How sex-biased dispersal affects conflict over parental investment

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Abstract

Existing models of parental investment have mainly focused on interactions at the level of the family, and have paid much less attention to the impact of population-level processes. Here we extend classical models of parental care to assess the impact of population structure and limited dispersal. We find that sex-differences in dispersal substantially affect the amount of care provided by each parent, with the more philopatric sex providing the majority of the care to young. This effect is most pronounced in highly viscous populations: in such cases, when classical models would predict stable biparental care, inclusion of a modest sex difference in dispersal leads to uniparental care by the philopatric sex. In addition, mating skew also affects sex-differences in parental investment, with the more numerous sex providing most of the care. However, the effect of mating skew only holds when parents care for their own offspring. When individuals breed communally, we recover the previous finding that the more philopatric sex provides most of the care, even when it is the rare sex. Finally, we show that sex-differences in dispersal can mask the existence of sex-specific costs of care, because the philopatric sex may provide most of the care even in the face of far higher mortality costs relative to the dispersing sex. We conclude that sex-biased dispersal is likely to be an important, yet currently overlooked driver of sex-differences in parental care.

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1   Introduction

Although mothers and fathers share a common genetic stake in the survival of their young, their evolutionary interests are rarely fully aligned [1–3]. Each parent typically stands to gain if the other bears more of the costs of raising the young, leading to sexual conflict over the provision of parental care [4–7]. Such conflict is thought to be an important driver of between-species variation in forms of care [8] and is associated with a range of conspicuous behaviours, such as brood concealment [9], infanticide [10, 11], brood desertion [12, 13] and negotiation between parents over care [e.g., 14–16].

Over the years, a substantial body of theory has been developed to explain the evolution sex-differences in parental care [for reviews see 6, 7], focusing chiefly on behavioural interactions within the family (e.g., negotiation or coercion between parents [17–23]) or between parents and helpers [24, 25]). This emphasis on interactions at the family level can perhaps be attributed to the self-contained nature of the family-unit, which allows researchers to concentrate on the behaviour of a small number of family members in the context of a clearly defined "nursery" environment [26]. However, the downside of such a narrow focus is that the potential impact of processes at the population level has been largely ignored in existing models of parental investment. So far, the only population-level process that has received much attention is the feedback between parental investment and mate availability [8, 27–29]. The possible influence of other population-scale processes on the provision of care remains poorly understood.

Dispersal is one such population-level process, which is thought to influence the resolution of other forms of family conflict (e.g., genomic imprinting: [30–32], parent-offspring conflict [33] and infanticide [34]). The importance of dispersal in the familial context raises the question whether it might also affect the outcome of sexual conflict between parents over care. A key hint that dispersal may influence investment decisions comes from models that focus on more abstract social behaviour (e.g., helping and harming) [35, 36]. These models show that sex-differences in dispersal can favour substantial asymmetries in helping behaviours between the two sexes. Given that sex-biases in dispersal are common in the animal kingdom [37–39], it seems likely that patterns of dispersal might provide useful insights into the evolution of uniparental and biparental care.

Here, we set out to examine the impact of sex-biased dispersal on parental care, in particular on sex-differences in parental investment. We build on the classical theoretical model of biparental care by Houston & Davies [17] embedding it in a demographically explicit framework familiar from recent models of social evolution in structured populations [35, 40–43].

2   The model

A demographical model of parental care   Our approach is to develop an evolutionary demographic model [40, 44–47] of the provision of care to a brood by male and female parents.

Consider a population distributed over infinitely many territories [48, 49], in which individuals reproduce sexually and generations are overlapping. Each territory contains n_f adult female breeders and n_m adult male breeders. Time proceeds in a series of discrete breeding seasons, during each of which a given female mates at random within her patch to produce a large number of offspring, in a $1 : 1$ sex ratio. We assume that all males on the patch have identical mating success. When $n_f = n_m$, this could entail females and males on a patch pairing up at random, with each female's offspring all being fathered by the same male, or each of a female's offspring might be fathered by a randomly chosen male; both scenarios give identical results. When $n_f \neq n_m$, the latter interpretation is more natural.

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The individual parental efforts of males and females are given by u_m and u_f respectively, and offspring survival, which depends upon the combined efforts of both parents, is given by $b(u_f + u_m)$. Following classical models of parental investment [4, 5, 19, 50, 51], we assume that b increases, at a diminishing rate, with an increase in either parent's level of effort u_x, $x \in \{m, f\}$ (so that $\partial b / \partial u_x > 0$ and $\partial^2 b / \partial u_x^2 < 0$). In addition, an increased level of parental effort u_x is assumed to come at a cost to the parent's future fitness, through an increase in its mortality probability $\mu_x \equiv \mu_x(u_x)$ [4]. Again, in accordance with previous models (e.g., [19, 21]), we assume that parental mortality increases in accelerating fashion with an individual's effort $\partial \mu_x / \partial u_x > 0$ and $\partial^2 \mu_x / \partial u_x^2 > 0$.

Of all offspring produced during each time step that survive, a fraction h_m of sons and a fraction h_f of daughters remain on the natal patch, while fractions $d_m = 1 - h_m$ and $d_f = 1 - h_f$ disperse to other randomly chosen patches. After dispersal, offspring on a patch (both native and immigrant) compete for any breeding vacancies created by the mortality of adult members of their own sex. The offspring that fail to claim a breeding vacancy die, after which the same sequence of events is repeated in the next time step.

