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# Kinship dynamics: patterns and consequences of changes in local relatedness

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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.

## 1. Introduction

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] recognized 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 formalization 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

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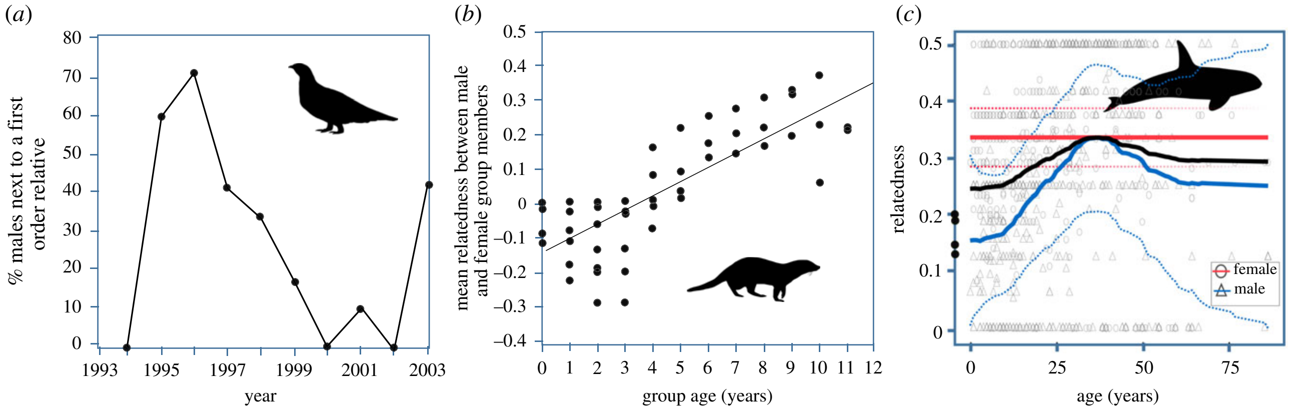

**Figure 1.** Examples of different patterns of kinship dynamics. (*a*) Population kinship dynamics in red grouse (*Lagopus lagopus scoticus*) using data from an 8-year cycle in a natural population (figure redrawn from [14]). Here kinship dynamics show a cyclical pattern with local relatedness increasing 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 outweigh 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 licence (https://creativecommons.org/publicdomain/zero/1.0/); banded mongoose image by Birgit Lang published under Public Domain Dedication 1.0 licence (https://creativecommons.org/publicdomain/zero/1.0/); killer whale image by Chris Huh published under Creative Commons Licence 3.0 (https://creativecommons.org/licenses/by-sa/3.0/). (Online version in colour.)

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.

## 2. Patterns of kinship dynamics

Here we identify three levels at which kinship dynamics may occur in natural populations (figure 1). First, average local relatedness may change over time at the level of the population (population kinship dynamics; figure 1*a*). 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 (figure 1*b*). 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] (figure 1*c*). 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.

### (a) 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] (figure 1*a*). 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 (figure 1*a*).

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 programme) 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, such as 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.

## (b) 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] (figure 1*b*). 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 (figure 1*b*). 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.

## (c) 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; figure 1*c*). Individual kinship dynamics were first formalized in theoretical models examining the evolution of menopause in humans and some species of toothed whales [11,12] (figure 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 & 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 (figure 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] (figure 2*a*(ii)). 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 (figure 2*a*(ii)). Even when there is no sex biased dispersal, kinship dynamics can still occur [12] (figure 2*a*(iii)). For example, in some species of toothed whales, neither sex disperses nor 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

