Group size modulates kinship dynamics and selection on social traits

Peng He[1,7], **Michael N. Weiss**[2,3], **Samuel Ellis**[2], **Daniel W. Franks**[4,5], **Michael A. Cant**[6], **Darren P. Croft**[2] and **Rufus A. Johnstone**[1,7]

[1]Department of Zoology, University of Cambridge, Cambridge, CB2 3EJ, UK
[2]Centre for Research in Animal Behaviour, University of Exeter, Exeter, EX4 4QG, UK
[3]Center for Whale Research, Friday Harbour, Washington, 98250, USA
[4]Department of Biology, University of York, York, YO10 5DD, UK
[5]Department of Computer Science, University of York, York, YO10 5GH, UK
[6]Centre for Ecology and Conservation, University of Exeter, Cornwall, TR10 9FE, UK
[7]Correspondence: peng.he@outlook.de (PH), raj1003@cam.ac.uk (RAJ)

ABSTRACT

The mean relatedness of an individual to others in its social group may change with age. Such kinship dynamics, which are expected to influence sex- and age-specific social behaviours, are sensitive to demography. Existing models of kinship dynamics, however, have focused chiefly on the influences of population-level demographic parameters (e.g., sex-specific dispersal rate and mating pattern). Here, we extend these models to explore the effects of local group size on kinship dynamics and the resulting patterns of selection for sex- and age-specific helping and harming. We show that individuals' average relatedness to others is higher in smaller than larger groups, and consequently, selective pressure for helping or harming is generally stronger in smaller than larger groups. Moreover, relatedness changes faster with age in smaller groups, particularly at younger ages. These patterns favour more extreme social traits in smaller groups and especially so at earlier life history stages. In particular we highlight that, while social systems

characterized by bi-sexual philopatry with non-local mating (e.g., whales) are known to favour a shift from more helpful to more harmful behaviour as females age — a trend that has been invoked to explain the evolution of menopause and post-reproductive helping — the timing of this shift is predicted to be sensitive to local group size, potentially favouring earlier female reproductive cessation in smaller groups. Our study generates new insights into the effects of local group properties on kinship dynamics, and suggests that such effects might also help to explain widespread variation in age-linked social traits, such as the timing of menopause in social mammals.

KEYWORDS: Group size variation | Inclusive fitness | Life history evolution | Menopause | Population asymmetric subdivision | Social evolution

INTRODUCTION

There is clear evidence that the mean relatedness of an individual to others in its social group may change systematically with age [1, 2]. Such kinship dynamics, which are sensitive to a species' demography, are predicted to influence sex- and age-specific social behaviours such as helping and harming [1-4]. For example, among social mammals, only humans and some toothed whales [5] exhibit a life history pattern of early reproductive cessation (compared to males), followed by an extended period of post-reproductive life during which they assist kin [3, 4, 6, 7]. This unusual life history pattern is associated with unusual kinship dynamics: females in these species typically experience an increase in their relatedness to others in their social groups as they age, a trend that has been invoked to help explain the evolution of menopause and post-reproductive helping [2-4, 6].

Despite growing interest in kinship dynamics, existing models have focused chiefly on how these dynamics are shaped by population-level demographic parameters, such as typical rates of female and male philopatry versus dispersal [3, 8], and of local versus non-local mating [2, 4]. It remains unclear how local variation in demographic factors such as social group size modulates local kinship dynamics, and the temporal patterns of social behaviours expected under such dynamics. There is abundant evidence that group size varies within populations of many species [9-18], and that it is often correlated with social behaviours such as the amount of assistance provided by non-breeding helpers in cooperative breeders [19-23]. But the impacts of group size on kinship dynamics, and on predicted changes in social behaviour with age, remain unclear.

Here, we extend existing models of kinship dynamics [2, 4] in a group-structured population to incorporate local variation in group size. We compare kinship dynamics in smaller and larger groups, and explore how these dynamics influence patterns of age-specific selection for helping versus harming behaviours in both sexes. Inspired by model predictions, we also use a long-term census dataset of the southern resident killer whale (*Orcinus orca*) population to explore how young versus old mothers vary in their propensity to give births in social groups of varying sizes. By doing so, we highlight a group-size-related mechanism that may help to explain widespread variation in the expression of social and life history traits, such as the timing of reproductive cessation observed in social mammals [24, 25].