Selection gradients To model the evolution of male and female parental care, we use an adaptive dynamics approach [40, 52, 53]. This method assumes that evolutionary change in female and male care levels u_f and u_m occurs through the successive invasion and substitution of mutations of slight effect. In the Appendix, we derive fitness expressions $W(u_f + \delta u_f; u_f, u_m)$ (or $W(u_m + \delta u_m; u_f, u_m)$) for the fitness of a mutant female (or male) with care level $u_f + \delta u_f$ ($u_m + \delta u_m$) in a resident population that has female care levels u_f and male care levels u_m. When mutations in male and female care levels occur independently (i.e., no pleiotropy), the rate and direction of evolutionary change in u_f and u_m, is then proportional to the selection gradients $\partial W (u_f + \delta u_f; u_f, u_m) / \partial \delta u_f$ and $\partial W (u_m + \delta u_m; u_f, u_m) / \partial \delta u_m$ evaluated at $\delta u_f = \delta u_m = 0$. Expressions for these selection gradients are derived using a neighbour-modulated fitness (also called direct fitness) approach [45, 46, 54] in the Appendix. Consequently, we can solve for the equilibrium levels of female and male care (u_f^* and u_m^*) at which both selection gradients vanish.

Individual-based simulations We also ran individual-based simulations to corroborate our analytical results. We simulated a population of 2000 patches, each containing n_f female breeders and n_m male breeders. Each individual bears two unlinked, diploid loci u_f and u_m. Alleles at each locus interact additively. Each allele mutates with a per-generation probability of $\nu = 0.01$. In case a mutation occurs, a random number is drawn from a normal distribution with mean zero and variance $\sigma_\nu^2 = 0.0001$ and added to current allelic value. During each time step, a female chooses a random partner and produces $M \cdot b(u_f + u_m)$ offspring, where $M = 200$. Male and female offspring disperse to a random patch with probability d_m or d_f or remain at the natal patch with probability $1 - d_m$ and $1 - d_f$. After the offspring production stage, female and male breeders die with respective probabilities $\mu_m(u_m)$ and $\mu_f(u_f)$. In case of a death, a new offspring is randomly sampled from the pool of immigrant and local offspring in each patch, after which the next time step begins. Simulations ran for $100\,000$ generations. The simulations are coded in C and are available from the first author's website.

Male and female care in well-mixed populations We first focus on a simple 'baseline' scenario in which the number of breeding adults per patch is identical for both sexes, $n = n_f = n_m$, and in which males and females care only for their own offspring (i.e., no communal breeding [55, 56]), so that the survival of an individual offspring depends only upon the efforts of its own

father and mother. For a well-mixed population ($h_f = h_m = 0$), we then find that the equilibrium parental efforts u_f^* and u_m^* of mothers and fathers satisfy:

$$\frac{\mu_m'\left(u_m^*\right)}{\mu_m\left(u_m^*\right)} = \frac{b_{u_m}'\left(u_f^* + u_m^*\right)}{b\left(u_f^* + u_m^*\right)} \tag{1}$$

$$\frac{\mu_f'\left(u_f^*\right)}{\mu_f\left(u_f^*\right)} = \frac{b_{u_f}'\left(u_f^* + u_m^*\right)}{b\left(u_f^* + u_m^*\right)}, \tag{2}$$

where $b_x'(u_f^* + u_m^*)$ reflects the partial derivative of juvenile reproductive value with respect to the variable x. In other words, for each parental sex, the proportional increase in parental mortality due to a slight increase in effort (corresponding to the left-hand side of the equations) must precisely balance the proportional increase in offspring survival (corresponding to the right-hand side of the equations).

Sex-specific care when dispersal is limited   Again, we focus on a scenario where parents care only for their own offspring (no communal breeding). We now consider a viscous population in which dispersal is limited ($h_f, h_m > 0$) and where the number of male breeders n_m is not necessarily identical to the number of female breeders n_f (mating skew). Dependent on the level of mating skew, males sire, on average, offspring from multiple females and hence provide care for multiple broods (when males are rare, $n_m < n_f$) or sire only part of a brood of a single female (when males are common, $n_m > n_f$) and thus only care for that part of the brood. As the offspring survival function $b(u_f + u_m)$ measures effort at the level of a single brood, we thus need to weigh a male's contribution by his expected number of mates n_f/n_m, so that we have $b(u_f + u_m/\frac{n_f}{n_m})$. Incorporating these assumptions in a demographical model of parental care set out in the Supplement, we show that equilibrium female and male parental effort (eqns. [S24, S25]) now satisfy:

$$\left[r_{\text{self}} - r_{f \to \text{locally competing juv}}\right] \frac{\mu_f'\left(u_f^*\right)}{\mu_f\left(u_f^*\right)} = 2\left[r_{f \to \text{own juv}} - r_{f \to \text{competing juv}}\right] \frac{b_{u_f}'\left(u_f^* + \frac{n_m}{n_f}u_m^*\right)}{b\left(u_f^* + \frac{n_m}{n_f}u_m^*\right)} \tag{3}$$

$$\frac{n_f}{n_m}\left[r_{\text{self}} - r_{m \to \text{locally competing juv}}\right] \frac{\mu_m'\left(u_m^*\right)}{\mu_m\left(u_m^*\right)} = 2\left[r_{m \to \text{own juv}} - r_{m \to \text{competing juv}}\right] \frac{b_{u_m}'\left(u_f^* + \frac{n_m}{n_f}u_m^*\right)}{b\left(u_f^* + \frac{n_m}{n_f}u_m^*\right)}, \tag{4}$$

Here, terms on the left-hand side show that the proportional increase in parental mortality due to a slight increase in effort by each sex is weighted by the difference between r_{self}, which denotes the relatedness of the focal breeder to itself ($r_{\text{self}} = 1$), and $r_{x \to \text{locally competing juv}}$, which denotes the relatedness of a focal breeder of sex x to locally competing juveniles of the same sex, one of which will replace the focal breeder when it dies. On the right-hand side, the proportional increase in offspring survival due to a slight increase in parental effort is weighted by twice the difference between $r_{x \to \text{own juv}}$, which denotes the relatedness of a focal to its own juvenile offspring and $r_{x \to \text{competing juv}}$, which denotes its relatedness to offspring competing with its own young (the factor of two appears because in a sexual population every parent produces on average two offspring, one of each sex). Note that these relatedness coefficients depend, in turn, on a number of demographical parameters, including the sex-specific dispersal probabilities h_f and h_m, the sex-specific mortality rates $\mu_m(u_m)$ and $\mu_f(u_f)$ and the number of male and female

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breeders n_m and n_f. Explicit expressions for these relatedness coefficients are derived in the Supplementary Information, section S1.4.