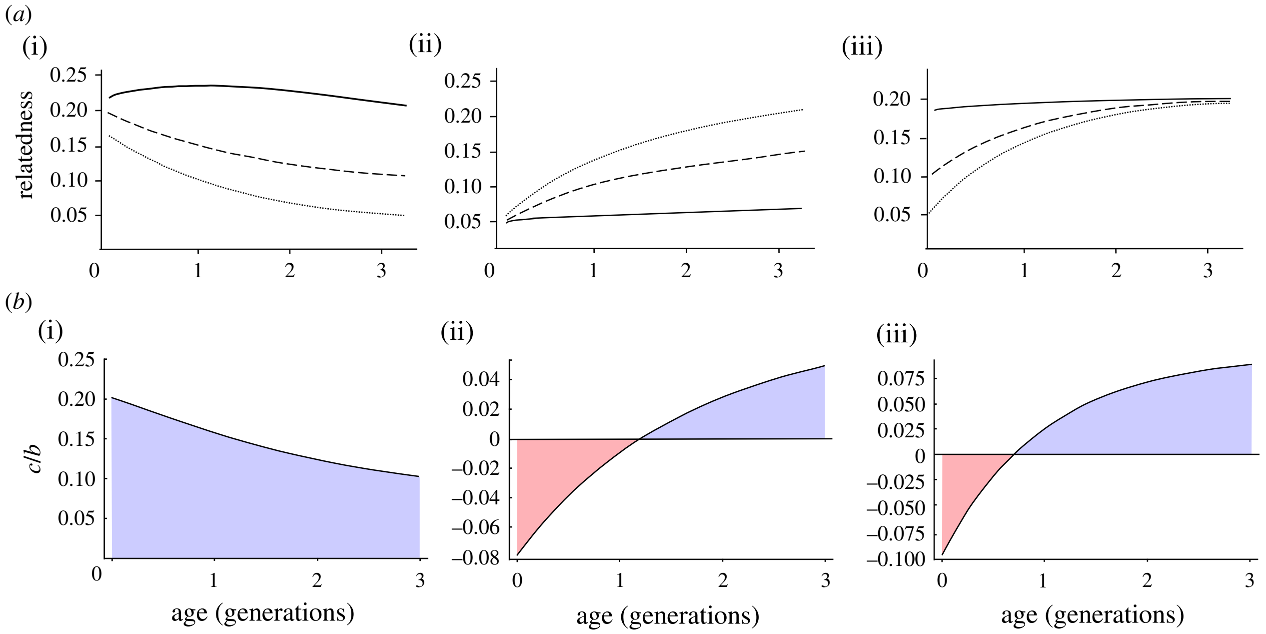

**Figure 2.** Age-dependent kinship dynamics and their consequences for selection on social traits under different demographic patterns (modified from [12]). (*a*) Predicted age-dependent kinship dynamics, showing age-specific relatedness to a breeding female of other local males (dotted lines) and females (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]. (Online version in colour.)

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 (figures 1*c* and 2*a*(iii)) [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].

## 3. 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 (figure 1*c*) 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] (figure 2). Johnstone & Cant [12] formalized 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 [45]) 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 [45]. There is strong support in both humans and killer whales that there is intergenerational conflict between old and young females [16,46,47] 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 versus 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) [48,49]. For example, Lehmann [48] 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 (see also [49]). Sozou [50] 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 [51,52]. If individuals can provide benefits to kin in late life it may select for longevity [45,53–55]. 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 [56]. Thus, we hypothesize 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 [51]. For example, theoretical work has reported that low juvenile dispersal reduces the strength of selection on adult survival [52], favouring the evolution of shorter lifespans [57,58]. 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 [52]. 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 [52]. 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 versus 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 [59]. 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 [60]. In addition, theoretical work has demonstrated that changes in within-group or population relatedness can change the nature of intergroup violence and warfare [61]. 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 [61]. 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 [62]. 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 [62]. 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 [62]. 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.

## 4. 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 [63] 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 [64]. Currently, however, how the sexes differ in patterns of kinship dynamics and the resulting implications for sex differences in behaviour and life-history evolution remains unexplored. Moreover, within a sex it is well documented that both dispersal patterns [65] 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 have 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 [66]. It would then be possible to quantify local kin structure using weighted measures of association strength, using association indices [67] to weight relatedness between individuals by the strength (weight) of their association.

## 5. Conclusion

Kinship dynamics mean that the strength and direction of kin selection can change systematically over time [11,12,16,63]. 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 [68]. 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 [69]) 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 [70]. This can include the propensity to engage in social interactions, the capability to influence others and the positive versus negative valence of social interactions [71]. 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*) have shown that following a mother's death, maternal sisters strengthen their social bond whereas the bonds with maternal aunts are weakened [72]. 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 minimize 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 formalized 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 [73] 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 [74]. 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 [75]. In many species, the ability of individuals to help and provide benefits to kin may also be age-dependent [76]. For example, as individuals age, they develop skills, knowledge and experience that increase the benefits they can pass on to kin [77–80]. 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 [79,80]. 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 [78]. 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.

Data accessibility. This article has no additional data.

Authors' contributions. All authors contributed to the development of the ideas in the paper. D.P.C. wrote the original draft of the paper, with all authors contributing to reviewing and editing subsequent drafts. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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