal (down to up) rate. Predictions are generated from the analytical model with male and female dispersal rates as individuated in the panel and other variables set to $m = 0.82$, $n = 10$, $\mu = 0.1$. 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.

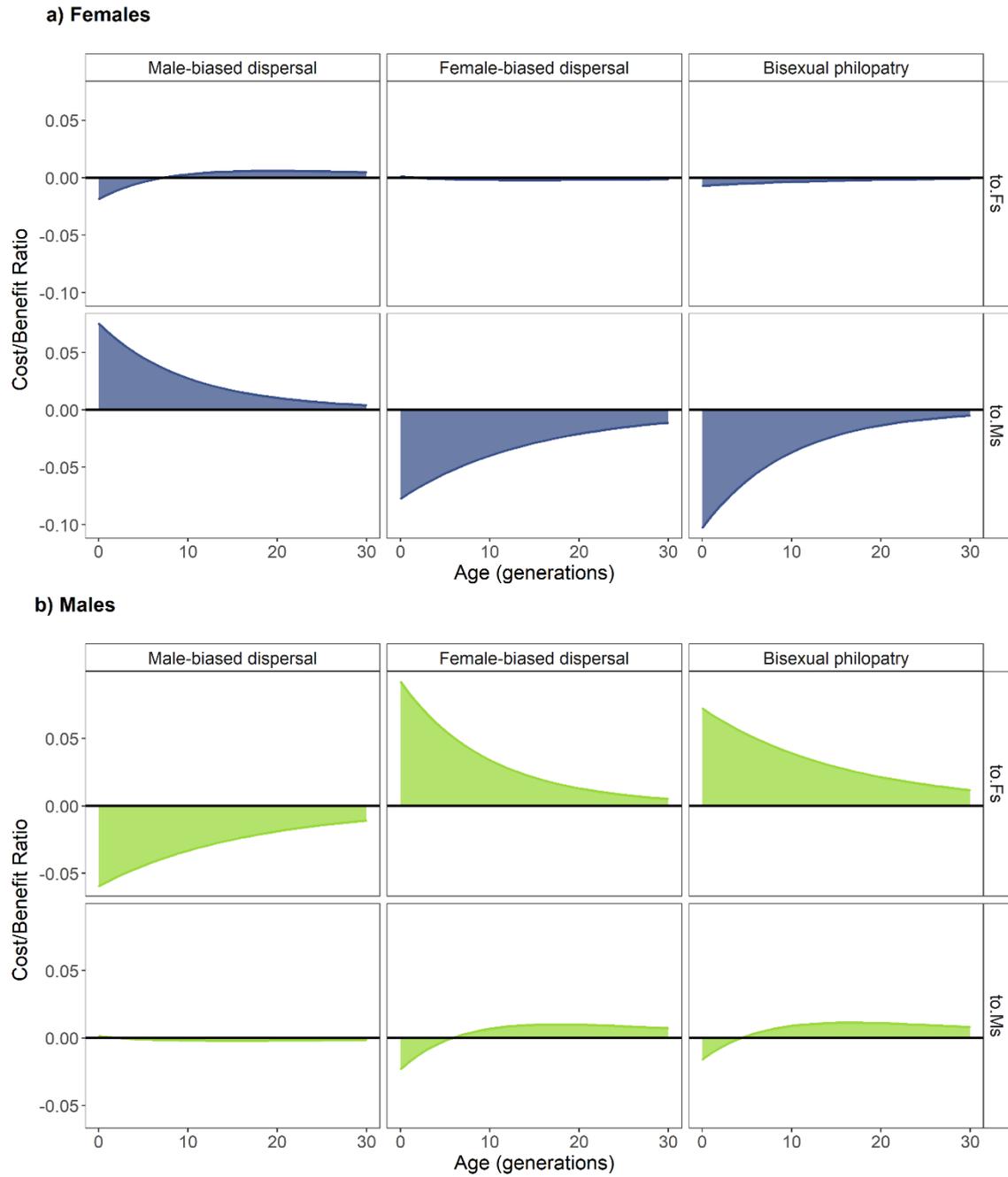
Patterns and consequences of age-linked change in local relatedness in animal societies