Note that in a well-mixed population, in which there is no philopatry $h_f = h_m = 0$, we have $r_{f \to \text{own juv}} = r_{m \to \text{own juv}} = \frac{1}{2}$, $r_{f \to \text{locally competing juv}} = r_{m \to \text{locally competing juv}} = r_{f \to \text{competing juv}} = r_{m \to \text{competing juv}} = 0$, so that equations (3,4) reduce to eqns. (1,2).

Eqns. (3,4) can be used to investigate the influence of sex-biased philopatry on caring effort, for example by considering a scenario in which males are more philopatric than are females ($h_m > h_f$). As a result of such a dispersal asymmetry, a male's average relatedness $r_{m \to \text{local juv}}$ to local juveniles of his own sex increases compared to a female's average relatedness $r_{f \to \text{local juv}}$ to juveniles of her own sex. The left-hand side in eq. (4) therefore becomes smaller relative to the left-hand side in eq. (3). One can interpret this as a decrease in the effective mortality cost of care for males compared to females, due to the fact that in dying, a male breeder is more likely than is a female to free up a breeding spot for a related offspring. However, inspecting the right-hand side of eq. (4), $h_m > h_f$ also entails a decrease in the marginal benefits of increased male effort. This is because the term $r_{m \to \text{competing juv}}$ becomes larger, as a philopatric male who raises more surviving young is also more likely than is a female to displace related offspring. The balance between these two effects, however, favours greater parental effort by the more philopatric sex (here males), because it can be shown that $r_{m \to \text{competing juv}}$ on the right-hand side is smaller to an order $(h_f^2 + h_m^2)/h_m$ relative to the coefficient $r_{m \to \text{local juv}}$ on the left-hand side (see eqns. S27, S29). As a result, male-biased philopatry leads males to increase their level of parental effort, while females reduce theirs.

2.1   Result 1: the philopatric sex provides more care to the brood

Figure 1 provides a simple illustration of the dramatic effect that sex-differences in philopatry can have on the levels of parental effort provided by males and females: in contrast to classical models [17, 19], which predict that both parents should invest equally in their young (Figure 1A), even modest sex-biases in philopatry lead to the more philopatric sex (males in this example) providing the majority of care to young (Figure 1B). Stronger sex-biases in philopatry can even lead to scenarios in which the philopatric sex effectively become sole carers, while the contribution by the dispersing sex to the brood is negligible (Figure 1C). This pattern is robust to variation in absolute sex-specific dispersal probabilities, provided that the direction of sex-specific bias is unchanged, as shown in Figure 2. The effect is most pronounced when a single breeding pair occupies a patch (Figure 2A). With a larger number of breeding pairs per patch, the overall asymmetry may be less pronounced (as relatedness to young is reduced due to the presence of other breeding pairs), but the most philopatric sex still provides the majority of care (Figure 2B).

2.2   Result 2: the most common sex does not always provide more care

Next, we consider the effect of mating skew, where the number of female breeders in a patch differs from that of the male breeders, $n_f \neq n_m$. Note that the left-hand side of eq. (4) is multiplied by n_f/n_m, which shows that mating skew directly affects the equilibrium balance of sex-specific care. When males are the more common sex, for example, the left hand side in eq. (4) is reduced relative to that in eq. (3), so that an increase in male parental effort has a smaller effective mortality cost relative to an increase in female effort. Selection thus favours greater caring effort by males when they are the more common sex (and less caring effort when they are the rarer sex). That the more common sex cares more is a well-known result from studies

modeling how the adult sex ratio (ASR) affects sex differences in parental care in well-mixed populations [8, 29].

However, mating skew also affects sex differences in parental effort indirectly, by modulating the relatedness coefficients (3, 4). When males are the more common sex, individual males have a lower genetic share in the next generation in the local patch (as they compete more strongly for matings), thus reducing a male's relatedness $r_{\mathrm{m}\to\text{locally competing juv}}$ to any locally competing juveniles. Vice versa, the coefficient $r_{\mathrm{f}\to\text{locally competing juv}}$ for females is increased, as individuals of the rare sex have a greater genetic share in the next generation. In dying, males are therefore less likely to be replaced by a related juvenile in comparison to females, so that the effective mortality cost of care is larger for the more common sex. For the same reasons, $r_{\mathrm{m}\to\text{competing juv}}$ on the right-hand side of eq. (4) is also reduced when males are the common sex, reducing the fecundity benefit of increased care for the more common sex. However, $r_{\mathrm{m}\to\text{competing juv}}$ is smaller than $r_{\mathrm{m}\to\text{locally competing juv}}$ on the left hand side (compare eqns. [S29, S27]), any indirect effects of mating skew via relatedness cause the more common sex to provide less care relative to the rare sex.

Individual care: the common sex cares more What is the overall consequence of both indirect and direct effects on the evolution of sex-differences in care? When individuals care only for their own offspring, Figure 3A-C shows that the more numerous sex always provides the majority of care to the young. In other words, the indirect effect of mating skew via relatedness does is not enough to alter the well-established result that the more common sex cares more [8, 29]. Nonetheless, the amount of care provided by each sex is still affected by sex differences in dispersal, as levels of sex-specific care increase with philopatry (contour lines in Figure 3A-C).