METHODS

Population demographic assumptions

Building on the models of Johnstone and Cant [4] and Ellis et al [2], we consider an infinite, diploid, bisexual population, divided into discrete social groups [aka islands, demes or patches, 26, 27], a proportion u of which are of α-type consisting of $n_{f\alpha}$ female and $n_{m\alpha}$ male breeders, while the remaining fraction $1-u$ are of β-type consisting of $n_{f\beta}$ female and $n_{m\beta}$ male breeders (previous models assumed that all groups contained the same number of female and male breeders). Group or patch type is defined solely by size, and we suppose that $n_{f\alpha}+n_{m\alpha}<n_{f\beta}+n_{m\beta}$, implying that smaller groups are of α-type while larger groups are of β-type. Time proceeds in discrete steps, in each of which every female breeder produces some very large number, p, of offspring, a fraction x of which are females while the rest are males (fecundity p and primary sex ratio $x:(1-x)$ do not influence predicted kinship dynamics but are introduced here for clarity — see details in the supplement). The probability that an offspring in an α-type or β-type group is sired by a male from the same group is m_α or m_β, respectively (while the probability of being sired by a male breeder from a different group is $1-m_\alpha$ or $1-m_\beta$, respectively). After reproduction, each female offspring produced in an α-type or β-type group remains in its natal group with probability $\pi_{f\alpha}$ or $\pi_{f\beta}$, respectively (while with probability $1-\pi_{f\alpha}$ or $1-\pi_{f\beta}$ it disperses to a random patch in the population); similarly, each male offspring produced in an α-type or β-type group remains in its natal patch with probability $\pi_{m\alpha}$ or $\pi_{m\beta}$, respectively. After dispersal, offspring in each patch (both those born locally that did not disperse, together with immigrants from the rest of the population) compete in a fair lottery for breeding vacancies created by deaths of adults of their own sex in that patch — we assume that from one time step to the next each female breeder dies with the probability μ_f, and each male breeder does so with the probability μ_m (i.e., mortality rates are independent of group type). Offspring that fail to obtain any breeding vacancy die, and the cycle then repeats.

Modelling kinship dynamics

Given above demographic assumptions, we derive in the appendix expressions for the expected relatedness of males and females of varying ages to others in the same social group — distinguishing between smaller (α-type) and larger (β-type) groups. In the results section, we explore the predicted patterns of kinship dynamics in populations in which the proportion of α-type patches is either low ($u = 0.1$), medium ($u = 0.5$) or high ($u = 0.9$). For simplicity, we assume that $n_{f\alpha} = n_{m\alpha} = 5$ and $n_{f\beta} = n_{m\beta} = 20$ throughout (i.e., a smaller group contains 10 individuals, while a larger group contains 40 individuals, with the same number of males and females in either type of groups; under this sex ratio, changes in the numbers of females and males in groups of either type do not qualitatively alter the predicted effects of group size variation on kinship dynamics and age-related selective pressures). The mortality rate of female and male breeders at each timestep across their lifespan in both types of patches is $\mu_f = \mu_m = 0.1$. To make our explorations biologically relevant, we consider the three typical dispersal and mating patterns of social mammals addressed by Johnstone and Cant [4] and Ellis et al [2], represented by (**I**) whales: *bisexual philopatry with non-local mating*, where $1 - \pi_{f\alpha} = 1 - \pi_{f\beta} = 0.15$, $1 - \pi_{m\alpha} = 1 - \pi_{m\beta} = 0.15$, and $m_\alpha = m_\beta = 0$, (**II**) apes: *female-biased dispersal with local mating*, where $1 - \pi_{f\alpha} = 1 - \pi_{f\beta} = 0.85$, $1 - \pi_{m\alpha} = 1 - \pi_{m\beta} = 0.15$, and $m_\alpha = m_\beta = .82$, and (**III**) typical mammals: *male-biased dispersal with local mating*, where $1 - \pi_{f\alpha} = 1 - \pi_{f\beta} = 0.15$, $1 - \pi_{m\alpha} = 1 - \pi_{m\beta} = 0.85$, and $m_\alpha = m_\beta = .82$ (to reveal the effects of group size variation on kinship dynamics, under each of these scenarios, we also show in the appendix for comparison the kinship dynamics in a counterpart 'homogeneous' population consisting of either all α-type or all β-type groups as defined for the 'heterogeneous' population, while keeping all other parameter values for such 'homogeneous' populations the same as those for the 'heterogeneous' populations of interest).