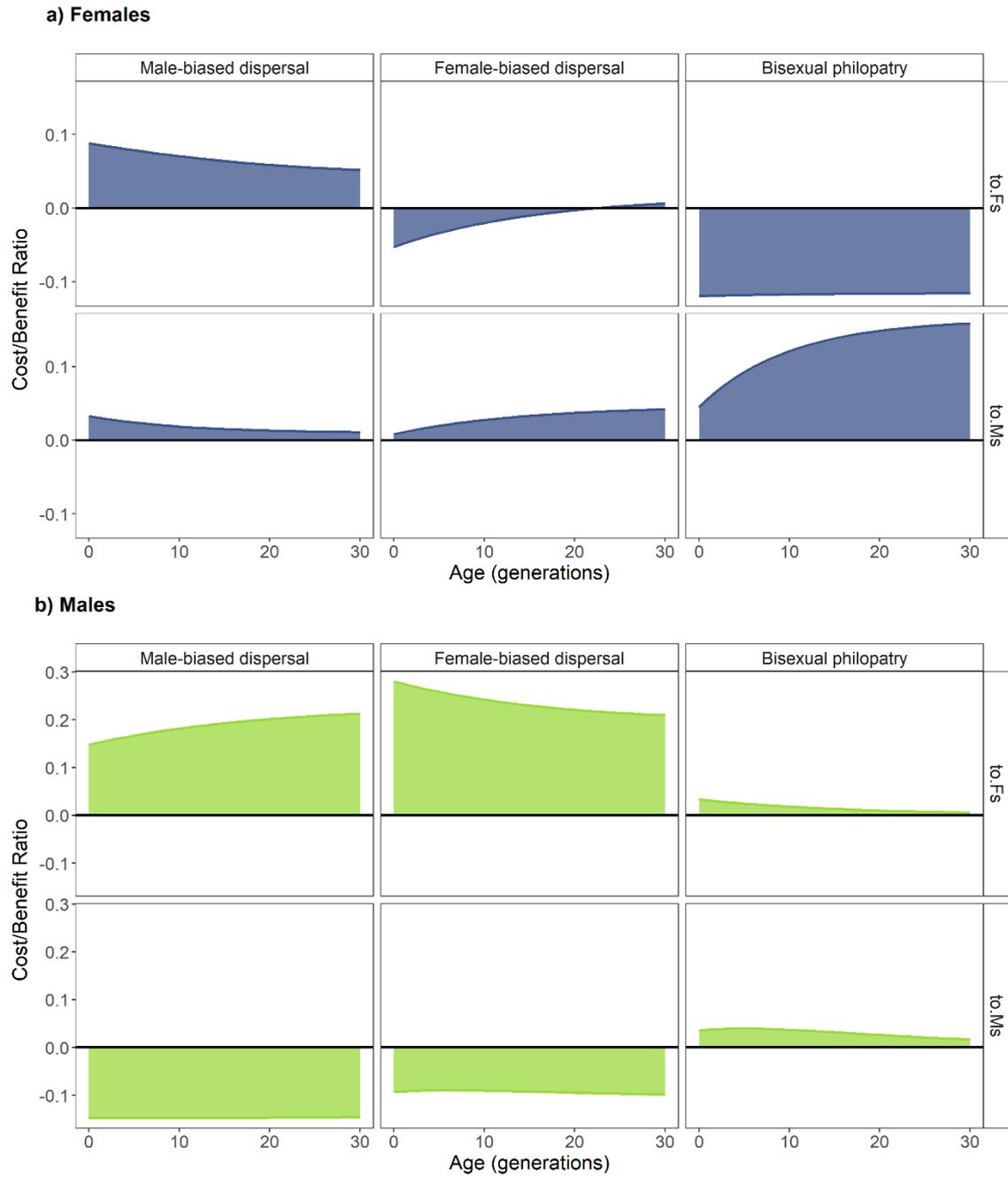
Supplementary Figure 3 Predicted (orange outline panels; i) and observed (black outlined panel; ii) kinship dynamics for males (green) and females (purple) in 7 species of mammal: banded mongooses (A), chimpanzees (B), European badgers (C), killer whales (D), rhesus macaques (E), spotted hyena (F) and 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.



