Title

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

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Abstract

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

Main text

Introduction

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

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

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

In this study, we combine theoretical modelling with long term individual-based data from several species of group-living mammals to investigate the predictability and consequences of sex differences in kinship dynamics in animals. Specifically, we: (1) develop a theoretical model to predict male and female kinship dynamics under different rates of dispersal and local mating; (2) compare these predicted kinship dynamics with empirical data from seven mammal systems with contrasting social and mating systems; (3) use a model to demonstrate that these patterns of kinship dynamics can select for age-linked behavioural change and that these changes can differ by sex.

Results and Discussion

Sex differences in kinship dynamics

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

Kinship dynamics in mammals

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

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

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

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

Rhesus macaques, spotted hyenas and yellow baboons all have strongly male-biased dispersal, very rare female dispersal and high rates of local mating[32–38]. In both spotted hyenas and yellow baboons, male local relatedness increased with age (spotted hyenas: $\beta = 0.12$ [0.105 – 0.135], $\Delta r = +72\%$; yellow baboons: $\beta = 0.033$ [0.009 – 0.058], $\Delta r = +23\%$) as predicted by our simulation models (figures 2F, 2G). In yellow baboons, this increase is more pronounced after age 14 when their own adult offspring begin joining the reproductive pool of the group ($\beta = 2.18$ [1.398 – 2.96]). While our modelling predicts that rhesus macaque males will show a modest increase in local relatedness with age (figure 2E), this is not reflected in the observed data where male rhesus macaques showed an age-linked decrease in local relatedness ($\beta = -0.143$ [-0.149 – -0.137], $\Delta r = -40\%$). There is, however, a positive relationship between the number of years a male has been in their group (their group-tenure) and their local relatedness (β = 0.85 [0.79 – 0.92]). This suggests that the common secondary dispersal in rhesus macaques[36,37] is nullifying age-linked kinship dynamics, but that local relatedness is still dynamic in this species.

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

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

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

Supplementary Table

The consequences of kinship dynamics

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

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

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

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

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

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

General Discussion

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

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

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

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

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

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

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

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

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

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

Methods

Analytical kinship dynamics model

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

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

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

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

Kinship dynamics in mammals

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

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

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

Kinship dynamics simulation model

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

The agents in the model are adult individuals. Each model iteration is considered to be a year, and agents increase their age each iteration. The agents inhabit groups of fixed size and even sex ratio. At each time step, the agents have a fixed probability of mortality, determined by sex-specific expected lifespan. Dead agents are replaced by either a philopatric or immigrant of the same sex. All agents join a group at a fixed age input as 'age at maturity'. The probability that individuals are philopatric or immigrants is determined by the sex-specific rates of dispersal. Philopatric individuals have a mother chosen from within the group, and the rate of in-group mating determines the probability that the father is also from within the group. Immigrants are unrelated to the other members of their group. The model is run until 2000 individuals have lived in the group- for some species due to computational limitations the target of 2000 was reached by running the model 4 times to 500 individuals. Patterns of kinship dynamics from the simulation model are robust and qualitatively identical for 500 and 2000 individuals. If juveniles are being included in the analysis, after the model of adults has run, non-breeding juveniles are added to each group-year *post-hoc*. Juvenile group size is an inputted model parameter and is filled by maturing philopatric individuals and other offspring who are considered to die or disperse before reaching maturity. More details about the formulation of the simulation model can be found in supplementary 3. The model outputs the age and pedigree of all individuals in the group in each model-year. We use this information to calculate kinship dynamics (see *calculating relatedness* and *statistically modelling* sections).

Calculating relatedness

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

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

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

equation 1.

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

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

equation 2

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

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

equation 3.

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

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

Statistical modelling

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

equation 4

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

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

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Author contributions

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

Data availability

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

Code availability

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

Competing interests

The authors declare no competing interests.