Communal care: the philopatric sex cares more Things are different, however, when we consider a scenario of communal care, in which individuals provide care to all locally born offspring. Figures 3D, F show that effect of mating skew (causing the more common sex to provide more care) is now markedly reduced relative to that of sex-biased dispersal. Only when dispersal patterns are relatively similar across both sexes (i.e., close to the line $h_{\mathrm{m}} = h_{\mathrm{f}}$), do we find that mating skew determines which sex provides most of the care. Otherwise, we retrieve the interesting result that the more philopatric sex provides most of the care.

Why does communal care change our conclusions? When parents care for all locally born offspring, coefficients $r_{\mathrm{f}\to\text{own juv}}$ and $r_{\mathrm{m}\to\text{own juv}}$ in equations (3,4) for the case of individual care are now replaced by the coefficients $r_{\mathrm{f}\to\text{locally born juv}}$ and $r_{\mathrm{m}\to\text{locally born juv}}$. Hence, whether focal gene copies benefit from any changes in the focal's care now depends on mating skew: when males are the more common sex ($n_{\mathrm{m}} > n_{\mathrm{f}}$), individual males have a smaller expected genetic share in the next generation relative to females. As a consequence, a slight increase in a mutant male's parental effort is less likely to benefit copies of that mutant gene present in offspring, because $r_{\mathrm{m}\to\text{locally born juv}}$ becomes smaller relative to $r_{\mathrm{f}\to\text{locally born juv}}$ as n_{m} increases. Going back to eqns. (3,4), communal care substantially reduces the fecundity benefit of effort by the more common sex (right-hand side), thus offsetting the previously found reduction in the effective mortality cost of increased care by the more common sex (left-hand side). All in all, the effect of mating skew is therefore largely cancelled out in taxa with communal care, causing the effects of sex-biased dispersal to prevail (Figures 3D, F).

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2.3 Result 3: sex-biased dispersal can mask sex-specific costs of care

Well-established predictions on sex-biases in care often focus on differences in costs and constraints between the sexes [17, 57, 58], which raises the question how sensitive our conclusions are to asymmetries in costs between the sexes. Figure 4 varies the mortality cost of male care relative to female care, $(1-k_{\mathrm{m}})/(1-k_{\mathrm{f}})$. Unsurprisingly, when male philopatry is low the proportion of male care rapidly decreases with increasing mortality costs of male care. However, for taxa with high levels of male philopatry, we would predict that males still provide the majority of care in the face of considerable costs. Consequently, sex-biased dispersal can mask the effect that sex differences in cost have on the relative amount of care that males and females provide to their young.

3 Discussion

Our analysis reveals that sex differences in dispersal can have a substantial effect on the resolution of sexual conflict over parental care: when females are the dispersing sex, our model predicts that males should typically invest more in caring for young. Vice versa, when males are the dispersing sex, females should invest more in care. These predictions contrast strikingly with those of classical models assuming well-mixed populations (e.g., [17]); the impact of sex-biased dispersal may even be sufficient to destabilise biparental care and lead to uniparental care by the philopatric sex (see Figure 1). Although the effect of sex-biased dispersal can be outweighed by that of mating skew in certain breeding systems (such that the more common sex provides most of the care, even if it is more prone to dispersal; Figure 3), all other things being equal, parental investment by a given sex always increases with the relative level of philopatry of that sex.

Why does sex-biased dispersal have such marked effects? Previous models of the evolution of reproductive effort in asexual populations have shown that greater effort is selectively favoured, at a cost to adult survival, when dispersal is more limited[59–61]. Our model reveals that the same holds true in populations with two sexes: where males are the philopatric sex, for example, they value the production of offspring more relative to their own survival, thus selectively favouring higher levels of male care. By contrast, the dispersing sex, in this case females, value their own survival more relative to the production of offspring, selectively favouring reduced levels of female care. These effects arise because, in dying, an adult of the philopatric sex is likely to free up a breeding vacancy that may be occupied by a local, related offspring; this indirect, kin-selected benefit partially offsets the cost of death. By contrast, when an adult of the dispersing sex dies, the vacancy created is more likely to be filled by an unrelated, immigrant offspring. Consequently, as sex-biased dispersal changes the trade-off between adult survival and offspring production to diverge between the sexes, sex-biases in parental care are likely to arise.

Our model also shows that mating skew can substantially influence sex-specific patterns of parental care, with the more numerous sex (all other things being equal) providing more of the care. This finding corroborates previous studies on the relationship between the ASR and sex roles in well-mixed populations [8, 28, 29]. As one sex becomes more numerous, investment in survival becomes less advantageous due to increased competition over future breeding opportunities, favouring increased investment in current reproductive output. Consequently, we expect the more numerous sex to provide most of the care regardless of the degree of sex-biased dispersal (e.g., Figure 3A-C). However, the same does not hold in populations with communal care, in which local males and females care for all locally born offspring. In the case of com-

munal care, parental investment by individuals of the more numerous sex yields fewer benefits because care is distributed among offspring other than one's own, favouring lower levels of investment.

Our prediction that the philopatric sex provides more care could be tested using available data on parental care and sex-biased dispersal in well-studied taxonomic groups. One may, for instance, contrast dispersal and parental care in birds and mammals: in mammals, males are typically the dispersing sex [37, 39, 62] and indeed we find that the more philopatric sex (females) provide most of the care: in 90% of all mammalian taxa female care predominates, while male-only care is completely absent [63]. In birds, by contrast, females are typically the sex more prone to dispersal [37, 38, 64], and male contribution to parental care is much more common in birds than in mammals, with the vast majority of all bird species (90%) exhibiting biparental care [63]. Obviously, there are other differences between birds and mammals that might account for these broad differences, and a more detailed comparative analysis would be needed to test our predictions properly. Nevertheless, our model clearly suggests that spatial structure and sex-differences in dispersal have been largely overlooked in existing meta-analyses (e.g., [65–67]) that aim to understand the social and ecological factors influencing sex role evolution.

