**Kinship Dynamics: Patterns and Consequences of Changes in Local Relatedness**

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**Abstract**

Mounting evidence suggests that patterns of local relatedness can change over time in predictable ways, a process termed kinship dynamics. Kinship dynamics may occur at the level of the population or social group, where the mean relatedness across all members of the population or group changes over time, or at the level of the individual where an individual’s relatedness to its local group changes with age. Kinship dynamics are likely to have fundamental consequences for the evolution of social behaviour and life history because they alter the inclusive fitness payoffs to actions taken at different points in time. For instance, growing evidence suggests that individual kinship dynamics have shaped the evolution of menopause and age-specific patterns of helping and harming. To date, however, the consequences of kinship dynamics for social evolution have not been widely explored. Here we review the patterns of kinship dynamics that can occur in natural populations and highlight how taking a kinship dynamics approach has yielded new insights into behaviour and life history evolution. We discuss areas where analysing kinship dynamics could provide new insight into social evolution and we outline some of the challenges in predicting and quantifying kinship dynamics in natural populations.

For over half a century kin selection has been a cornerstone of evolutionary biology, providing a fundamental theoretical framework for understanding the evolution of social behaviour [1]. When developing the theory of kin selection, Hamilton [1] recognised that a key factor influencing kin structure is the degree to which individuals disperse away from their natal habitat or social group. In Hamilton’s original formalisation of kin selection, however, the behavioural/demographic mechanisms by which the relatedness coefficient *r* was generated were left undefined [1]. The effects of population structure and demography (group size and dispersal rates) on patterns of local relatedness (mean pairwise relatedness to nearby individuals) were explored by Taylor [2]. Rather than specifying the level of relatedness, Taylor [2] allowed relatedness to emerge from the model. Taylor demonstrated that although a decrease in dispersal generated an increase in local relatedness in structured populations, the benefits of helping kin were cancelled out by the costs of an increase in competition among kin [2]. In this pivotal finding, Taylor highlighted the importance of considering how dispersal generates patterns of relatedness in structured populations. Over the last 30 years, a significant focus of theoretical work has been in identifying the factors that influence local relatedness [3]. As well as patterns of dispersal, mating patterns, overlapping generations and social-partner choice can all influence local relatedness [4-10].

Although often considered a static property of a group, population, or species, local relatedness can be dynamic, changing predictably with time - referred to as kinship dynamics [11, 12]. When kinship dynamics are predictable and repeatable, then they may have profound implications for social evolution [11, 12]. Currently, however, despite many species living in kin-structured populations [13], studies of social evolution have tended not to consider the rich implications of kinship dynamics. Here we review the different patterns of kinship dynamics that can occur in natural populations and the potential consequences of kinship dynamics for behaviour and life history evolution. We outline current gaps in our understanding of the patterns and consequences of kinship dynamics and highlight priorities for future research.

1. **Patterns of Kinship Dynamics**

Here we identify three levels at which kinship dynamics may occur in natural populations (Fig 1). First, average local relatedness may change over time at the level of the population (population kinship dynamics; Fig 1A). Second, kinship dynamics may occur at the group level (group kinship dynamics), where the average local relatedness of members of a social group changes over time (Fig 1B). Finally, kinship dynamics may occur at the individual level (individual kinship dynamics), where the relatedness of a focal individual to its local group changes systematically over time, often with age [11, 12] (Fig 1C). These levels can act either independently or concurrently. For example, group level kinship dynamics may occur independent of population kinship dynamics - the local mean relatedness of a social group may change over time while the average local relatedness of the population remains constant over time. Likewise, individual kinship dynamics do not imply population or group kinship dynamics and the overall mean local relatedness (of a group or population) may remain constant over time, even though the average relatedness of an individual female or male to the rest of its group may increase or decrease.

* 1. **Population kinship dynamics**

Population kinship dynamics can be driven by temporal shifts in population density, fecundity (reproductive success), reproductive skew, dispersal and mortality. For example, some species of voles, mice and grouse exhibit cyclical kinship dynamics, linked to changes in population density [14, 17, 18] (Fig 1A). For example, in male red grouse (*Lagopus lagopus scoticus*) males form territories to gain access to females. In the autumn, young of the year males compete to gain a territory and recruitment of males to a population is dependent on them successfully securing a territory. At low population density, males are less aggressive towards kin than non-kin and can even help young related males to gain a territory by relinquishing territory or by helping in territorial contests with unrelated males [19]. This process forms clusters of territories held by related males [20], which in turn generates a positive feedback that leads to the proliferation of kin clusters. A point is reached, however, where space is limited due to the density of the population and the inclusive fitness benefits of helping kin no longer outweigh the direct costs of increased competition. At this point, cooperation breaks down and all individuals behave aggressively. This suppresses recruitment of new males as territory holders and the population spirals into decline and kin clusters break up [14]. This process continues until the population reaches a point where competition is low and the males once again start to help recruit related males to local territories setting the population off on another cycle (Fig 1A).

Changes in patterns of reproductive success and survival may also change patterns of local relatedness over time [21]. In China, for example, demographic transitions have resulted from a reduction in the number of children per family (due to the country’s family planning program) while life expectancy has increased. The combined effects are a decline in the number of kin relationships over time but the kin relationships that do occur are longer lasting [22]. Ecological forces such as predation risk and disease may generate substantial variation in fecundity between groups, which can have consequences for population relatedness [23-25]. Under conditions where the variance in fecundity is high, for example, a predator wiping out an entire family (clutch) of offspring, rather than removing individuals from multiple clutches, then this can lead to high proportions of close kin being recruited to the population in comparison to a scenario where mortality occurs at the level of the individual [25]. Cyclical changes in predation or disease risk could, therefore, in theory, drive cyclical kinship dynamics at the level of the population. The potential for such processes to drive population kinship dynamics, however, remain uninvestigated.

