

How sex-biased dispersal affects sexual conflict over care

Bram Kuijper^{1,*} & Rufus A Johnstone²

February 23, 2018

¹) Environment and Sustainability Institute, University of Exeter, Penryn Campus, TR11 9FE Penryn, United Kingdom

²) Department of Zoology, University of Cambridge, Downing Street, CB2 3EJ Cambridge, United Kingdom

*) Corresponding author: a.l.w.kuijper@exeter.ac.uk

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. We conclude that sex-biased dispersal is likely to be an important, yet currently overlooked driver of sex-differences in parental care.

Introduction

Although mothers and fathers share a common genetic stake in the survival of their young, their evolutionary interests are rarely fully aligned (Parker, 1979; Arnqvist and Rowe, 2005; Wedell et al., 2006). 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 (Trivers, 1972; Parker et al., 2002; Houston et al., 2005; Lessells, 2012). Such conflict is thought to be an important driver of between-species variation in forms of care (Kokko and Jennions, 2008) and is associated with a range of conspicuous behaviors, such as brood concealment (Valera et al., 1997), infanticide (Hrdy, 1979; Hausfather and Hrdy, 1984), brood desertion (Székely et al., 1996; Van Dijk et al., 2007) and negotiation between parents over care (e.g., Schwagmeyer et al., 2002; Smiseth and Moore, 2004; Hinde and Kilner, 2007).

Over the years, a substantial body of theory has been developed to explain the evolution of parental care (for reviews see Houston et al., 2005; Alonzo, 2010; Lessells, 2012), focusing chiefly on behavioral interactions within the family (e.g., negotiation or coercion between parents [Houston and Davies, 1985; McNamara et al., 1999, 2003; Johnstone and Hinde, 2006; Lessells and McNamara, 2012; Johnstone et al., 2014] or between parents and helpers [Johnstone, 2011; Savage et al., 2013]). 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 behavior of a small number of family members in the context of a clearly defined “nursery” environment (Mock and Parker, 1997). 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 (Parker and Simmons, 1996; McNamara et al., 2000; Kokko and Johnstone, 2002; Kokko and Jennions, 2008; Alonzo, 2012). 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 [Haig, 2000; Van Cleve et al., 2010; Úbeda and Gardner, 2010], parent-offspring conflict [Kuijper and Johnstone, 2012], female harming [Rankin, 2011; Wild et al., 2011; Faria et al., 2015] and infanticide [Lion and Van Baalen, 2007]). The importance of dispersal in the familial context raises the question of whether it might also affect the outcome of sexual conflict between parents over care. In related contexts such as sex allocation, sex-biased dispersal is well known to result in conflict between males and females over the sex ratio (Wild and Taylor, 2005). In addition, models that focus on more abstract social behavior (e.g., helping and harming) have shown that sex-differences in dispersal can favor substantial asymmetries in helping behaviors between the two sexes (Johnstone and Cant, 2008; Gardner, 2010). Given that sex-biases in dispersal are common in the animal kingdom (Greenwood, 1980; Greenwood and Harvey, 1982; Lawson Handley and Perrin, 2007), 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 (Houston and Davies, 1985) embedding it in a demographically explicit framework familiar from models of social evolution in structured populations (Taylor, 1988, 1992; Rousset, 2004; Gardner and West, 2006; Lehmann et al., 2006; Johnstone et al., 2012).

The model

A demographical model of parental care Our approach is to develop an evolutionary demographic model (Hamilton, 1964a; Taylor and Frank, 1996; Rousset, 2004; Taylor et al., 2007; Lion et al., 2011) of the provision of care to a brood by male and female parents. Consider a population distributed over infinitely many

territories (Wright, 1931, 1951), 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 (see section S3 in the Online Supplement which shows that sex ratio biases do not affect sex-differences in care). We assume that all males on the patch have identical mating success. When $n_f = n_m$, this could entail a female pairing up with a randomly chosen local male, and that male fathers all her offspring, 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 and is assumed to apply here.

The individual parental efforts of males and females are given by u_m and u_f respectively, and the number of surviving offspring $b(u_f, u_m)$ depends upon the combined efforts of both parents. Following the classical model by Houston and Davies (1985), we assume that male and female efforts contribute additively to offspring survival. In addition, we assume that the number of surviving offspring $b(u_f, u_m)$ measures effort at the level of a single brood: consequently, we need to weigh a male's contribution to the current brood by his expected number of mates n_f/n_m , so that a male's effort to a single brood is given by u_m/n_f . Hence, offspring survival can be written as $b(u_f, u_m) \equiv b(u_f + u_m \frac{n_m}{n_f})$.