Tables

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

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

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

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

Figure legends

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

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

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

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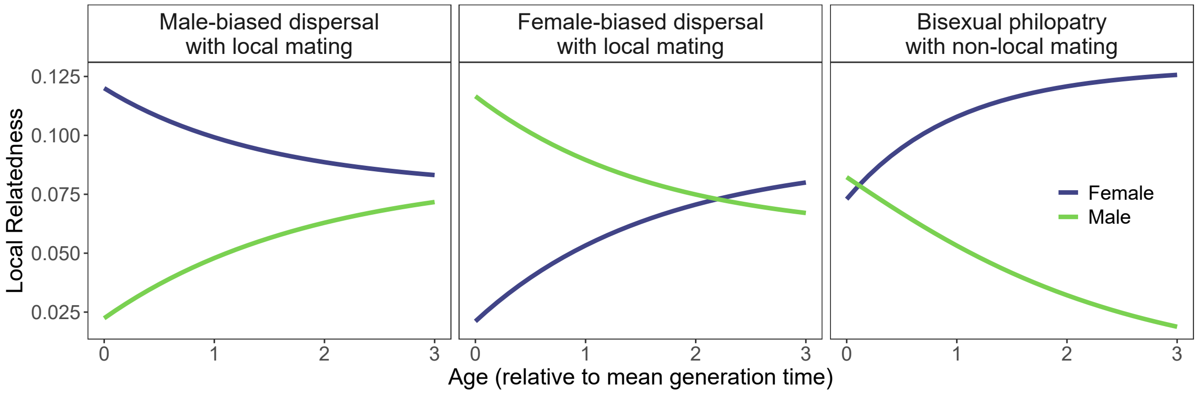


Fig 1

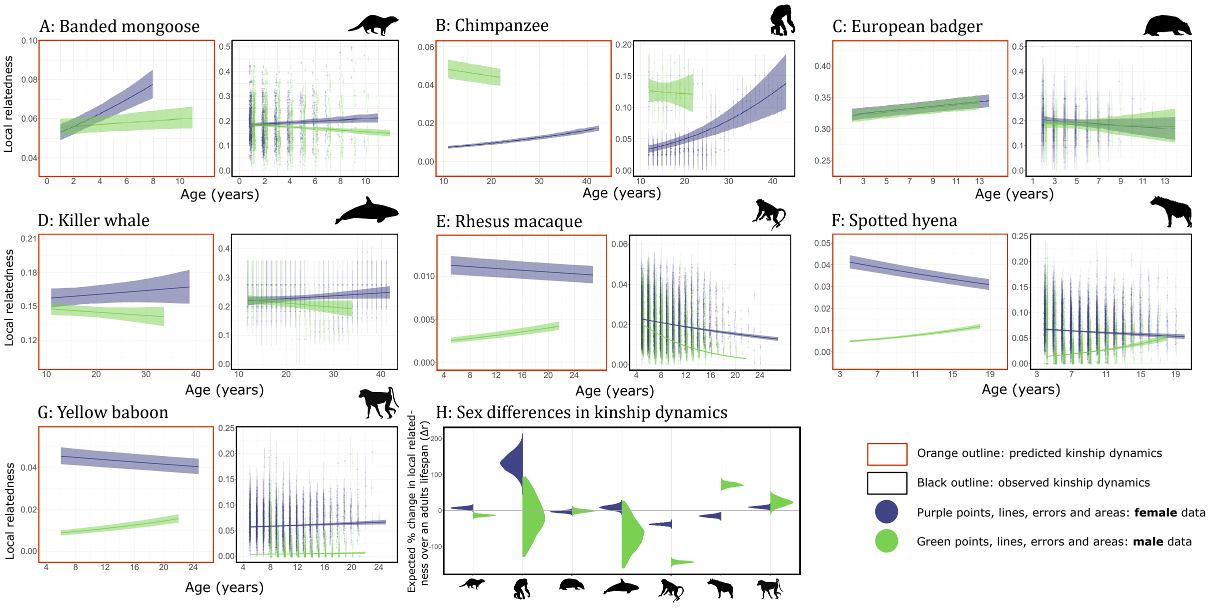
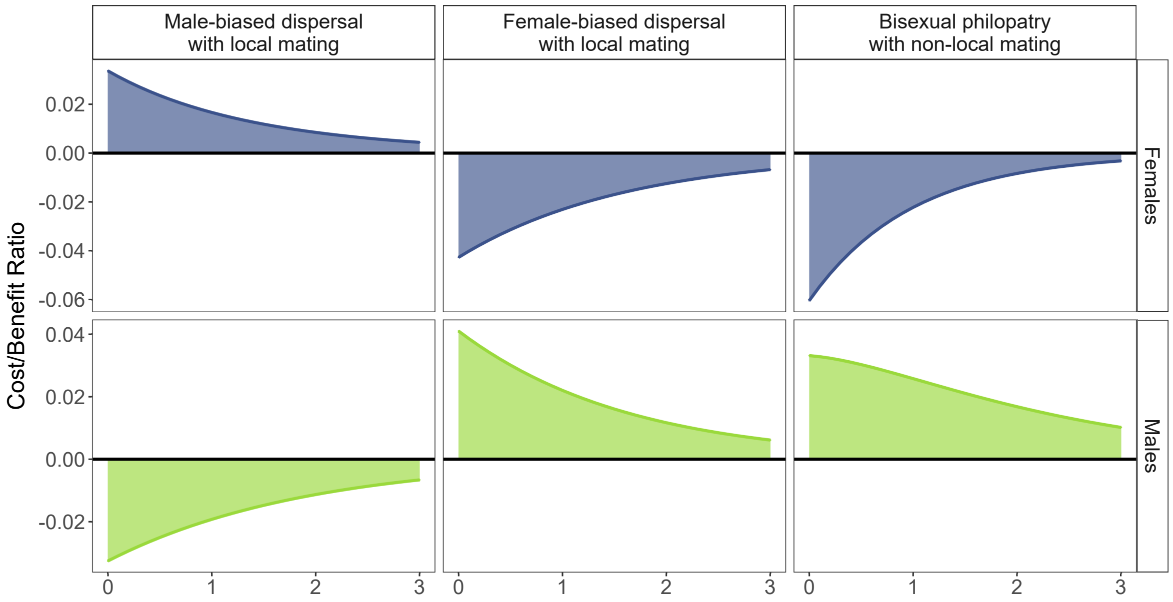