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.



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.

Supplementary References

0. Lehmann, L. & Rousset, F. When do individuals maximize their inclusive fitness? *Am. Nat.* **195**, 717–732 (2020).
1. Cant, M. A., Nichols, H. J., Thompson, F. J. & Vitikainen, E. I. K. Banded mongooses: Demography, life history, and social behavior. *Coop. Breed. Vertebr. Stud. Ecol. Evol. Behav.* 318–337 (2016). doi:10.1017/CBO9781107338357.019
2. Thompson, F. J., Marshall, H. H., Vitikainen, E. I. K. & Cant, M. A. Causes and consequences of intergroup conflict in cooperative banded mongooses. *Anim. Behav.* **126**, 31–40 (2017).
3. Cant, M. A. Social control of reproduction in banded mongooses. *Anim. Behav.* **59**, 147–158 (2000).
4. Vitikainen, E. I. K. *et al.* Biased escorts: Offspring sex, not relatedness explains alloparental care patterns in a cooperative breeder. *Proc. R. Soc. B* **284**, 20162384 (2017).
5. Inzani, E. L. *et al.* Female reproductive competition explains variation in prenatal investment in wild banded mongooses. *Sci. Rep.* **6**, 1–6 (2016).
6. Inzani, E. *et al.* Spontaneous abortion as a response to reproductive conflict in the banded mongoose. *Biol. Lett.* **15**, 4–8 (2019).
7. Thompson, F. J. *et al.* Reproductive competition triggers mass eviction in cooperative banded mongooses. *Proc. R. Soc. B Biol. Sci.* **283**, (2016).
8. Nichols, H. J., Cant, M. A., Hoffman, J. I. & Sanderson, J. L. Evidence for frequent incest in a cooperatively breeding mammal. *Biol. Lett.* **10**, 3–6 (2014).
9. Nichols, H. J., Cant, M. A. & Sanderson, J. L. Adjustment of costly extra-group paternity according to inbreeding risk in a cooperative mammal. *Behav. Ecol.* **26**, 1486–1494 (2015).
10. Wells, D. A. *et al.* Extra-group paternity varies with proxies of relatedness in a social mammal with high inbreeding risk. *Behav. Ecol.* **32**, 94–104 (2021).
11. Nichols, H. J., Jordan, N. R., Jamie, G. A., Cant, M. A. & Hoffman, J. I. Fine-scale spatiotemporal patterns of genetic variation reflect budding dispersal coupled with strong natal philopatry in a cooperatively breeding mammal. *Mol. Ecol.* **21**, 5348–5362 (2012).
12. Wells, D. A., Cant, M. A., Nichols, H. J. & Hoffman, J. I. A high-quality pedigree and genetic markers both reveal inbreeding depression for quality but not survival in a cooperative mammal. *Mol. Ecol.* **27**, 2271–2288 (2018).
13. Wittig, R. M. & Boesch, C. Demography and life history of five chimpanzee communities in the Tai National Park. in *The chimpanzees of the Tai forest: 40 years of research* (eds. Boesch, C. *et al.*) 125–140 (Cambridge University Press, 2019).
14. Boesch, C., Kohou, G., Néné, H. & Vigilant, L. Male competition and paternity in wild chimpanzees of the Tai forest. *Am. J. Phys. Anthropol.* **130**, 103–115 (2006).