Evaluating selective pressures

Having derived the sex- and age-specific average relatedness of individuals to their social group of given type, we then use these values to determine the sex- and age-specific strength of selection for helping or harming behaviours by individuals in both smaller and larger social

groups, following the inclusive fitness approach of Ellis et al [2], under the three typical cases of mating and dispersal described above (we assume helping or harming is genetically determined by a mutant allele). Briefly, this is done by firstly deriving expressions for the reproductive values of individuals of both sexes given our demographic assumptions, and then using these expressions to derive a fitness function for an individual of either sex at a given age in either type of patch in relation to its own fecundity and mortality performances and those of others in its group (see details in the appendix). Lastly, using these fitness functions, we derive expressions for the inclusive fitness impact on the individual at a given age should it express a 'harmful' or 'helpful' behaviour that affects the fecundity or mortality of itself and others in an α-type or β-type group, and from these the sex- and age-specific strength of selection (or selective pressure) on the behaviour.

More specifically, when evaluating such inclusive fitness effects, we assume the behaviour imposes some total marginal fitness benefits or costs of magnitude b (say $0 < |b| \ll 1$) on the local recipients of either sex in terms of either fecundity or mortality, where $b > 0$ implies a 'helpful' and $b < 0$ a 'harmful' act. We assume this benefit or cost is equally divided among these recipients, and conducting this behaviour confers some marginal but constant fitness costs on the actor of magnitude $0 < c \ll 1$ (i.e., either fecundity or mortality costs, respectively; see details of the expressions evaluating the inclusive fitness effects of the social behaviour in both these contexts in the appendix). Under such assumptions and the given costs of conducting the behaviour (e.g., here $c = 10^{-5}$), we can find the critical value of b^* at which the behaviour would have no net fecundity or mortality impact, and use the $\frac{c}{b^*}$ as a measure of the sex- and age-specific selective pressure on the behaviour. When $\frac{c}{b^*} > 0$, the more this (positive) ratio deviates from 0, the stronger the selective pressure for helping; by contrast, when $\frac{c}{b^*} < 0$, the more this (negative) ratio deviates from 0, the stronger the selective pressure for harming. To reveal how the prevalence of α-type (or β-type) groups in a population modulates the selective pressure on helping or harming, we explore populations with either low ($u = 0.1$), medium ($u = 0.5$) or high ($u = 0.9$) proportions of α-type (smaller) groups. As we did in our analysis of kinship dynamics, in the appendix we also show for comparison the sex- and age-specific selective pressures on the behaviour in a counterpart 'homogeneous' population [i.e., as in 2] that consists entirely of either α-type (smaller) or entirely of β-type (larger) groups (as defined in the 'heterogeneous'

population of interest), while keeping all other parameter values for such ‘homogeneous’ populations the same as those for the ‘heterogeneous’ populations of interest.

RESULTS

Local variation in kinship dynamics

We find, unsurprisingly, that individuals' average relatedness to their group is generally higher in smaller than larger groups. Of greater interest is the prediction that the rate of change in relatedness with age is typically higher in smaller than larger social groups — and that such differences are more pronounced at younger than older ages (Fig. 1). Intra-population variation in group size does not alter the general, qualitative patterns of kinship dynamics experienced by individuals of either sex [2], nor does the prevalence of smaller groups in the population. With given prevalence of smaller groups in the population, the differences in the patterns of kinship dynamics experienced by both sexes in smaller versus larger groups are most pronounced when both sexes are philopatric and mate non-locally (i.e., the whale case). With given patterns of mating and dispersal, the more prevalent the smaller groups are in the population (i.e., a higher u), the larger the differences in the patterns of kinship dynamics experienced by both sexes in smaller versus larger groups (Fig. 1).