A: Banded mongoose
B: Chimpanzee
C: European badger
D: Killer whale
E: Rhesus macaque
F: Spotted hyena
G: Yellow baboon
H: Sex differences in kinship dynamics
Local relatedness
Age (years)
Expected % change in local relatedness over an adults lifespan (Δr)
Orange outline: predicted kinship dynamics
Black outline: observed kinship dynamics
Purple points, lines, errors and areas: **female** data
Green points, lines, errors and areas: **male** data

Fig 2

a) Survival



b) Fecundity

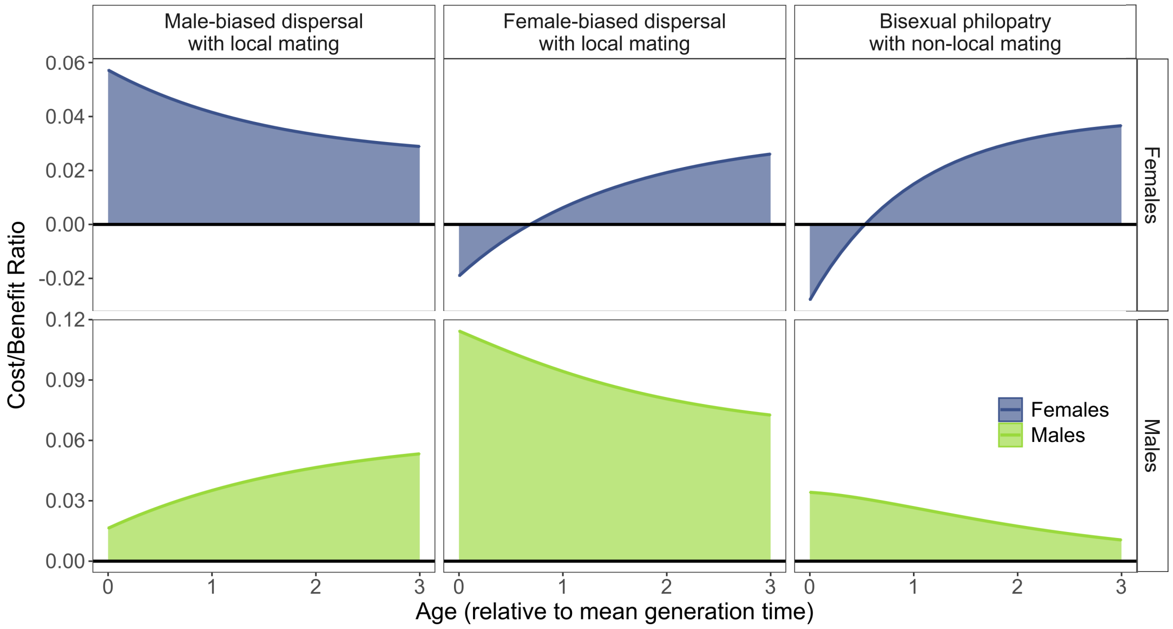


Fig 3