15. Vigilant, L., Hofreiter, M., Siedel, H. & Boesch, C. Paternity and relatedness in wild chimpanzee communities. *Proc. Natl. Acad. Sci. U. S. A.* **98**, 12890–12895 (2001).
16. *The Chimpanzees of the Tai Forest: 40 years of research.* (Cambridge University Press, 2019).
17. Wittig, R. M. & Boesch, C. Observational protocol and long-term data collection in Tai. in *The chimpanzees of the Tai forest: 40 years of research2* (eds. Boesch, C. *et al.*) 44–57 (Cambridge University Press, 2019).
18. Vigilant, L. Insights from genetic analyses of the Tai chimpanzees. in *The chimpanzees of the Tai forest: 40 years of research2* (eds. Boesch, C. *et al.*) 70–77 (Cambridge University Press, 2019).
19. McDonald, J. L., Robertson, A. & Silk, M. J. Wildlife disease ecology from the individual to the population: Insights from a long-term study of a naturally infected European badger population. *J. Anim. Ecol.* **87**, 101–112 (2018).

20. Rogers, L. M. *et al.* Movement of badgers (*Meles meles*) in a high-density population: Individual, population and disease effects. *Proc. R. Soc. B Biol. Sci.* **265**, 1269–1276 (1998).
21. Cheesman, C. L., Cresswell, W. J., Harris, S. & Mallinson, P. J. Comparison of dispersal and other movements in two Badger (*Meles meles*) populations. *Mamm. Rev.* **18**, 51–59 (1988).
22. Tuytens, F. A. M. *et al.* Spatial perturbation caused by a badger (*Meles meles*) culling operation: Implications for the function of territoriality and the control of bovine tuberculosis (*Mycobacterium bovis*). *J. Anim. Ecol.* **69**, 815–828 (2000).
23. Carpenter, P. J. *et al.* Mating system of the Eurasian badger, *Meles meles*, in a high density population. *Mol. Ecol.* **14**, 273–284 (2005).
24. Marjamäki, P. H. *et al.* Individual variation and the source-sink group dynamics of extra-group paternity in a social mammal. *Behav. Ecol.* **30**, 301–312 (2019).
25. Delahay, R. J., Langton, S., Smith, G. C., Clifton-Hadley, R. S. & Cheeseman, C. L. The spatio-temporal distribution of *Mycobacterium bovis* (bovine tuberculosis) infection in a high-density badger population. *J. Anim. Ecol.* **69**, 428–441 (2000).
26. Marjamäki, P. H., Dugdale, H. L., Delahay, R., McDonald, R. A. & Wilson, A. J. Genetic, social and maternal contributions to *Mycobacterium bovis* infection status in European badgers (*Meles meles*). *J. Evol. Biol.* **34**, 695–709 (2021).
27. Ford, J. K. B. & Ellis, G. M. Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. *Mar. Ecol. Prog. Ser.* **316**, 185–199 (2006).
28. Hanson, M. B. *et al.* Species and stock identification of prey consumed by endangered southern resident killer whales in their summer range. *Endanger. Species Res.* **11**, 69–82 (2010).
29. Hanson, M. B. *et al.* Endangered predators and endangered prey : Seasonal diet of Southern Resident killer whales. *PLoS One* **16**, e0247031 (2021).
30. Bigg, M. A., Olesiuk, P. F., Ellis, G. M., Ford, J. K. B. & Balcomb, K. C. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Rep. Int. Whal. Comm. Spec.* 383–405 (1990).
31. Parsons, K. M., Balcomb, K. C., Ford, J. K. B. & Durban, J. W. The social dynamics of southern resident killer whales and conservation implications for this endangered population. *Anim. Behav.* **77**, 963–971 (2009).