Following classical models of parental investment (Trivers, 1972, 1974; Parker and Macnair, 1978; Parker et al., 2002; McNamara et al., 2003), 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 $\mu_x \equiv \mu_x(u_x)$ (Trivers, 1972). Again, in accordance with previous models (e.g., McNamara et al., 2003; Johnstone and Hinde, 2006), we assume that parental mortality increases in accelerating fashion with an individual's effort $\partial \mu_x/\partial u_x > 0$ and $\partial^2 \mu_x/\partial u_x^2 > 0$. To generate the figures below, the fecundity of a pair with effort levels u_f and u_m is given by the decelerating function $b(u_f + \frac{n_m}{n_f} u_m) = 1 - \exp[-(u_f + \frac{n_m}{n_f} u_m)]$ (e.g., see Parker and Macnair, 1978; Houston and Davies, 1985). The mortality $\mu_i(u_i)$ of individuals of sex i is given by the accelerating function (e.g., McNamara et al., 2003) $\mu_i(u_i) = k_i + (1 - k_i)u_i^2$, where k_i reflects the baseline mortality per breeding season and $1 - k_i$ the strength with which the square of sex-specific effort u_i^2 increases mortality.

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 (Rousset, 2004; McGill and Brown, 2007; Dercole and Rinaldi, 2008). 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. For the sake of simplicity, u_f and u_m are represented by haploid, autosomal gene loci with full recombination between them (although individual-based simulations with diploid inheritance give identical results, see below). Moreover, we assume sex-limited expression, so that u_f and u_m are only expressed in females and males respectively. In the Appendix, we derive fitness expressions $W(u_f + \delta u_f; u_f, u_m)$ and $W(u_m + \delta u_m; u_f, u_m)$ for the fitness of a mutant female and male respectively. The mutant females and males have care levels $u_f + \delta u_f$ and $u_m + \delta u_m$ respectively, 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 a 'personal fitness') approach (Hamilton, 1964b; Taylor and Frank, 1996; Taylor et al., 2007;

Gardner et al., 2011) 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 . Similar to the analytical model, we assume sex-limited expression, so that u_f and u_m are only expressed in females and males respectively. The two alleles at each gene locus determine the value of u_f (or u_m) additively (no dominance or epistasis). 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 produces M ova, where $M = 200$. Each ovum is then fertilized by a randomly sampled male that lives in the local patch, after which offspring sex is assigned randomly (offspring are born as male with a 50% probability). Subsequently, we allow each newborn offspring to survive with probability $b(u_f + u_m \frac{n_m}{n_f})$. When parents only care for their own offspring, u_f and u_m are the phenotypes of the offspring's genetic mother and father. When parents care communally, u_f and u_m are the phenotypes of a randomly sampled female and male, which both live the local patch. Male and female offspring subsequently 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 100000 generations. The simulations are coded in C and are available at <http://dx.doi.org/10.5281/zenodo.168166>.

Results

For the sake of brevity, we only treat a numerical analysis of our model in the main text. However, the reader interested in formal results can consult the Appendix, where we provide expressions of the equilibrium levels of male and female care and how they are affected by dispersal and mating skew.

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

Figure 1 provides a simple illustration of the effect that sex-differences in philopatry can have on the levels of parental effort provided by males and females: in contrast to classical models (Houston and Davies, 1985; McNamara et al., 2003), 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).

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 (Pen, 2000; Ronce and Promislow, 2010; Johnstone and Kuijper, 2014). 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 (see the Appendix for analytical results). By contrast, when an adult of the dispersing sex dies, the vacancy created

is more likely to be filled by an unrelated, immigrant offspring. Hence, due to sex-biases in dispersal, the trade-off between adult survival and offspring production diverges between the sexes. As a result, sex-biases in parental care are likely to arise.

The finding that the more philopatric sex provides more care to young 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 territory, the overall sex difference in care 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).

Result 2: the commonest 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, $n_f \neq n_m$. When individuals care only for their own offspring, Figure 3A-C shows that the more numerous sex provides the majority of care to the young (see Figure S3A-F for corresponding absolute values of female and male effort). Taking a scenario where females are the more numerous sex as an example (Figure 3A), males sire two broods on average (as there are twice as many females as males), yet males only provide the minor share of care to each of their young. For example, the $u_m/(u_m + u_f) = 0.25$ line in Figure 3A illustrates that the total amount of care that males give to young throughout their life constitutes 25% of the total amount of lifetime effort given by both females and males.

The result that the commonest sex (females in this case) provides most of the care is in line with previous results (Kokko and Monaghan, 2001; Kokko and Johnstone, 2002; Kokko and Jennions, 2008; Houston et al., 2005): for the common sex, investment in survival is less advantageous as it faces increased competition over future breeding opportunities, thus favouring increased investment in current reproductive output. 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).