Previous models have focused on behavioural interactions at the level of the family and on sex-specific costs of care as the main drivers of asymmetries in parental care between the males and females [17–23, 68, 69]. To our knowledge, there are currently no theoretical predictions that take account of ecological processes at population-level. Since our results show that dispersal and spatial population structure affect the outcome of conflict between parents over care, it seems likely that other ecological factors may also have a hitherto unforeseen impact on the relative level of investment by mothers and fathers. Factors such as spatiotemporal variation in resources, predation and disease are likely to be important factors [70], but the impact of such variation on parental care tactics remains to be explored.

Possible extensions to our model include analysing the coevolution of care and dispersal strategies. We have treated sex-specific dispersal rates as fixed parameters, and yet the evolution of sex-biased dispersal itself may well be affected by male and female parental effort. So far, studies of the evolution of sex-differences in dispersal have focused on inbreeding avoidance and sex differences in kin competition as drivers of sex-biases in dispersal [71–74], . overlooking the impact of sex-differences in care. In the absence of any sex-specific fitness consequences of parental effort , investment in care should affect competition among kin of both sexes equally and thus is unlikely to lead to sex-differences in dispersal. However, when parental care is more beneficial for offspring of one sex versus the other (e.g., [75]), parental effort is likely to affect sex-biases in dispersal.

Another key assumption of our model is that parental strategies specify investment in care as a 'sealed bid' by both parents, as in the classical model by Houston & Davies [17]. In other words, parents are unable to respond to each other's efforts on a behavioural time scale. By contrast, more recent models of negotiation over care have begun to explore the evolution of sex-differences in the degree of responsiveness to the amount of effort invested by a partner [18, 19, 21, 22]. When responding to each other's efforts is costly, our study suggests that sex-biases in dispersal are likely to affect the degree of sex-specific responsiveness, simply because the effective cost of being more responsive will be lower for the philopatric sex. In general, sex differences in phenotypic plasticity (of which parental responsiveness is an example) are likely to be affected by the degree of philopatry.

To summarise, more studies that place models of family conflict in their population-level, ecological context are likely to enhance our understanding of the great variation in family life histories that we observe in nature.

References

[1] Parker, G. A., 1979 Sexual selection and sexual conflict. In *Sexual selection and Reproductive Competition in the Insects* (eds. N. S. Blum & N. B. Blum). New York: Academic Press, pp. 123–166.

[2] Arnqvist, G. & Rowe, L., 2005 *Sexual Conflict.* Princeton University Press, Princeton.

[3] Wedell, N., Kvarnemo, C., Lessells, C. M. & Tregenza, T., 2006 Sexual conflict and life histories. *Anim. Behav.* **71**, 999–1011. doi:10.1016/j.anbehav.2005.06.023.

[4] Trivers, R., 1972 Parental investment and sexual selection. In *Sexual Selection and the Descent of Man* (ed. B. Campbell). Chicago: Aldine Publishing Company, pp. 136–179.

[5] Parker, G. A., Royle, N. J. & Hartley, I. R., 2002 Intrafamilial conflict and parental investment: a synthesis. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **357**, 295–307. doi:10.1098/rstb.2001.0950.

[6] Houston, A. I., Szèkely, T. & McNamara, J. M., 2005 Conflict between parents over care. *Trends Ecol. Evol.* **20**, 33–38. doi:10.1016/j.tree.2004.10.008.

[7] Lessells, C. M., 2012 Sexual conflict. In *The Evolution of Parental Care* (eds. N. J. Royle, P. T. Smiseth & M. Kolliker). Oxford, UK: Oxford University Press, pp. 150–170. doi:10.1093/acprof:oso/9780199692576.001.0001.

[8] Kokko, H. & Jennions, M. D., 2008 Parental investment, sexual selection and sex ratios. *J. Evol. Biol.* **21**, 919–948. doi:10.1111/j.1420-9101.2008.01540.x.

[9] Valera, F., Hoi, H. & Schleicher, B., 1997 Egg burial in penduline tits, *Remiz penudlinus*: its role in mate desertion and female polyandry. *Behav. Ecol.* **8**, 20–27. doi:10.1093/beheco/8.1.20.

[10] Hrdy, S. B., 1979 Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethol. Sociobiol.* **1**, 13–40. doi:10.1016/0162-3095(79)90004-9.

[11] Hausfather, G. & Hrdy, S. (eds.), 1984 *Infanticide: Comparative and Evolutionary Perspectives*. New York: Aldine.

[12] Székely, T., Webb, J. N., Houston, A. I. & McNamara, J. M., 1996 An evolutionary approach to offspring desertion in birds. *Curr. Ornithol.* **13**, 271–330. doi:10.1007/978-1-4615-5881-1_6.

[13] Van Dijk, R. E., Szentirmai, I., Komdeur, J. & Székely, T., 2007 Sexual conflict over parental care in penduline tits *Remiz pendulinus*: the process of clutch desertion. *Ibis* **149**, 530–534.

[14] Schwagmeyer, P. L., Mock, D. W. & Parker, G. A., 2002 Biparental care in house sparrows: negotiation or sealed bid? *Behav. Ecol.* **13**, 713–721. doi:10.1093/beheco/13.5.713.

[15] Smiseth, P. T. & Moore, A. J., 2004 Behavioral dynamics between caring males and females in a beetle with facultative biparental care. *Behav. Ecol.* **15**, 621–628. doi:10.1093/beheco/arh053.

[16] Hinde, C. A. & Kilner, R. M., 2007 Negotiations within the family over the supply of parental care. *Proc. R. Soc. Lond. B Biol. Sci.* **274**, 53–60. doi:10.1098/rspb.2006.3692.

[17] Houston, A. & Davies, N., 1985 The evolution of cooperation and life history in the dunnock, *Prunella modularis*. In *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (eds. R. Sibley & R. Smith). Oxford, UK: Blackwell Publishing Inc, pp. 471–487.