* 1. **Group kinship dynamics**

At the level of the social group, local relatedness may be dynamic and change over time. Such group level kinship dynamics can be driven by a range of demographic, social and ecological factors. For example, in mammalian social groups, smaller groups, with higher reproductive skew tend to have higher within-group average relatedness in comparison to larger groups [26-28]. Changes in group size, for example, as a result of changes in the ecological environment, may thus drive changes in patterns of relatedness within groups. Exactly how relatedness changes with a change in group size, however, will depend on the process of group formation. In banded mongooses (*Mungos mungo*), for example, new groups are founded when single sex groups disperse from their natal group and join with groups of dispersers from other packs to found a new group [15]. This “budding dispersal” can lead to an increase in local relatedness with group age [15] (Fig 1B). In recently founded groups, relatedness between the sexes is low. However, both males and females are highly philopatric, remaining in their natal group to breed, this drives an increase in local relatedness between males and females with the age of the group (Fig 1B). Such group based kinship dynamics can occur across multiple generations, with the longevity of the social group exceeding the longevity of individuals [15]. The process of group formation may be tightly linked to the quality of the environment, population density and mortality rate. For example, in white-winged choughs (*Corcorax melanorhamphos*)new groups were only observed after a period of unusually high mortality as a result of a drought [29]. The process of new group formation was associated with reduced intra-group relatedness due to fusions of unrelated groups/individuals [29]. At high population density, dispersal opportunities may be limited, meaning that individuals are more likely to remain with their local group [30] and thus changes in density at the local or population level may drive kinship dynamics. In some social systems, relatedness may actually decline with the age of the social group. For example, in several ant species, within-colony relatedness decreases with colony age [e.g. 31, 32]. This is driven by new queens being more likely to remain in their natal colony after mating, rather than dispersing to found new colonies as local colony density increases [32, 33]. Thus increasing the number of queens within the colony (increasing polygyny), diluting relatedness between workers and leading to long-term decreases in within-colony relatedness.

Group fission may also be a key process leading to group level changes in kin structure. For example, when the size of a social group exceeds the optimal group size, groups often split. During such fission events, individuals may segregate based on kinship resulting in daughter groups that are more assorted by kinship than the original group (e.g. [34, 35]). Group level changes in kin structure may also be driven by group takeovers, whereby the dispersing sex (usually males in the case of mammals), forcibly move into a group [36-38]. Such takeover events are often associated with the eviction of residents of the same sex and the infanticide of unrelated juvenile resident offspring [36-38]. If unrelated coalitions of males take over a group, then reproduction may be shared among the males [38], which will reduce the relatedness of resulting offspring in comparison to a group with high male reproductive skew. Group fission, fusion and takeover events clearly have the potential to drive group kinship dynamics. To date, however, previous work has not explicitly quantified patterns of kinship dynamics under these social processes.

* 1. **Individual kinship dynamics**

Due to demographic processes – particularly the degree of philopatry and the extent of local mating - local relatedness may change across an individual’s lifetime (individual kinship dynamics (Fig 1C)). Individual kinship dynamics were first formalised in theoretical models examining the evolution of menopause in humans and some species of toothed whales [11, 12] (see Fig 2). These models demonstrate that local relatedness can change as a function of age as some individuals disperse from their natal group, and others die and are replaced by relatives [11, 12]. Johnstone and Cant [12] investigated the consequences of different patterns of dispersal and mating for changes in female local relatedness across the lifespan, highlighting how demographic processes can drive individual kinship dynamics (Fig 2). Under sex biased dispersal and within-group mating, the relatedness of the dispersing sex to their group (after dispersal) is predicted to increase with age [11, 12] (Fig 2Aii). When the dispersing sex takes up residency with their new social group, they will initially have low local relatedness. Their relatedness, however, will increase with age as they reproduce and subsequently their philopatric offspring reproduce and produce philopatric grand offspring, which they are related to. Thus the increase in local relatedness for the dispersing individual joining a new social group is driven by an increase in relatedness to the philopatric sex (Fig 2 Aii). Even when there is no sex biased dispersal, kinship dynamics can still occur [12] (Fig 2 Aiii). For example, in some species of toothed whales, neither sex disperses and mating occurs outside of the social group. Under these conditions, females are born into a group without their father and have comparatively low relatedness to males in the group. As females age and reproduce, their sons will remain in the local group and their relatedness to local males is predicted to increase over time [12]. Work to date on patterns of individual kinship dynamics has tended to consider the general pattern of kinship dynamics at the level of the population for individuals belonging to a particular class (e.g. males or females). However, within a given class of individuals, there is likely considerable variation in the kinship dynamics that individuals experience, for example, due to individual differences in dispersal and fecundity.

Few empirical studies have quantified age-dependent kinship dynamics in natural populations. In a comparative study across 19 human communities with diverse patterns of residence and dispersal, Koster et al. [39] examined the prediction that immigrants to a community will initially have low relatedness to the local group with few kinship ties, but that their local relatedness will increase as they populate the local group with their descendants [11, 12]. The general predicted pattern was observed, with patterns of local relatedness increasing with age in both immigrant males and females where they were the more commonly dispersing sex. Some communities, however, displayed very different patterns, which were likely due to unstable settlement histories, fluid patterns of residency and community size [39]. In human societies, analysis of kinship dynamics could be extended to include affinal kin (in-laws) who may be treated more like biological kin than unrelated friends [40], because they share genetic interests in future generations [41].