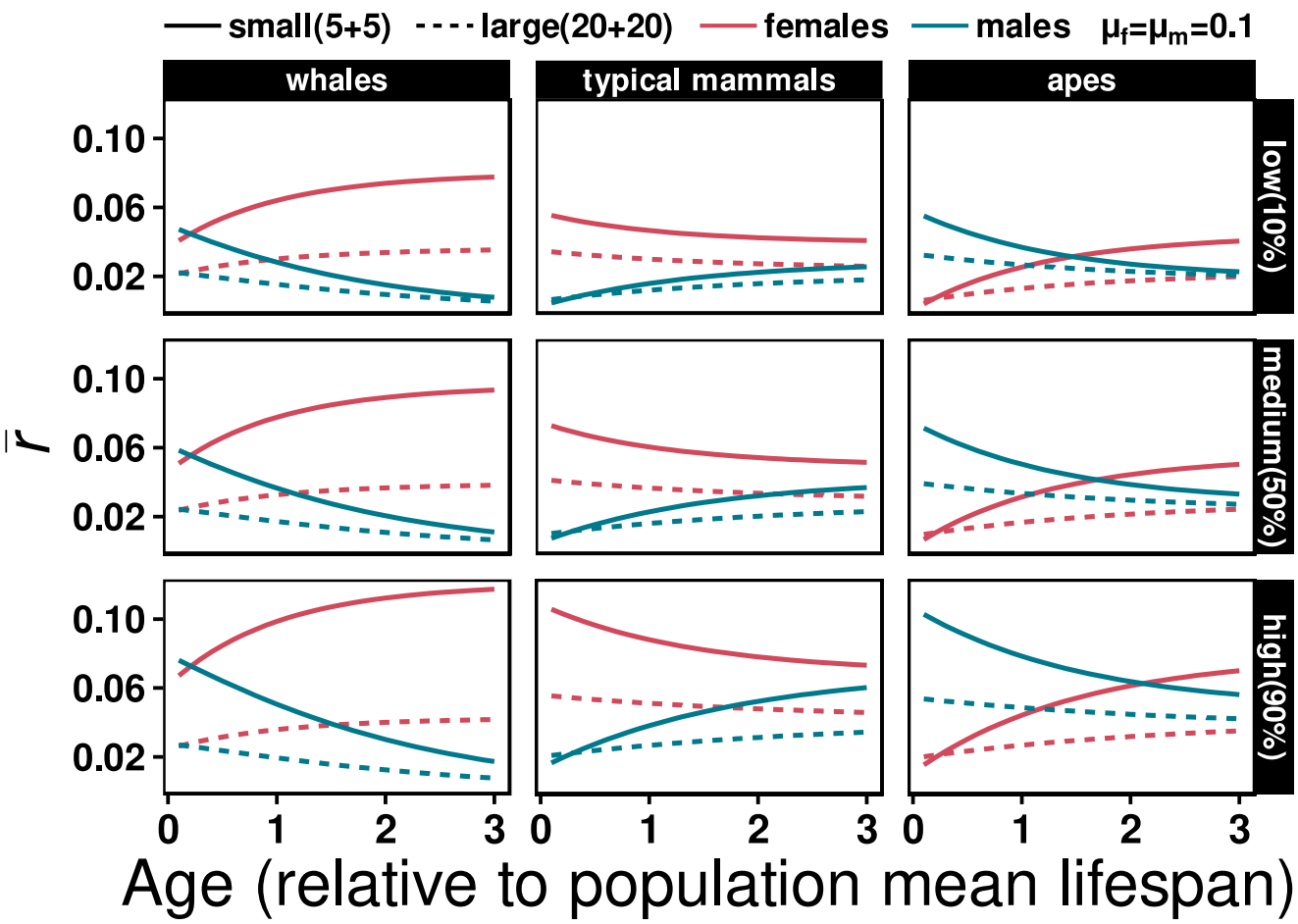

Fig. 1 Curves show the predicted mean relatedness of an individual female (red) or male(blue) to others in its social group (small: 5 females and 5 males, large: 20 females and 20 males), as a function of its age (scaled relative to the mean lifespan in the population under constant female and male mortality rate $\mu_f = \mu_m = 0.1$ at each timestep). In each panel, solid curves show results for small groups, dashed lines for large groups. The three columns show results for three different patterns of dispersal and mating, referred to as: the 'whale' case (*bisexual philopatry with non-local mating*), the typical mammal case (*male-biased dispersal with local mating*), and the 'ape' case (*female-biased dispersal with local mating*), as detailed in the main texts. The three rows show results for three different proportions of smaller groups in the population: low ($u = 10\%$), medium ($u = 50\%$), or high ($u = 90\%$).