[18] McNamara, J. M., Gasson, C. E. & Houston, A. I., 1999 Incorporating rules for responding into evolutionary games. *Nature* **401**, 368–371. doi:10.1038/43869.

[19] McNamara, J. M., Houston, A. I., Barta, Z. & Osorno, J.-L., 2003 Should young ever be better off with one parent than with two? *Behav. Ecol.* **14**, 301–310. doi:10.1093/beheco/14.3.301.

[20] Härdling, R., Kokko, H. & Arnold, K., 2003 Dynamics of the caring family. *Am. Nat.* **161**, 395–412. doi:10.1086/367587.

[21] Johnstone, R. A. & Hinde, C. A., 2006 Negotiation over offspring care – how should parents respond to each other's efforts? *Behav. Ecol.* **17**, 818–827. doi:10.1093/beheco/arl009.

[22] Lessells, C. M. & McNamara, J. M., 2012 Sexual conflict over parental investment in repeated bouts: negotiation reduces overall care. *Proc. R. Soc. Lond. B Biol. Sci.* **279**, 1506–1514. doi:10.1098/rspb.2011.1690.

[23] Johnstone, R. A., Manica, A., Fayet, A. L., Stoddard, M. C., Rodriguez-Gironés, M. A. & Hinde, C. A., 2014 Reciprocity and conditional cooperation between great tit parents. *Behav. Ecol.* **25**, 216–222. doi:10.1093/beheco/art109.

[24] Johnstone, R. A., 2011 Load lightening and negotiation over offspring care in cooperative breeders. *Behav. Ecol.* **22**, 436–444. doi:10.1093/beheco/arq190.

[25] Savage, J. L., Russell, A. F. & Johnstone, R. A., 2013 Maternal costs in offspring production affect investment rules in joint rearing. *Behav. Ecol.* **24**, 750–758. doi:10.1093/beheco/ars203.

[26] Mock, D. & Parker, G., 1997 *The Evolution of Sibling Rivalry*. Oxford, UK: Oxford University Press.

[27] Parker, G. A. & Simmons, L. W., 1996 Parental investment and the control of sexual selection: predicting the direction of sexual competition. *Proc. R. Soc. Lond. B Biol. Sci.* **263**, 315–321. doi:10.1098/rspb.1996.0048.

10

[28] McNamara, J. M., Székely, T., Webb, J. N. & Houston, A. I., 2000 A dynamic game-theoretic model of parental care. *J. Theor. Biol.* **205**, 605–623. doi:10.1006/jtbi.2000.2093.

[29] Kokko, H. & Johnstone, R. A., 2002 Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **357**, 319–330. doi:10.1098/rstb.2001.0926.

[30] Haig, D., 2000 Genomic imprinting, sex-biased dispersal, and social behavior. *Ann. NY. Acad. Sci.* **907**, 149–163. doi:10.1111/j.1749-6632.2000.tb06621.x.

[31] Van Cleve, J., Feldman, M. W. & Lehmann, L., 2010 How demography, life history, and kinship shape the evolution of genomic imprinting. *Am. Nat.* **176**, 440–455. doi:10.1086/656277.

[32] Úbeda, F. & Gardner, A., 2010 A model for genomic imprinting in the social brain: juveniles. *Evolution* **64**, 2587–2600. doi:10.1111/j.1558-5646.2010.01015.x.

[33] Kuijper, B. & Johnstone, R. A., 2012 How dispersal influences parent-offspring conflict over investment. *Behav. Ecol.* **23**, 898–906. doi:10.1093/beheco/ars054.

[34] Lion, S. & Van Baalen, M., 2007 From infanticide to parental care: why spatial structure can help adults be good parents. *Am. Nat.* **170**, E26–E46. doi:10.1086/519462.

[35] Johnstone, R. A. & Cant, M. A., 2008 Sex differences in dispersal and the evolution of helping and harming. *Am. Nat.* **172**, 318–330. doi:10.1086/589899.

[36] Gardner, A., 2010 Sex-biased dispersal of adults mediates the evolution of altruism among juveniles. *J. Theor. Biol.* **262**, 339–345. doi:10.1016/j.jtbi.2009.09.028.

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

[38] Greenwood, P. J. & Harvey, P. H., 1982 The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Evol. Syst.* **13**, 1–21. doi:10.1146/annurev.es.13.110182.000245.

[39] Lawson Handley, L. J. & Perrin, N., 2007 Advances in our understanding of mammalian sex-biased dispersal. *Mol. Ecol.* **16**, 1559–1578. doi:10.1111/j.1365-294X.2006.03152.x.

[40] Rousset, F., 2004 *Genetic Structure in Subdivided Populations*. Princeton: Princeton University Press.

[41] Gardner, A. & West, S. A., 2006 Demography, altruism, and the benefits of budding. *J. Evol. Biol.* **19**, 1707–1716. doi:10.1111/j.1420-9101.2006.01104.x.

[42] Lehmann, L., Perrin, N. & Rousset, F., 2006 Population demography and the evolution of helping behaviors. *Evolution* **60**, 1137–1151. doi:10.1111/j.0014-3820.2006.tb01193.x.

[43] Johnstone, R. A., Cant, M. A. & Field, J., 2012 Sex-biased dispersal, haplodiploidy and the evolution of helping in social insects. *Proc. R. Soc. Lond. B Biol. Sci.* **279**, 787–793. doi:10.1098/rspb.2011.1257.

[44] Hamilton, W. D., 1964 The genetical evolution of social behaviour. I. *J. Theor. Biol.* **7**, 1–16. doi:10.1016/0022-5193(64)90038-4.

11

[45] Taylor, P. D. & Frank, S. A., 1996 How to make a kin selection model. *J. Theor. Biol.* **180**, 27–37. doi:10.1006/jtbi.1996.0075.