32. Ford, M. J. *et al.* Inbreeding in an endangered killer whale population. *Anim. Conserv.* **21**, 423–432 (2018).
33. Ellis, S. *et al.* Mixture models as a method for comparative sociality: social networks and demographic change in resident killer whales. *Behav. Ecol. Sociobiol.* **75**, 1–15 (2021).
34. Cords, M. The behavior, ecology, and social evolution of Cercopithecine monkeys. in *The Evolution of Primate Societies* (eds. Mitani, J. C., Call, J., Kappeler, P. M., Palombit, R. A. & Silk, J. B.) 91–112 (The University of Chicago Press, 2012).
35. Thierry, B. Unity in diversity: Lessons from macaque societies. *Evol. Anthropol.* **16**, 224–238 (2007).
36. Brent, L. J. N. The causes and consequences of sociality in adult female rhesus macaques using a social network approach. (University of Roehampton, London, UK, 2010).
37. Drickamer, L. C. & Vessey, S. H. Group changing in free-ranging male rhesus monkeys. *Primates* **14**, 359–368 (1973).
38. Weiß, B. M., Kulik, L., Ruiz-Lambides, A. V. & Widdig, A. Individual dispersal decisions affect fitness via maternal rank effects in male rhesus macaques. *Sci. Rep.* **6**, 1–10 (2016).
39. Larson, S. M., Ruiz-Lambides, A., Platt, M. L. & Brent, L. J. N. Social network dynamics precede a mass eviction in group-living rhesus macaques. *Anim. Behav.* **136**, 185–193 (2018).
40. Widdig, A. *et al.* A longitudinal analysis of reproductive skew in male rhesus macaques. *Proc. R. Soc. B*

- 271, 819–826 (2004).
41. Dubuc, C., Ruiz-Lambides, A. & Widdig, A. Variance in male lifetime reproductive success and estimation of the degree of polygyny in a primate. *Behav. Ecol.* **25**, 878–889 (2014).
 42. Blomquist, G. E., Sade, D. S. & Berard, J. D. Rank-related fitness differences and their demographic pathways in semi-free-ranging rhesus macaques (*Macaca mulatta*). *Int. J. Primatol.* **32**, 193–208 (2011).
 43. Ruiz-Lambides, A. V. *et al.* Long-term analysis on the variance of extra-group paternities in rhesus macaques. *Behav. Ecol. Sociobiol.* **71**, (2017).
 44. Ruiz-Lambides, A. V., Weiß, B. M., Kulik, L. & Widdig, A. Which male and female characteristics influence the probability of extragroup paternities in rhesus macaques, *Macaca mulatta*? *Anim. Behav.* **140**, 119–127 (2018).
 45. Rawlings, R. & Kessler, M. *The Cayo Santiago Macaques: History, Behaviour and Biology*. (State University of New York Press, 1986).
 46. Widdig, A. *et al.* Genetic studies on the Cayo Santiago rhesus macaques: A review of 40 years of research. *Am. J. Primatol.* **78**, 44–62 (2016).
 47. Smith, J. E., Kolowski, J. M., Graham, K. E., Dawes, S. E. & Holekamp, K. E. Social and ecological determinants of fission-fusion dynamics in the spotted hyaena. *Anim. Behav.* **76**, 619–636 (2008).
 48. Davidian, E. *et al.* The interplay between social rank, physiological constraints and investment in courtship in male spotted hyenas. *Funct. Ecol.* **35**, 635–649 (2021).
 49. Hofer, H. & East, M. L. The commuting system of Serengeti spotted hyenas: how a predator copes with migratory prey. II. Intrusion pressure and commuters' space use. *Anim. Behav.* **46**, 559–574 (1993).
 50. Höner, O. P., Wachter, B., East, M. L., Runyoro, V. A. & Hofer, H. The effect of prey abundance and foraging tactics on the population dynamics of a social, territorial carnivore, the spotted hyena. *Oikos* **108**, 544–554 (2005).
 51. Davidian, E., Courtiol, A., Wachter, B., Hofer, H. & Höner, O. P. Why do some males choose to breed at home when most other males disperse? *Sci. Adv.* **2**, 1–10 (2016).