Local variation in selection

We find that selective pressures on helping or harming are generally higher in smaller than larger groups, and the rate of change in selective pressures with age is higher in smaller than larger social groups, especially at earlier than later life history stages (Fig. 2, A and B). The presence of group size variation does not qualitatively alter the predicted patterns of selective pressures on the social behaviour [2], neither does the prevalence (u) of smaller groups in the population. In the whale and ape cases, we find that females in both smaller and larger groups experience a significant shift in selective pressures from harming to helping when the behaviour affects fecundity, and that such shifts occur earlier in smaller groups (Fig. 2-A). With given prevalence of smaller groups in the population, the differences in the critical ages of these shifts between small and large groups are less significant in the ape than in the whale case; however, the impacts of the prevalence of smaller groups differs between the cases: in the whale case, such differences in critical age are more marked when smaller groups are more prevalent, while in the ape case such differences are most pronounced at low but least pronounced at intermediate prevalence of smaller groups in the population (Fig. 2-B).

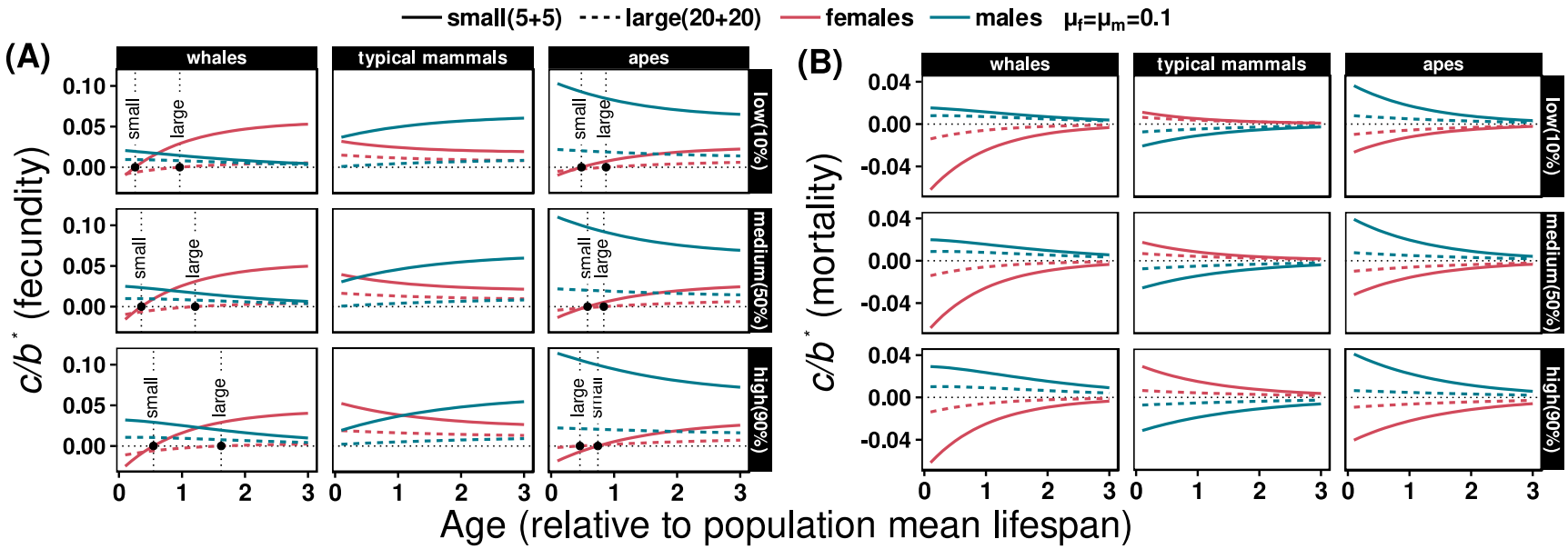

Fig. 2 Curves show the predicted strength of selection for helping (positive values) or harming (negative values) as a function of age (scaled relative to the mean lifespan in the population under constant female and male mortality rate $\mu_f = \mu_m = 0.1$ at each timestep) given the sex- and group-size-specific kinship dynamics shown in Fig.1, should the behaviour affect the fecundity (A) or fecundity (B) of an actor and the recipients. Dotted black horizontal lines in (A) and (B) marking the condition at which the behaviour is selectively neutral ($\frac{c}{b^*} = 0$) and dotted black vertical lines in (A) highlighting the critical age (marked by black dots at the intersections between the curves and the horizontal dotted black line) at which selection on females switches from favouring harming to helping in small (5 females and 5 males) and large (20 females and 20 males) groups. In each graph, solid curves show results for small groups, dashed lines for large groups. The three columns in (A) or (B) show results for three different patterns of dispersal and mating, referred to as: the 'whale' case (*bisexual philopatry with non-local mating*), the typical mammal case (*male-biased dispersal with local mating*), and the 'ape' case (*female-biased dispersal with local mating*), as detailed in 'METHODS', while the three rows show results for three different proportions of smaller groups in the population: low ($u = 10\%$), medium ($u = 50\%$), or high ($u = 90\%$).

DISCUSSION