Support for individual kinship dynamics also comes from work on non-human animals. For example, in work on wild populations of killer whales that show bisexual philopatry, we have found a strong match with the theoretical prediction of increasing female relatedness with age (Fig 1C, Fig 2Aiii) [16]. Analogous patterns have been found in several species of cooperative breeders where relatedness of an individual to the local group changes as a function of age [42-44]. For example, in African wild dogs (*Lycaon pictus*), dwarf mongooses (*Helogale parvula*) and Lake Tanganyika cichlids (*Neolamprologus pulcher*) the relatedness of non-breeding helpers to the dominant breeders decreases with helper age due to a combination of breeder turnover, extra-pair paternity and helper immigration [42-44].

**2. The consequences of kinship dynamics for social evolution**

Individual kinship dynamics may directly impact patterns of helping and harming behaviour across the lifespan due to a change in the immediate availability of kin with age, which will drive changes in patterns of social behaviour. However, when individual kinship dynamics show predictable changes, they have the potential to influence the evolution of optimal life history and behaviour [11, 12]. For example, models of life history evolution in humans and toothed whales predict that kinship dynamics shape the selective pressures on reproductive lifespan and can help explain why females undergo menopause [11, 12]. Under patterns of kinship dynamics where female relatedness increases with age (which occurs in resident killer whales (Fig 1C) and is thought to be the case in ancestral humans [11, 12]) younger females are predicted to be under strong selection for harming behaviour, whereas older females are under stronger selection for helping behaviour [11, 12 see Fig 2]. Cant and Johnstone formalised these asymmetries in selection for helping and harming behaviour as the reproductive conflict hypothesis, which predicts that when old and young females in the same local group compete for reproduction, younger females should outcompete older females (because they are under stronger selection for harming behaviour). When taken together with the benefits grandmothers can gain by helping their kin (the grandmother hypothesis [49]) the reproductive conflict hypothesis provides a mechanism to explain why females undergo menopause – they are under selection to switch from a harming strategy where they reproduce to a helping strategy where they invest in helping their kin and no longer reproduce themselves [49]. There is strong support in both humans and killer whales that there is intergenerational conflict between old and young females [16, 50, 51] and that this can contribute to selection for the evolution of menopause. For example, in work on resident killer whales using over 40 years of individual-based demographic and social data we showed that when mothers and daughters co-breed, the offspring from the older generation had a significantly higher risk of mortality than offspring from the younger generation female [16].

Evolutionary models of individual kinship dynamics to date, have tended to focus on life history trade-offs at a given point in time [11, 12]. Selection, however, may act on temporal trade-offs between current vs future fitness, which will be shaped by individual kinship dynamics. Such trade-offs would not require an individual to project likely changes in kinship dynamics itself - selection on social traits will be influenced by the expected future kin structure and the associated fitness costs and benefits. Although there has been little explicit analysis of how kinship dynamics (i.e. changing levels of relatedness over time) influence inter-temporal trade-offs,  models have shown that kin selection can modulate the balance between current and future costs and benefits (even when relatedness remains constant) [52, 53]. For example, Lehmann [52] demonstrated that when there is a tendency for future members of an individual’s community to be kin, then selection can act on organisms in a way that produces future benefits to its community. Sozou [53] extended this concept further to examine how an individual should value future benefits to itself (individual discounting) or its social community (social discounting), finding that the social discounting rate was generally lower than the individual (private) discounting rate. The extension of kinship dynamic models to consider temporal trade-offs and social/individual discounting provides an exciting avenue for future research.

To date, models examining the evolutionary consequences of individual kinship dynamics have been restricted to studies investigating the evolution of menopause in humans and toothed whales. There is no reason to expect, however, that the behaviour and life-history implications of kinship dynamics are restricted to the evolution of this unusual life-history trait. Kin selection models have been integrated with life-history theory in considering the evolution of senescence, where an individual's longevity can influence the vital rates of local relatives [54, 55]. If individuals can provide benefits to kin in late life it may select for longevity [49, 56-58]. In support of this prediction, recent work comparing the longevity of females across non-human mammals found that females in species with grandparental care lived longer [59]. Thus we hypothesise that in species where relatedness increases with individual age selection will favour longevity if there are opportunities for late life helping. The costs of interacting with kin, which can reduce the fitness of relatives, may also drive life history evolution [54]. For example, theoretical work has reported that low juvenile dispersal reduces the strength of selection on adult survival [55], favouring the evolution of shorter lifespans [60, 61]. Thus we predict that in species where interacting with kin carries significant costs, individual kinship dynamics, where relatedness increases with age could result in selection for shorter lifespans. Future research is needed to understand how kinship dynamics interact with both the opportunities for helping kin and the costs of interacting with kin to shape the evolution of senescence. Theoretical work has also shown that competition among kin can shape age-specific fecundity [55]. When dispersal is limited and competition among siblings is intense, selection will favour individuals to reduce competition among kin during times of peak fertility and spread reproduction throughout life [55]. Kinship dynamics thus have the potential to shape reproductive decisions across the lifespan, well beyond the evolution of menopause and new work is needed to examine how kinship dynamics influence reproductive decisions across the lifespan.

At the level of the group - group kinship dynamics generate the possibility that patterns of helping and harming within and between groups may change over time. For example, in the case of the banded mongoose, an increase in within-group relatedness will select for increased helping within groups which could manifest as increased helping in rearing pups and/or dominant individuals being more tolerant of the breeding attempts of related subordinate individuals in older vs younger groups [15]. Moreover, in social groups that have high levels of within-group relatedness selection can favour indiscriminate helping whereby individuals do not adjust the level of help they provide other individuals within the group in response to their relatedness to them [45]. Group based kinship dynamics may have consequences for the success of the group. For example, in matrilineal groups of red howler monkeys, the average group relatedness predicts female reproductive success with females in kin groups having significantly higher reproductive success [46]. In addition, theoretical work has demonstrated that changes in within-group or population relatedness can change the nature of intergroup violence and warfare [47]. For example, an increase in within-group relatedness may increase selection for belligerence and bravery behaviours, which can result in individuals paying a personal cost of death so that relatives in the group can gain benefits such as new mating opportunities or additional resources [47]. Predictable changes in patterns of local relatedness at a group level may shape how social relationships form in groups. For example, one possibility is that founding animals may invest more in forming stronger social relationships in groups where kinship increases over time. Future empirical and theoretical work is needed to examine the ontogeny of social relationships in social groups that are undergoing different patterns of group kinship dynamics.