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 (see Figure S3G-L for corresponding absolute values of female and male effort). Only when dispersal patterns are relatively similar across both sexes (i.e., close to the line $h_m = h_f$), do we find that mating skew determines which sex provides most of the care. Otherwise, we retrieve the notable result that the more philopatric sex provides most of the care.

Why do we find that dispersal (rather than the adult sex ratio [ASR]) typically determines which sex provides most care in communal breeders? As mating skew still causes the more numerous sex to face increased competition for future breeding opportunities, we would still expect increased investment in current reproductive output. However, the benefits of such investment in current reproductive output are substantially lower in communally breeding taxa, as parents now also provide care to offspring other than their own. This is particularly the case for parents of the more numerous sex, as an individual parent of the more numerous sex has a lower genetic share in any locally born offspring, relative to a parent belonging to the rarer sex. As a consequence, the benefits of current parental investment by the commoner sex are now diluted, so that the effects of the ASR are largely undone. By contrast, sex-differences in dispersal still drive sex-differences in parental care, as a breeder of the philopatric sex is still more likely to be replaced by a relative than the dispersing sex, thus reducing the effective mortality cost of care as in result 1.

Result 3: the more philopatric sex cares more despite higher costs

Well-established predictions on sex-biases in care often focus on differences in costs and constraints between the sexes (Houston and Davies, 1985; Gross and Sargent, 1985; Liker and Székely, 2005), which raises the question how sensitive our conclusions are to asymmetries in costs between the sexes. For an example scenario where females remain at the natal site with probability $h_f = 0.8$, Figure 4 varies the mortality cost of male care relative to female care, $(1 - k_m)/(1 - k_f)$ (see Figure S4 for the corresponding absolute values of female and male effort). When males nearly always disperse ($h_m \rightarrow 0$) while females are philopatric, the proportion of male care rapidly decreases with increasing mortality costs of male care. Consequently, we find that males provide equal or less care to young than females do (proportion of male care falls below black line of equal effort between the sexes), despite lower mortality costs of male care relative to female care (i.e., $(1 - k_m)/(1 - k_f) < 1$). As females are the more philopatric sex, they value production of offspring more than their own survival, causing them to provide more care in the face of high female costs of care. By contrast, for taxa with high levels of male philopatry ($h_m \approx 1$), Figure 4 predicts that males provide the majority of care despite that males face mortality costs that are up to 1.5 times higher than those in females. 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.

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. Conversely, 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., Houston and Davies, 1985); the impact of sex-biased dispersal may even be sufficient to destabilize 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 increases with the relative level of philopatry of that sex.

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. By our knowledge, all meta-analyses on the selective causes of sex-differences in parental care focus on birds (Olson et al., 2008; Liker et al., 2013), so we discuss the ramifications of our model below in the context of birds. Nonetheless, we emphasize that evolutionary transitions between female-only, male-only and biparental care also occur in fish, reptiles and amphibians (Goodwin et al., 1998; Balshine, 2012), and given the recent accumulation of studies on sex-biased dispersal in these groups (e.g., Palo et al., 2004; Liebgold et al., 2011; Wang et al., 2012; Hutchings, 2003) assessing the consequences of our model should be a goal of future meta-analyses.

In birds, existing studies mainly focus on the role of polygamy and the adult sex ratio (ASR) as drivers of sex differences in parental care (Olson et al., 2008; Liker et al., 2013). Notably, these studies find that the ASR is strongly correlated with sex-differences in care (i.e., the more common sex provides more care), in line with previous models (McNamara et al., 2000; Kokko and Johnstone, 2002; Kokko and Jennions, 2008) and the current study (at least when communal care is absent). However, studies have yet to consider the role of dispersal as an additional explanatory variable. Our model suggests that the role of sex-biased dispersal may be particularly important for those species in which biases in the ASR and polygamy/polygyny are small or absent, yet still have substantial biases in parental care. One intriguing case in point from a meta analysis by Liker et al. (2013) is the red-necked phalarope (*Phalaropus lobatus*), in which parental care is heavily male-biased (Rubega et al., 2000) while biases in the ASR are absent (Hildén and Vuolanto, 1972;

Reynolds et al., 1986; Whitfield, 1990) (see Table S5 in Liker et al., 2013). Notably, red-necked phalaropes are characterized by male-biased philopatry (Reynolds and Cooke, 1988; Schamel and Tracy, 1991), and our model suggests that this favors male biases in parental care. By contrast, the other species from the dataset by Liker et al. (2013) in which biases in the ASR are absent is the semipalmated plover (*Charadrius semipalmatus*), which has biparental care (Sullivan Blanken and Nol, 1998; Nol and Blanken, 2000) and, interestingly, identical rates of philopatry between the sexes (Nol et al., 2010). As most non-communally breeding species live with only a single male and female per territory, our model suggests that philopatry can have substantial effects (see Figure 2A). However, in case territory structure is weaker or multiple breeders breed in a single territory, effects of philopatry only lead to limited (but nonetheless measurable) sex-differences in parental care (see Figure 2A). Hence, these examples suggest that more should be done to relate sex-differences in dispersal to quantitative estimates in parental care.