Group size is a key component of social evolution [9, 11, 13, 15, 17, 28-31]. Building on existing models of kinship dynamics, we generated new insights into how local group size influences selection for social traits in dynamic yet locally varying kinship environments.

Comparing distinct, homogeneous populations, individuals are typically more related to others in populations characterised by smaller groups [29, 32]. We show this prediction also applies to differently sized groups within a single, heterogeneous population, suggesting the robustness of the predictions by these previous studies to group size heterogeneity. In our model, individuals in all groups within a population have the same underlying survival and fecundity schedules, sex-specific dispersal rates, and mating pattern. The qualitative patterns of kinship dynamics for both sexes, and the way they relate to the underlying demographic processes, are the same for both smaller and larger groups. Differences in local kinship dynamics nevertheless result from the asymmetric impact of demographic turnover between smaller and larger groups. The same event, such as the recruitment of a new group member after losing one, has a greater impact on average relatedness to others in a smaller group. Consequently, the kinship ties that build up as an immigrant ages do so slower in a larger group, leading to both slower rates of change in age-specific relatedness and a lower mean relatedness averaging over all ages.

Despite the general demographic mechanism by which group size modulates relatedness, empirically testing the predicted patterns of age-linked expression of social behaviours (or life history traits they outline) by our model is challenging. We theoretically demonstrated that the locally varying kinship dynamics can lead to variations in age-linked trends in social behaviours, such as the timing of switching from harming to helping or the timing of reproductive cessation observed in social mammals [24, 25]. However, a common complication that may come into play when testing such predictions is that natural group sizes often fluctuate (at both the ecological and evolutionary temporal scales) such that one cannot easily identify consistently smaller or larger groups — for instance in fission-fusion societies where not only the size but also the membership of a group often change. While the effects of group size on kinship dynamics may be detectable in cases where populations are clearly demographically and socially structured,

inferring the more profound evolutionary causal link between group size and age-related trends in social traits is empirically more difficult. It is important, however, to identify the social organizational scales at which groups can be biologically most easily identified and categorised as smaller or larger. For example, at a higher social organizational scale, one might contrast smaller vs larger sub-populations, while at a finer scale within these, one could also identify smaller and larger social groups.