Because kin selection is conditional on the kin structure in the social environment, kinship dynamics may result in cyclical shifts in selection which could reduce the long term efficiency of kin selection [48]. Under population and group kinship dynamics, which can occur across many generations, different social traits may be selected for under different levels of local relatedness. Such condition-dependent selection may dilute the strength of selection when social conditions change across generations or differ between social groups [48]. In periods when social traits are not under strong selection, genetic drift may be enhanced, which can lead to accelerated evolution – referred to as the Red King process [48]. The efficiency of kin selection thus may be weaker under greater conditionality (i.e. when periods of high relatedness occur infrequently). Future work is needed to directly explore the consequences of population and group kinship dynamics for the efficiency of kin selection.

**3. Predicting and quantifying individual kinship dynamics**

Current models predicting patterns of kinship dynamics have tended to focus on the consequences of variation in dispersal and mating [11, 12]. It is likely however that other factors also play a role in driving kinship dynamics in animal societies, including group size, mortality patterns and variation in fecundity. How well model predictions match empirical patterns of kinship dynamics will depend on how well they capture the key processes driving relatedness patterns [26]. Some insight into how population traits other than dispersal and mating patterns may influence individual kinship dynamics comes from a study by Rodrigues [62] who examined how variation in age-dependent changes in patterns of fecundity drive age-dependent kinship dynamics which in turn is expected to drive age-dependent patterns of helping behaviour. Rodrigues found that in populations where fecundity increases with age, the average local relatedness of an individual to their local group is predicted to increase with age, which will select for an increase in helping with the actor’s age. In predicting patterns of kinship dynamics, it is important to accurately evaluate demographic features of the population that can drive kinship dynamics (e.g. dispersal patterns). In some instances, the predictability of kinship dynamics may be limited due to stochasticity in demographic variables (including, for example, mortality, reproductive success and dispersal).

New work is needed to fully examine how demographic and life history traits impact on patterns of kinship dynamics. Kinship dynamics are likely to show considerable differences between the sexes. For example, work in humans illustrates that kinship dynamics can show surprisingly diverse patterns across communities and the sexes [39] with local relatedness both increasing and decreasing as a function of age. In the vast majority of natural populations, there is a bias towards one sex dispersing. It is well documented that sex differences in dispersal mean that kin selection can affect males and females very differently [63]. Currently, however, how the sexes differ in patterns of kinship dynamics and the resulting implications for sex differences in life history evolution remains unexplored. Moreover, within a sex it is well documented that both dispersal patterns [64] and reproductive success can vary among individuals, which will generate inter-individual variation in kinship dynamics. The consequences of this inter-individual variation in patterns of kinship dynamics for social evolution has not been explored.

To quantify patterns of kinship dynamics, we need to decide how to quantify local relatedness. In species where individuals form stable social groups, we can track patterns of kinship by examining patterns of relatedness between individuals within a local group over time. However, in many animal societies, social groups are dynamic and individuals interact and cooperate with animals from different social units. Here we need to capture social interactions within and between groups. One approach is to use social network theory and community detection algorithms to define local kinship networks [65]. It would then be possible to quantify local kin structure using weighted measures of association strength, using association indices [66] to weight relatedness between individuals by the strength (weight) of their association.

**4. Conclusions**

Kinship dynamics mean that the strength and direction of kin selection can change systematically over time [11, 12, 16, 62]. To date however, very few studies have incorporated kinship dynamics into models of social evolution. Current theory, predicting the evolutionary consequences of kinship dynamics has tended to focus on species that undergo menopause. However, the evolutionary consequences of kinship dynamics are likely to extend well beyond this unusual life history trait and new work is needed to develop a general understanding of the evolutionary consequences of kinship dynamics at the level of the population, group and individual.

A particularly exciting avenue for future research is the comparison of kinship dynamics between the sexes. Life history differences between the sexes within a species are widespread and significant attention has been given to examining the mechanisms driving sex differences in life history evolution [67]. It is possible that in many species, the sexes experience very different patterns of kinship dynamics that could have been a significant force driving sex differences in life history evolution. Because kinship dynamics are driven by demographic processes, kinship dynamics are likely to show profound differences between species. For example, individual kinship dynamics are dependent on patterns of philopatry, the general pattern of which differs between birds and mammals (e.g. in birds females normally disperse more than males whereas in contrast in mammals males typically disperse more than females [68]) leading to the prediction that general patterns of kinship dynamics may differ between taxa. Moreover, because group size, predation and fecundity likely play a key role in driving patterns of kinship dynamics, it is likely that patterns of kinship dynamics differ between populations of the same species living under different ecological conditions. Future work comparing patterns of kinship dynamics between species, populations and the sexes is eagerly anticipated.

Patterns of kinship dynamics may help explain variation in social behaviour across the lifespan and contribute to patterns of social ageing. In humans and non-human primates there may be fundamental shifts in social interactions as individuals age [69]. This can include the propensity to engage in social interactions, the capability to influence others and the positive vs negative valence of social interactions [70]. How patterns of individual kinship dynamics influence the cost-benefit trade-off of social interactions across the lifespan and thus patterns of social ageing remains unexplored.