 52. Höner, O. P. *et al.* Female mate-choice drives the evolution of male-biased dispersal in a social mammal. *Nature* **448**, 798–801 (2007).
 53. Frank, L. G. Social organization of the spotted hyaena *Crocuta crocuta*. II. Dominance and reproduction. *Anim. Behav.* **34**, 1510–1527 (1986).
 54. Vulllioud, C. *et al.* Social support drives female dominance in the spotted hyaena. *Nat. Ecol. Evol.* **3**, 71–76 (2019).
 55. Smith, J. E. *et al.* Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behav. Ecol.* **21**, 284–303 (2010).
 56. East, M. L., Burke, T., Wilhelm, K., Greig, C. & Hofer, H. Sexual conflicts in spotted hyenas: Male and female mating tactics and their reproductive outcome with respect to age, social status and tenure. *Proc. R. Soc. B Biol. Sci.* **270**, 1247–1254 (2003).
 57. East, M. L., Hofer, H. & Wickler, W. The erect 'penis' is a flag of submission in a female-dominated society: greetings in Serengeti spotted hyenas. *Behav. Ecol. Sociobiol.* **33**, 355–370 (1993).
 58. Hofer, H. & East, M. L. Behavioral processes and costs of co-existence in female spotted hyenas: a life history perspective. *Evol. Ecol.* **17**, 315–331 (2003).
 59. Höner, O. P. *et al.* The fitness of dispersing spotted hyaena sons is influenced by maternal social status. *Nat. Commun.* **1**, 60 (2010).
 60. East, M. L. *et al.* Maternal effects on offspring social status in spotted hyenas. *Behav. Ecol.* **20**, 478–483 (2009).
 61. Matthews, L. H. Reproduction in the spotted hyaena, *Crocuta crocuta* (Erleben). *Philos. Trans. R. Soc.*

- B* **230**, 1–78 (1939).
62. Hofer, H. & East, M. L. Virilized sexual genitalia as adaptations of female spotted hyaenas. *Rev. suisse Zool.* **102**, 895–906 (1995).
 63. Frank, L. G., Glickman, S. E. & Powch, I. Sexual dimorphism in the spotted hyaena (*Crocuta crocuta*). *J. Zool.* **221**, 308–313 (1990).
 64. Wilhelm, K. *et al.* Characterization of spotted hyena, *Crocuta crocuta* microsatellite loci. *Mol. Ecol. Notes* **3**, 360–362 (2003).
 65. Kalinowski, S. T., Taper, M. L. & Marshall, T. C. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol. Ecol.* **16**, 1099–1106 (2007).
 66. Fischer, J. *et al.* Insights into the evolution of social systems and species from baboon studies. *Elife* **8**, 1–16 (2019).
 67. Altmann, S. A. *Foraging for survival: yearling baboons in Africa*. (University of Chicago Press, 1998).
 68. Alberts, S. C. & Altmann, J. Balancing costs and opportunities : dispersal in male baboons. *Am. Nat.* **145**, 279–306 (1995).
 69. Charpentier, M. J. E., Tung, J., Altmann, J. & Alberts, S. C. Age at maturity in wild baboons: Genetic, environmental and demographic influences. *Mol. Ecol.* **17**, 2026–2040 (2008).
 70. Onyango, P. O., Gesquiere, L. R., Altmann, J. & Alberts, S. C. Puberty and dispersal in a wild primate population. *Horm. Behav.* **64**, 240–249 (2013).
 71. Lea, A. J., Learn, N. H., Theus, M. J., Altmann, J. & Alberts, S. C. Complex sources of variance in female dominance rank in a nepotistic society. *Anim. Behav.* **94**, 87–99 (2014).
 72. Packer, C., Collins, D. A. & Eberly, L. E. Problems with primate sex ratios. *Philos. Trans. R. Soc. B Biol. Sci.* **355**, 1627–1635 (2000).