[46] Taylor, P. D., Wild, G. & Gardner, A., 2007 Direct fitness or inclusive fitness: how shall we model kin selection? *J. Evol. Biol.* **20**, 301–309. doi:10.1111/j.1420-9101.2006.01196.x.

[47] Lion, S., Jansen, V. A. & Day, T., 2011 Evolution in structured populations: beyond the kin versus group debate. *Trends Ecol. Evol.* **26**, 193–201. doi:10.1016/j.tree.2011.01.006.

[48] Wright, S., 1931 Evolution in Mendelian populations. *Genetics* **16**, 97–159.

[49] Wright, S., 1951 The genetical structure of populations. *Annals Eugen.* **15**, 323–354. doi:10.1111/j.1469-1809.1949.tb02451.x.

[50] Trivers, R. L., 1974 Parent-offspring conflict. *Am. Zool.* **14**, 249–264. doi:10.1093/icb/14.1.249.

[51] Parker, G. A. & Macnair, M. R., 1978 Models of parent–offspring conflict. I. Monogamy. *Anim. Behav.* **26**, 97–110. doi:10.1016/0003-3472(78)90009-X.

[52] McGill, B. J. & Brown, J. S., 2007 Evolutionary game theory and adaptive dynamics of continuous traits. *Annu. Rev. Ecol. Evol. Syst.* **38**, 403–435. doi:10.1146/annurev.ecolsys.36.091704.175517.

[53] Dercole, F. & Rinaldi, S., 2008 *Analysis of Evolutionary Processes: the Adaptive Dynamics Approach and its Applications*. Princeton: Princeton University Press.

[54] Hamilton, W. D., 1964 The genetical evolution of social behaviour. II. *J. Theor. Biol.* **7**, 17–52. doi:10.1016/0022-5193(64)90039-6.

[55] Brown, J. L., 1978 Avian communal breeding systems. *Annu. Rev. Ecol. Evol. Syst.* **9**, 123–155. doi:10.1146/annurev.es.09.110178.001011n.

[56] Cant, M. A., 2012 Cooperative breeding systems. In *The Evolution of Parental Care* (eds. N. J. Royle, P. T. Smiseth & M. Kölliker). Oxford: Oxford University Press, pp. 206–225. doi:10.1093/acprof:oso/9780199692576.003.0012.

[57] Gross, M. R. & Sargent, R. C., 1985 The evolution of male and female parental care in fishes. *Am. Zool.* **25**, 807–822. doi:10.1093/icb/25.3.807.

[58] Liker, A. & Székely, T., 2005 Mortality costs of sexual selection and parental care in natural populations of birds. *Evolution* **59**, 890–897. doi:10.1111/j.0014-3820.2005.tb01762.x.

[59] Pen, I., 2000 Reproductive effort in viscous populations. *Evolution* **54**, 293–297. doi:10.1111/j.0014-3820.2000.tb00030.x.

[60] Ronce, O. & Promislow, D., 2010 Kin competition, natal dispersal and the moulding of senescence by natural selection. *Proc. R. Soc. Lond. B Biol. Sci.* **277**, 3659–3667. doi:10.1098/rspb.2010.1095.

[61] Johnstone, R. A. & Kuijper, B., 2014 Kin competition and the evolution of sex differences in development time and body size. *Am. Nat.* **183**, 537–546. doi:10.1086/675392.

[62] Dobson, S. F., 1982 Competition for mates and predominant juvenile male dispersal in mammals. *Anim. Behav.* **30**, 1183–1192. doi:10.1016/S0003-3472(82)80209-1.

[63] Clutton-Brock, T. H., 1991 *The Evolution of Parental Care*. Princeton: Princeton University Press.

[64] Clarke, A. L., Sæther, B.-E. & Røskaft, E., 1997 Sex biases in avian dispersal: a reappraisal. *Oikos* **79**, 429–438. doi:10.2307/3546885.

[65] Harrison, F., Barta, Z., Cuthill, I. & Székely, T., 2009 How is sexual conflict over parental care resolved? A meta-analysis. *J. Evol. Biol.* **22**, 1800–1812. doi:10.1111/j.1420-9101.2009.01792.x.

[66] Olson, V., Liker, A., Freckleton, R. & Székely, T., 2008 Parental conflict in birds: comparative analyses of offspring development, ecology and mating opportunities. *Proc. R. Soc. Lond. B Biol. Sci.* **275**, 301–307. doi:10.1098/rspb.2007.1395.

[67] Liker, A., Freckleton, R. P. & Székely, T., 2013 The evolution of sex roles in birds is related to adult sex ratio. *Nat. Commun.* **4**, 1587. doi:10.1038/ncomms2600.

[68] Jones, K. M., Ruxton, G. D. & Monaghan, P., 2002 Model parents: is full compensation for reduced partner nest attendance compatible with stable biparental care? *Behav. Ecol.* **13**, 838–843. doi:10.1093/beheco/13.6.838.

[69] Van Dijk, R. E., Székely, T., Komdeur, J., Pogány, Á., Fawcett, T. W. & Weissing, F. J., 2012 Individual variation and the resolution of conflict over parental care in penduline tits. *Proc. R. Soc. Lond. B Biol. Sci.* **279**, 1927–1936. doi:10.1098/rspb.2011.2297.

[70] Quinlan, R. J., 2007 Human parental effort and environmental risk. *Proc. R. Soc. Lond. B Biol. Sci.* **274**, 121–125. doi:10.1098/rspb.2006.3690.

[71] Gandon, S., 1999 Kin competition, the cost of inbreeding and the evolution of dispersal. *J. Theor. Biol.* **200**, 345–364. doi:10.1006/jtbi.1999.0994.

[72] Perrin, N. & Mazalov, V., 1999 Dispersal and inbreeding avoidance. *Am. Nat.* **154**, 282–292. doi:10.1086/303236.