Future research should examine how active partner preferences shape kinship dynamics and how individuals respond to demographic events in their social network and the consequences of these events for kinship dynamics. For example, long term observations on female baboons (*Papio cynocephalus*) has shown that following a mother’s death, maternal sisters strengthen their social bond whereas the bonds with maternal aunts are weakened [71]. Feedbacks may exist between changes in behaviour and changes in relatedness that generate further changes in relatedness and behaviour. For example, excluding individuals from groups to minimise competition could generate increases in local relatedness which further selects for increased investment exclusion (since this is an altruistic act that benefits everyone in the group, it is favoured by higher *r*). In principle, this kind of positive feedback could lead to a runaway outcome that results in a very high level of local relatedness over time. Such feedbacks however, have not been formalised in models of group formation and social evolution, providing an exciting opportunity for future research.

Here we have focused on changes in local relatedness over time, however, the other terms in Hamilton’s rule – the costs (*c*) and benefits (*b*) may also change over time [72] and interact with individual kinship dynamics. For example, reproductive value (the expected contribution of an individual to the future population) can significantly impact kin directed behaviours [73]. The costs of a social act depend in part on the reproductive value of the actor and the benefits on the reproductive value of the recipient, both of which can change with age [74]. In many species, the ability of individuals to help and provide benefits to kin may also be age-dependent [75]. For example, as individuals age, they develop skills, knowledge and experience that increase the benefits they can pass on to kin [76-79]. For example, in African elephants (*Loxodonta africana*) older females are better able to assess social and predatory threats, which can increase the survival of their younger kin [78, 79]. Similar results have been reported in resident killer whales where old post-reproductive females lead their group around foraging grounds, especially in times of low food abundance [77]. Kinship dynamic models provide a conceptual framework to be able to examine how changes in patterns of local relatedness with age interact with changes in the costs and benefits of social acts.

Given the ubiquity of kin-structured social groups in populations [13], kinship dynamics are likely to have widespread consequences for the evolution of social behaviour and life history in both males and females. Researchers working on kin structured social species often have the data needed to quantify kinship dynamics. We encourage researchers to consider patterns of kinship dynamics in their study systems and the potential consequences that they may have for social evolution.

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**References**

1. Hamilton W.D. 1964 The genetical evolution of social behaviour. I and II. *J Theor Biol* **7**(1), 1-52 10.1016/0022-5193(64)90039-6.

2. Taylor P. 1992 Altruism in viscous populations—an inclusive fitness model. *Evolutionary Ecology* **6**(4), 352-356 <https://doi.org/10.1007/BF02270971>.

3. Cooper G.A., Levin S.R., Wild G., West S.A. 2018 Modeling relatedness and demography in social evolution. *Evol Lett* **2**(4), 260-271 <https://doi.org/10.1002/evl3.69>.

4. Boomsma J.J. 2007 Kin selection versus sexual selection: why the ends do not meet. *Curr Biol* **17**(16), R673-R683 <https://doi.org/10.1016/j.cub.2007.06.033>.

5. Boomsma J.J. 2009 Lifetime monogamy and the evolution of eusociality. *Philos Trans R Soc Lond B Biol Sci* **364**(1533), 3191-3207 10.1098/rstb.2009.0101.

6. Lukas D., Clutton-Brock T. 2012 Cooperative breeding and monogamy in mammalian societies. *Proc R Soc Biol Sci Ser B* **279**(1736), 2151–2156 10.1098/rspb.2011.2468.

7. Eliassen S., Jørgensen C. 2014 Extra-pair mating and evolution of cooperative neighbourhoods. *PLOS ONE* **9**(7), e99878 10.1371/journal.pone.0099878.

8. Taylor P.D., Irwin A.J. 2000 Overlapping generations can promote altruistic behavior. *Evolution* **54**(4), 1135-1141

9. Sharp S.P., McGowan A., Wood M.J., Hatchwell B.J. 2005 Learned kin recognition cues in a social bird. *Nature* **434**(7037), 1127-1130 10.1038/nature03522.

10. Vastenhouw N., Brunschwig K., Okihara K., Müller F., Tijsterman M., Plasterk R. 2006 Social evolution: kin preference in a social microbe. *Nature* **442**, 882 <https://doi.org/10.1038/442881a>.

11. Cant M.A., Johnstone R.A. 2008 Reproductive conflict and the separation of reproductive generations in humans. *Proc Natl Acad Sci USA Biol Sci* **105**(14), 5332-5336 10.1073/pnas.0711911105.

12. Johnstone R.A., Cant M.A. 2010 The evolution of menopause in cetaceans and humans: the role of demography. *Proc R Soc Biol Sci Ser B* **277**(1701), 3765-3771 10.1098/rspb.2010.0988.

13. Hatchwell B.J. 2010 Cryptic kin selection: kin structure in vertebrate populations and opportunities for kin-directed cooperation. *Ethology* **116**(3), 203-216 <https://doi.org/10.1111/j.1439-0310.2009.01732.x>.

14. Piertney S.B., Lambin X., Maccoll A.D., Lock K., Bacon P.J., Dallas J.F., Leckie F., Mougeot F., Racey P.A., Redpath S. 2008 Temporal changes in kin structure through a population cycle in a territorial bird, the red grouse *Lagopus lagopus scoticus*. *Mol Ecol* **17**(10), 2544-2551 <https://doi.org/10.1111/j.1365-294X.2008.03778.x>.

15. Nichols H.J., Jordan N.R., Jamie G.A., Cant M.A., Hoffman J.I. 2012 Fine‐scale spatiotemporal patterns of genetic variation reflect budding dispersal coupled with strong natal philopatry in a cooperatively breeding mammal. *Mol Ecol* **21**(21), 5348-5362 10.1111/mec.12015.

16. Croft D.P., Johnstone R.A., Ellis S., Nattrass S., Franks D.W., Brent L.J., Mazzi S., Balcomb K.C., Ford J.K., Cant M.A. 2017 Reproductive conflict and the evolution of menopause in killer whales. *Curr Biol* **27**(2), 298-304 10.1016/j.cub.2016.12.015.