To illustrate such challenges, we turn to the facts revealed by long-term census datasets from three killer whale populations. Starting at the largest social scale the data permits, a comparison among the northern and southern resident populations and the transient population [24] shows that 1) resident populations typically have larger pods than the transient population, and 2) females in the transient population achieve their 95% reproductive outputs earlier than those in the two resident populations [24]. This pattern fits the qualitative prediction of the model that smaller social group (pod) sizes should be associated with earlier selective shifts from harming to helping as females age. However, beyond the very small sample size at this social scale (i.e., 3 populations), which renders any strong test of our evolutionary predictions impossible, the resident and transient populations are also of different ecotypes, which leaves the causal basis of these observed life history differences unclear. Dropping down to a lower level of social organisation, while matrilines are the core social units within each of these populations, individuals from different matrilines typically form stable social clusters emerging as pods [2, 33]. Drawing on the long-term census data from the Southern resident population characterized by three stable pods since 1974 [34], we were able to explore how pod sizes are associated with females' reproductive strategies. In this case, younger killer whale mothers were relatively more likely to give birth in comparison to older mothers when in smaller than larger pods (Fig. 3). Once again, this fits the qualitative prediction that smaller social group sizes should be associated with earlier selective shifts from female harming to helping, but as at the larger social scale, the sample size for the comparison (i.e., 3 pods within one population) is much too low to provide a strong test of the model.

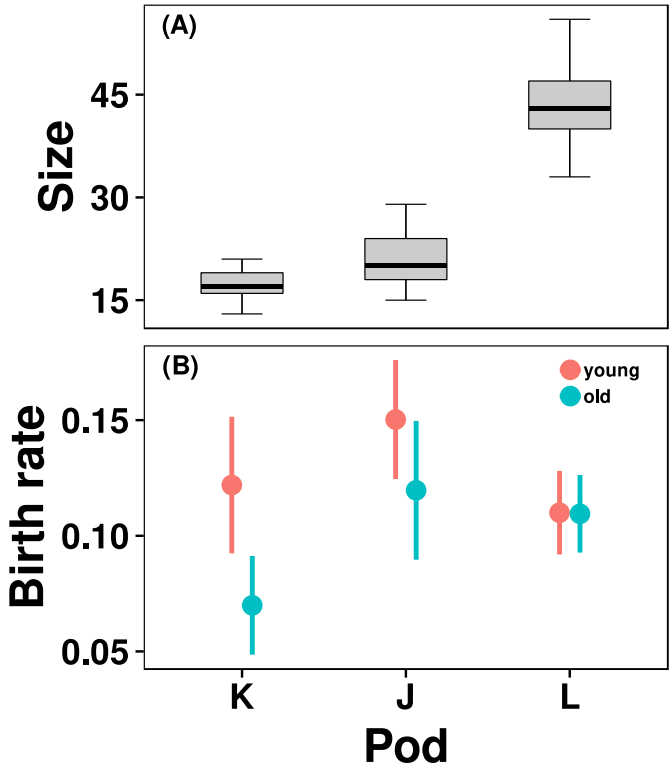

Fig. 3 Variation in the estimated propensity to give birth by the young ($9 \leq$ age < 24) versus old ($24 \leq$ age < 45) female killer whales (B) across the three pods (K, J, and L) with different sizes (A) in the southern resident population (where 24 is the median while 45 the average last reproductive age of females). The distributions of pod sizes are based on annual census data of the population between 1976 and 2022, while the birth rate (i.e., the predicted propensity or probability to give birth in a census year) of young and old (shown in red and blue in B, respectively, where vertical bars indicate the standard error of the estimates shown as dots) mothers are estimated from a logistic regression model fitted to the census data on the birth events recorded in females during this period (see in the appendix for details of model fitting).

In conclusion, while empirically testing the predicted patterns of age-linked trends in social behaviours in relation to group size remains challenging, we suggest the generality of the effects of group size on the locally dynamic kinship environments individuals experience and the social traits they express therein.

DATA AVAILABILITY

The expressions for calculating sex- and age-specific relatedness and selective pressures on social behaviours are given in the appendix. All the code and data used are available at https://github.com/ecopeng/GroupSize_KinshipDynamics_Selection.

AUTHORS' CONTRIBUTIONS

PH and RAJ led the conceptualization, modelling, and writing for this study with supports and inputs from other co-authors. MNW, SE and DPC led the data curation, analysis, and interpretation. DWF, MAC, DPC and RAJ contributed to acquiring funding for this study. All authors gave final approval for the publication of this study.

COMPETING INTERESTS

We do not have conflicts of interest to disclose.

ACKNOWLEDGEMENTS

We thank the Natural Environmental Research Council for granting us the funding (No. NE/S010327/1) to conduct this study.

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