 73. Alberts, S. C., Buchan, J. C. & Altmann, J. Sexual selection in wild baboons: from mating opportunities to paternity success. *Anim. Behav.* **72**, 1177–1196 (2006).
 74. Alberts, S. C., Watts, H. E. & Altmann, J. Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus* . *Anim. Behav.* **65**, 821–840 (2003).
 75. Van Horn, R. C., Buchan, J. C., Altmann, J. & Alberts, S. C. Divided destinies: Group choice by female savannah baboons during social group fission. *Behav. Ecol. Sociobiol.* **61**, 1823–1837 (2007).
 76. Slate, J., Marshall, T. & Pemberton, J. A retrospective assessment of the accuracy of the paternity inference program CERVUS. *Mol. Ecol.* **9**, 801–808 (2000).
 77. Buchan, J. C., Alberts, S. C., Silk, J. B. & Altmann, J. True paternal care in a multi-male primate society. *Nature* **425**, 179–181 (2003).
 78. R Development Core Team. R: A language and environment for statistical computing. (2019).
 79. Wickham, H., François, R. & Müller, K. dplyr: A Grammar of Data Manipulation. (2019).
 80. Clutton-Brock, T. H. & Lukas, D. The evolution of social philopatry and dispersal in female mammals. *Mol. Ecol.* **21**, 472–492 (2012).
 81. Clobert, J., Le Galliard, J. F., Cote, J., Meylan, S. & Massot, M. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol. Lett.* **12**, 197–209 (2009).
 82. Whitehead, H. *Analyzing Animal Societies: Quantative methods for vertebrate social analysis*. (University of Chicago Press, 2008).
 83. Kappeler, P. M. A framework for studying social complexity. *Behav. Ecol. Sociobiol.* **73**, 1–14 (2019).
 84. Isvaran, K. & Clutton-Brock, T. H. Ecological correlates of extra-group paternity in mammals. *Proc. R.*

- Soc. B* **274**, 219–224 (2007).
85. Griffith, S. C., Owens, I. P. F. & Thuman, K. A. Extra pair paternity in birds : a review of interspecific. *Mol. Ecol.* **11**, 2195–2212 (2002).
 86. Healy, K., Ezard, T. H. G., Jones, O. R., Salguero-Gómez, R. & Buckley, Y. M. Animal life history is shaped by the pace of life and the distribution of age-specific mortality and reproduction. *Nat. Ecol. Evol.* (2019). doi:10.1038/s41559-019-0938-7
 87. Ellis, S. *et al.* Postreproductive lifespans are rare in mammals. *Ecol. Evol.* **8**, 2482–2494 (2018).
 88. Johnstone, R. A. & Cant, M. A. The evolution of menopause in cetaceans and humans: The role of demography. *Proc. R. Soc. B* **277**, 3765–3771 (2010).
 89. Natrass, S. *et al.* Postreproductive killer whale grandmothers improve the survival of their grandoffspring. *Proc. Natl. Acad. Sci.* (2019). doi:10.1073/pnas.1903844116
 90. Charpentier, M. J. E., Van Horn, R. C., Altmann, J. & Alberts, S. C. Paternal effects on offspring fitness in a multimale primate society. *Proc. Natl. Acad. Sci. U. S. A.* **105**, 1988–1992 (2008).
 91. Alberts, S. C. & Altmann, J. Preparation and activation: determinants of age at reproductive maturity in male baboons. *Behav. Ecol. Sociobiol.* **36**, 397–406 (1995).
 92. Alberts, S. C. & Altmann, J. Matrix Models for Primate Life History Analysis. *Primate Life Histories and Socioecology* 66–102 (2003).
 93. Koster, J. *et al.* Kinship ties across the lifespan in human communities. *Philos. Trans. R. Soc. B Biol. Sci.* **374**, 20180069 (2019).