17. Borkowska A., Ratkiewicz M. 2004 Seasonal changes of population genetic structure and relatedness in the bank vole *Clethrionomys glareolus*: An analysis of age cohorts. *Ann Zool Fenn*, 661-670

18. Moss R., Watson A. 1991 Population cycles and kin selection in red grouse *Lagopus lagopus scoticus*. *Ibis* **133**, 113-120 <https://doi.org/10.1111/j.1474-919X.1991.tb07674.x>.

19. MacColl A.D., Piertney S.B., Moss R., Lambin X. 2000 Spatial arrangement of kin affects recruitment success in young male red grouse. *Oikos* **90**(2), 261-270 <https://doi.org/10.1034/j.1600-0706.2000.900206.x>.

20. Piertney S.B., MacColl A.D.C., Lambin X., Moss R., Dallas J.F. 1999 Spatial distribution of genetic relatedness in a moorland population of red grouse (*Lagopus lagopus scoticus*). *Biol J Linn Soc* **68**(1-2), 317-331

21. Caswell H. 2019 The formal demography of kinship: A matrix formulation. *Demogr Res* **41**(24), 679-712 10.4054/DemRes.2019.41.24.

22. Jiang L. 1995 Changing kinship structure and its implications for old-age support in urban and rural China. *Popul Stud* **49**(1), 127-145 <https://doi.org/10.1080/0032472031000148286>

23. Lehmann L., Balloux F.o. 2007 Natural selection on fecundity variance in subdivided populations: Kin selection meets bet hedging. *Genetics* **176**(1), 361-377 10.1534/genetics.106.066910.

24. Lehmann L., Rousset F. 2010 How life history and demography promote or inhibit the evolution of helping behaviours. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**(1553), 2599-2617 doi:10.1098/rstb.2010.0138.

25. Beckerman A.P., Sharp S.P., Hatchwell B.J. 2011 Predation and kin-structured populations: an empirical perspective on the evolution of cooperation. *Behav Ecol* **22**(6), 1294-1303 10.1093/beheco/arr131.

26. Lukas D., Reynolds V., Boesch C., Vigilant L. 2005 To what extent does living in a group mean living with kin? *Mol Ecol* **14**(7), 2181-2196 <https://doi.org/10.1111/j.1365-294X.2005.02560.x>.

27. Alvard M.S. 2003 Kinship, lineage, and an evolutionary perspective on cooperative hunting groups in Indonesia. *Human Nature* **14**(2), 129-163 10.1007/s12110-003-1001-5.

28. Spong G., Stone J., Creel S., Björklund M. 2002 Genetic structure of lions (*Panthera leo* L.) in the Selous Game Reserve: implications for the evolution of sociality. *J Evol Biol* **15**(6), 945-953 <https://doi.org/10.1046/j.1420-9101.2002.00473.x>.

29. Heinsohn R., Dunn P., Legge S., Double M. 2000 Coalitions of relatives and reproductive skew in cooperatively breeding white-winged choughs. *Proceedings of the Royal Society of London Series B: Biological Sciences* **267**(1440), 243-249 <https://doi.org/10.1098/rspb.2000.0993>.

30. Hatchwell B.J. 2009 The evolution of cooperative breeding in birds: kinship, dispersal and life history. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**(1533), 3217-3227 doi:10.1098/rstb.2009.0109.

31. Seppä P., Sundström L., Puntitila P. 1995 Facultative polygyny and habitat succession in boreal ants. *Biol J Linn Soc* **56**(4), 533-551 [https://doi.org/10.1016/0024-4066(95)90003-9](https://doi.org/10.1016/0024-4066%2895%2990003-9).

32. Ingram K.K. 2002 Plasticity in queen number and social structure in the invasive argentine ant (*Linepithema humile*). *Evolution* **56**(10), 2008-2016 <https://doi.org/10.1111/j.0014-3820.2002.tb00127.x>.

33. Pedersen J.S., Boomsma J.J. 1999 Effect of habitat saturation on the number and turnover of queens in the polygynous ant, *Myrmica sulcinodis*. *J Evol Biol* **12**(5), 903-917 <https://doi.org/10.1046/j.1420-9101.1999.00109.x>.

34. Widdig A., Nürnberg P., Bercovitch F.B., Trefilov A., Berard J.B., Kessler M.J., Schmidtke J., Streich W.J., Krawczak M. 2006 Consequences of group fission for the patterns of relatedness among rhesus macaques. *Mol Ecol* **15**(12), 3825-3832 10.1111/j.1365-294X.2006.03039.x.

35. Chepko-Sade B.D., Olivier T.J. 1979 Coefficient of genetic relationship and the probability of intragenealogical fission in *Macaca mulatta*. *Behav Ecol Sociobiol* **5**(3), 263-278 10.1007/BF00293675.

36. Morelli T.L., King S.J., Pochron S.T., Wright P.C. 2009 The rules of disengagement: takeovers, infanticide, and dispersal in a rainforest lemur, *Propithecus edwardsi*. *Behaviour* **146**(4-5), 499-523

37. Packer C., Pusey A.E. 1983 Adaptations of Female Lions to Infanticide by Incoming Males. *Am Nat* **121**(5), 716-728 10.1086/284097.

38. Packer C., Pusey A.E. 1982 Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature* **296**(5859), 740-742 10.1038/296740a0.

39. Koster J., Lukas D., Nolin D., Power E., Alvergne A., Mace R., Ross C.T., Kramer K., Greaves R., Caudell M., et al. 2019 Kinship ties across the lifespan in human communities. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**(1780), 20180069 doi:10.1098/rstb.2018.0069.

40. Burton-Chellew M.N., Dunbar R.I.M. 2011 Are affines treated as biological kin? A test of hughes’s hypothesis. *Curr Anthropol* **52**(5), 741-746 10.1086/661288.