[73] Perrin, N. & Mazalov, V., 2000 Local competition, inbreeding, and the evolution of sex-biased dispersal. *Am. Nat.* **155**, 116–127. doi:10.1086/303296.

[74] Lehmann, L. & Perrin, N., 2003 Inbreeding avoidance through kin recognition: choosy females boost male dispersal. *Am. Nat.* **162**, 638–652. doi:10.1086/378823.

[75] Lessells, C. M., 2002 Parentally biased favouritism: why should parents specialize in caring for different offspring? *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **357**, 381–403. doi:10.1098/rstb.2001.0928.

[76] Taylor, P. D., 1990 Allele-frequency change in a class-structured population. *Am. Nat.* **135**, 95–106. doi:10.1086/285034.

4   Figure captions

Figure 1   Sex-biases in dispersal can drive evolutionary transitions from biparental to near-uniparental care. The black dot in each panel shows the evolutionary stable level of female u_f^* and male parental care u_m^* for different combinations of male and female philopatry, h_m and h_f respectively. Panel A: the baseline case of a well-mixed population with complete migration, in which there are no sex-differences in care, $u_f = u_m$. Panel B: when males are more philopatric than females ($h_m > h_f$), males provide the majority of care to young. Panel C: when males are extremely philopatric in comparison to females, selection favours males to provide almost all care to young, whereas the amount of female care is negligible. Parameters: $n_m = n_f = 1$, $k_f = k_m = 0.1$. Red line: the selection differential of female effort vanishes, $dW/du_f = 0$. Blue line: the selection differential of male care vanishes, $dW/du_m = 0$. Light grey lines: individual-based simulations.

Figure 2   The equilibrium proportion of male care $u_m^*/(u_m^* + u_f^*)$ as a function of the amount of philopatry in both sexes. Panel A: in highly viscous populations with few individuals per patch ($n_f = n_m = 1$), slight sex-biases in philopatry cause pronounced sex-differences in care. In case sex-biases in philopatry are large, selection favours near uniparental care by the most philopatric sex. Panel B: in populations with multiple breeding pairs per patch, the effect of philopatry on sex-differences in care is less pronounced. Nonetheless, even here we find that the most philopatric sex always provides the majority of care to young. Parameters: $k_f = k_m = 0.1$.

Figure 3   The equilibrium fraction of male care $u_m^*/(u_m^* + u_f^*)$ for different degrees of mating skew n_m/n_f. Panels A-C: Parents care only for their own offspring. When mating skews occur for parents that care only for their own offspring, the more numerous sex (i.e., the sex with the lowest reproductive value) always provides the majority of care, regardless of the level of dispersal. Nonetheless, amount of care by a particular sex always increases with its level of natal philopatry. Panels D,F: in case parents provide care for all local offspring, the parameter space in which the more numerous sex provides most of the care is substantially decreased. Consequently, the level of philopatry becomes a more important determinant of the degree of sex-specific care, so that often the philopatric sex provides the majority of care. Parameters: $k_m = k_f = 0.1$.

Figure 4   The philopatric sex (here males) typically provides the majority of care, even when it has to pay a far higher mortality cost than the dispersing sex. The equilibrium fraction of male care $u_m^*/(u_m^* + u_f^*)$ when varying the cost of male care relative to that of female care, $(1-k_m)/(1-k_f)$ (x-axis) and by varying the level of male philopatry (y-axis). With low levels of philopatry, the proportion of male care rapidly declines from a pattern where males provide the majority of care to cases where females provide most of the care. However, when male dispersal is limited, males provide the majority of care to the brood, despite high sex-specific costs of male care. Parameters: $n_m = n_f = 2$, $d_f = 0.1$.
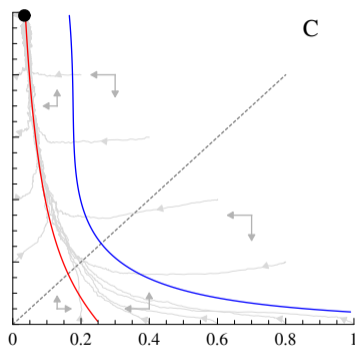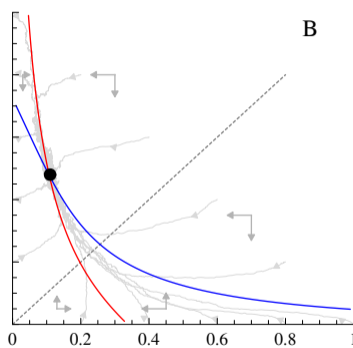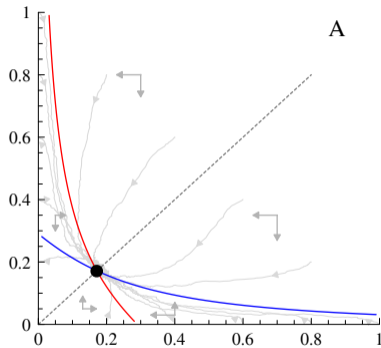
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Figure titles: $h_f = h_m = 0$ (A), $h_f = 0.5$, $h_m = 0.8$ (B), $h_f = 0.1$, $h_m = 0.9$ (C)

Legend:
$u_f = u_m$
u_f isocline
u_m isocline

X-axis: Female effort, u_f

Y-axis: Male effort, u_m

A $n_f = n_m = 1$

B $n_f = n_m = 3$

Male philopatry, h_m

Female philopatry, h_f

% male care

Figure panels A, B, C (top row): A — $n_f = 4, n_m = 2$; B — $n_f = 3, n_m = 3$; C — $n_f = 2, n_m = 4$. Right of top row: → parents care for own offspring. Legend: blue = male provides more care; white = female provides more care.

Panels D, E, F (bottom row). Right of bottom row: → parents care for all local offspring.

Axes: Female philopatry, h_f (horizontal); Male philopatry, h_m (vertical).