41. Hughes A.L. 1988 *Evolution and human kinship*. New York, Oxford University Press.

42. Creel S., Creel N.M. 2019 Patterns of relatedness and the fitness consequences of dispersal, philopatry, and reproductive suppression. In *The African Wild Dog*, pp. 223-244, Princeton University Press.

43. Creel S.R., Waser P.M. 1997 Variation in reproductive suppression among dwarf mongooses: interplay between mechanisms and evolution. In *Cooperative breeding in mammals* eds. Soloman N., French J., pp. 150-170. Cambridge, UK, Cambridge University Press.

44. Dierkes P., Heg D., Taborsky M., Skubic E., Achmann R. 2005 Genetic relatedness in groups is sex-specific and declines with age of helpers in a cooperatively breeding cichlid. *Ecol Lett* **8**(9), 968-975 10.1111/j.1461-0248.2005.00801.x.

45. Duncan C., Gaynor D., Clutton-Brock T., Dyble M. 2019 The evolution of indiscriminate altruism in a cooperatively breeding mammal. *Am Nat* **193**(6), 841-851 10.1086/703113.

46. Pope T.R. 2000 Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). *Behav Ecol Sociobiol* **48**(4), 253-267 10.1007/s002650000236.

47. Lehmann L., Feldman M.W. 2008 War and the evolution of belligerence and bravery. *Proc R Soc Biol Sci Ser B* **275**(1653), 2877-2885 10.1098/rspb.2008.0842.

48. de Oliveira J.L., Morales A.C., Stewart B., Gruenheit N., Engelmoer J., Brown S.B., de Brito R.A., Hurst L.D., Urrutia A.O., Thompson C.R.L., et al. 2019 Conditional expression explains molecular evolution of social genes in a microbe. *Nat Commun* **10**(1), 3284 10.1038/s41467-019-11237-2.

49. Hawkes K., O’Connell J.F., Jones N.B., Alvarez H., Charnov E.L. 1998 Grandmothering, menopause, and the evolution of human life histories. *Proc Natl Acad Sci USA Biol Sci* **95**(3), 1336-1339 10.1073/pnas.95.3.1336.

50. Lahdenperä M., Gillespie D.O.S., Lummaa V., Russell A.F. 2012 Severe intergenerational reproductive conflict and the evolution of menopause. *Ecol Lett* **15**(11), 1283-1290 10.1111/j.1461-0248.2012.01851.x.

51. Mace R., Alvergne A. 2012 Female reproductive competition within families in rural Gambia. *Proc R Soc Biol Sci Ser B* **279**(1736), 2219-2227 10.1098/rspb.2011.2424.

52. Lehmann L. 2007 The evolution of trans‐generational altruism: kin selection meets niche construction. *J Evol Biol* **20**(1), 181-189 <https://doi.org/10.1111/j.1420-9101.2006.01202.x>.

53. Sozou P.D. 2009 Individual and social discounting in a viscous population. *Proceedings of the Royal Society B: Biological Sciences* **276**(1669), 2955-2962 <https://doi.org/10.1098/rspb.2009.0401>.

54. Bourke A.F. 2007 Kin selection and the evolutionary theory of aging. *Annu Rev Ecol Evol Syst* **38**, 103-128 <https://doi.org/10.1146/annurev.ecolsys.38.091206.095528>.

55. Ronce O., Promislow D. 2010 Kin competition, natal dispersal and the moulding of senescence by natural selection. *Proc R Soc Biol Sci Ser B* **277**(1700), 3659-3667 10.1098/rspb.2010.1095.

56. Lee R.D. 2003 Rethinking the evolutionary theory of aging: transfers, not births, shape senescence in social species. *Proc Natl Acad Sci USA Biol Sci* **100**(16), 9637-9642 <https://doi.org/10.1073/pnas.1530303100>.

57. Pavard S., Koons D.N., Heyer E. 2007 The influence of maternal care in shaping human survival and fertility. *Evolution* **61**(12), 2801-2810 10.1111/j.1558-5646.2007.00236.x.

58. Hawkes K., Smith K.R. 2010 Do women stop early? Similarities in fertility decline in humans and chimpanzees. *Ann N Y Acad Sci* **1204**(1), 43-53 10.1111/j.1749-6632.2010.05527.x.

59. Péron G., Bonenfant C., Lemaitre J.-F., Ronget V., Tidiere M., Gaillard J.-M. 2019 Does grandparental care select for a longer lifespan in non-human mammals? *Biol J Linn Soc* **128**(2), 360-372 <https://doi.org/10.1093/biolinnean/blz078>.

60. Pen I. 2000 Reproductive effort in viscous populations. *Evolution* **54**(1), 293-297 10.1111/j.0014-3820.2000.tb00030.x.

61. Travis J.M. 2004 The evolution of programmed death in a spatially structured population. *J Gerontol A Biol Sci Med Sci* **59**(4), B301-B305 10.1093/gerona/59.4.b301.

62. Rodrigues A.M. 2018 Demography, life history and the evolution of age‐dependent social behaviour. *J Evol Biol* **31**(9), 1340-1353 10.1111/jeb.13308.

63. Johnstone R.A., Cant M.A. 2008 Sex differences in dispersal and the evolution of helping and harming. *American Naturalist* **172**(3), 318-330 10.1086/589899.

64. Gibbs M., Saastamoinen M., Coulon A., Stevens V.M. 2010 Organisms on the move: ecology and evolution of dispersal. *The Royal Society*, <https://doi.org/10.1098/rsbl.2009.0820>.

65. Croft D.P., James R., Krause J. 2008 *Exploring animal social networks*. Princeton, NJ, Princeton University Press.

66. Whitehead H. 2008 *Analyzing animal societies: quantitative methods for vertebrate social analysis*. Chicago, University of Chicago Press.

67. Maklakov A.A., Lummaa V. 2013 Evolution of sex differences in lifespan and aging: causes and constraints. *BioEssays* **35**(8), 717-724 10.1002/bies.201300021.

68. Greenwood P.J. 1980 Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* **28**, 1140-1162 [https://doi.org/10.1016/S0003-3472(80)80103-5](https://doi.org/10.1016/S0003-3472%2880%2980103-5).

69. Rosati A.G., Hagberg L., Enigk D.K., Otali E., Emery Thompson M., Muller M.N., Wrangham R.W., Machanda Z.P. 2020 Social selectivity in aging wild chimpanzees. *Science* **370**(6515), 473-476 10.1126/science.aaz9129.

70. Machanda Z.P., Rosati A.G. 2020 Shifting sociality during primate ageing. *Philos Trans R Soc Lond B Biol Sci* **375**(1811), 20190620 doi:10.1098/rstb.2019.0620.

71. Silk J.B., Altmann J., Alberts S.C. 2006 Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behav Ecol Sociobiol* **61**(2), 183-195 10.1007/s00265-006-0249-2.

72. Houston A.I., McNamara J.M. 1999 *Models of adaptive behaviour: an approach based on state*, Cambridge University Press.

73. Hasegawa M., Kutsukake N. 2019 Kin selection and reproductive value in social mammals. *J Ethol* **37**(2), 139-150 <https://doi.org/10.1007/s10164-019-00586-6>.

74. Milinski M. 1978 Kin selection and reproductive value. *Zeitschrift für Tierpsychologie* **47**(3), 328-329 <https://doi.org/10.1111/j.1439-0310.1978.tb01841.x>.

75. Li L., Peng H., Kurths J., Yang Y., Schellnhuber H.J. 2014 Chaos–order transition in foraging behavior of ants. *Proc Natl Acad Sci USA Biol Sci* **111**(23), 8392-8397 10.1073/pnas.1407083111.

76. Smith J.E., Estrada J.R., Richards H.R., Dawes S.E., Mitsos K., Holekamp K.E. 2015 Collective movements, leadership and consensus costs at reunions in spotted hyaenas. *Anim Behav* **105**, 187-200 <https://doi.org/10.1016/j.anbehav.2015.04.023>.

77. Brent L.J.N., Franks D.W., Foster E.A., Balcomb K.C., Cant M.A., Croft D.P. 2015 Ecological knowledge, leadership, and the evolution of menopause in killer whales. *Curr Biol* **25**(6), 746-750 10.1016/j.cub.2015.01.037.

78. McComb K., Moss C., Durant S.M., Baker L., Sayialel S. 2001 Matriarchs as repositories of social knowledge in African elephants. *Science* **292**(5516), 491-494 10.1126/science.1057895.

79. McComb K., Shannon G., Durant S., Sayiale K., Slotow R., Poole J., Moss C. 2011 Leadership in elephants: the adaptive value of age. *Proc R Soc Biol Sci Ser B* **278**(1722), 3270 - 3276 10.1098/rspb.2011.0168.

**Figure 1**. Examples of different patterns of kinship dynamics. (A) Population kinship dynamics in red grouse (*Lagopus lagopus scoticus*) using data from an 8-year cycle in a natural population [figure redrawn from 14]. Here kinship dynamics show a cyclical pattern with local relatedness increasing during population growth as established males help related males to establish a neighbouring breeding territory. As population density increases the costs of competition with neighbouring kin outweighs the benefits leading to increasing aggression and the break-up of kin clusters. (B) Group kinship dynamics of male – female relatedness in social groups of banded mongoose (*Mungos mungo*). New social groups form by the fission of unrelated male and female groups. As social groups age, male-female relatedness increases due to philopatric males and females inheriting the breeding positions [figure redrawn from 15]. (C) Individual kinship dynamics in Northern and Southern resident killer whales (*Orcinus orca*) showing patterns of maternal relatedness with female age for a total of 200 whales over 846 whale-years [figure redrawn from 16]. Figure shows the relationship between female age and mean relatedness to other females (red line), males (blue line) and average relatedness across both sexes (black line). Standard error of mean relatedness across both sexes is shown as dotted lines. As females age, their local relatedness to the group increases due to an increase in local relatedness to males. Animal images from PhyloPic: red grouse image (uncredited) published under Public Domain Dedication 1.0 license (<https://creativecommons.org/publicdomain/zero/1.0/>); banded mongoose image by Birgit Lang published under Public Domain Dedication 1.0 license (<https://creativecommons.org/publicdomain/zero/1.0/>); killer whale image by ChrisHuh published under Creative Commons Licence 3.0 (<https://creativecommons.org/licenses/by-sa/3.0/>).

**Figure 2.** Age-dependent kinship dynamics and their consequences for selection on social traits under different demographic patterns (modified from [12]). A) Predicted age-dependent kinship dynamics, showing age-specific relatedness to a breeding female of other local males (dotted lines) and females (solid lines) and the average relatedness across both sexes (dashed line). Age is scaled in mean generation lengths. Three different demographic patterns are plotted: (i) local mating within the group with high male dispersal and low female dispersal; (ii) local mating within the group with low male dispersal and high female dispersal; (iii) non-local mating (i.e. mating occurs outside the group) with low dispersal by both sexes. B). The consequences of age-dependent kinship dynamics for selection for helping (boosting the fecundity of other local breeders) and harming (reducing the fecundity of other local breeders) across the lifespan under different demographic patterns (i-iii as in A). A focal female can perform social acts that result in an immediate gain of *b* offspring for other breeders at an immediate cost *c* to herself. Selection for helping and harming are indicated by shading on the graph with blue areas indicating selection for helping and red areas indicate selection for harming. For further details, see Johnstone & Cant [12].