Future studies should also consider communally breeding species, as our model predicts that the ASR has a much weaker effect on sex-differences in care in those taxa (see Figure 3). In birds, a particularly interesting group to consider are joint-laying species like ratites (greater rhea, tinamou or ostrich), in which the ASR is female-biased (Donald, 2007), yet the father is the sole carer of the young (Vehrencamp and Quinn, 2004). Those patterns of care are difficult to reconcile with models exclusively relying on the ASR (McNamara et al., 2000; Kokko and Johnstone, 2002; Kokko and Jennions, 2008), so assessing the potential role of dispersal would be welcome in those taxa. In other joint-laying species, numbers of males and females at the nest appear more evenly distributed so the role of the ASR as a driver of sex-differences in care might be less important relative to dispersal (see table 11.1 in Vehrencamp and Quinn 2004). Numerous studies suggest that female-biased dispersal is the norm in these taxa (Greenwood and Harvey, 1982; Koenig et al., 2000; Eikenaar et al., 2008; Sankamethawee et al., 2010), suggesting that males should provide the majority of care. While little is known about sex differences in care by the dominant breeders, it is known that male helpers predominate in these species (Brown, 1987; Cockburn, 1998; Haig, 2000). Consequently, this corroborates the result by the current study (see also Johnstone and Cant, 2008; Gardner, 2010) that the more philopatric sex is typically the one that is more likely to engage in cooperative behavior than the dispersing sex.

The impact of limited dispersal on the evolution of parental care offers many possibilities for future extensions of this model. For example, would be interesting to assess whether the conclusion that the philopatric sex is always more cooperative extends to a broader range of social behaviors, such as social learning (Verzijden et al., 2012), defense of the local group (e.g., Kitchen and Beehner, 2007) or the establishment of dominance hierarchies (e.g., Kappeler, 1993). Next, future studies should consider the coevolution of sex differences in parental care with other traits (McNamara, 2013), such as sex-biased dispersal (Perrin and Mazalov, 2000; Lehmann and Perrin, 2003; Gros et al., 2008). In the absence of any sex-specific fitness consequences of parental effort, however, investment in care should affect competition among kin of both sexes equally and is thus unlikely to lead to sex-differences in dispersal. Only when parental care is more beneficial to offspring of a particular sex (Lessells, 2002), is parental effort more likely to lead to sex-biases in dispersal.

Another extension would be to assess the coevolution of the primary sex ratio with parental care. Section S3 in the Online Supplement therefore explores the simplest possible scenario where primary sex ratio coevolves with parental care, when parents care for their own young only. With regards to the primary sex ratio itself, we recover a previous result that the sex ratio is biased towards the dispersing sex in viscous populations (Hamilton, 1967; Bulmer and Taylor, 1980; Taylor, 1981; Frank, 1986; Taylor, 1994; Wild and Taylor, 2004; Pen, 2006). However, the presence of parental care causes the primary sex ratio to be more strongly biased towards the dispersing sex. The necessary assumption of overlapping generations (as current reproduction trades off with mortality: Trivers, 1972) causes an increase in relatedness among competing juveniles (e.g., Irwin and Taylor, 2001) relative to well-known sex allocation models assuming non-overlapping generations (e.g., Hamilton, 1967; Taylor, 1981). To avoid such increased competition between relatives, in-

creased investment towards the dispersing sex is therefore selectively favored, explaining the more strongly biased sex ratios in the current model.

What is the effect of such a biased primary sex ratio on the equilibrium level of care in each sex? Adding a biased sex ratios to fitness equations (S1-S12) shows that selection on sex-specific parental care is unaffected by a biased sex ratio, as any sex ratio terms in the numerator and the denominator cancel out against each other (see also Johnstone and Cant, 2008). Consequently, we conclude that sex-differences in parental care are robust to any biases in the primary sex ratio. This raises the question when biases in the sex ratio would start to affect patterns of parental care. In line with all other models on life-history evolution in viscous populations (e.g., Úbeda and Gardner, 2010; Rankin, 2011; Úbeda and Gardner, 2011, 2012; Van Cleve et al., 2010; Faria et al., 2015), we currently assume that the primary sex ratio does not change the number of adult breeding positions claimed by each sex. This is realistic when the number of adult breeding positions is environmentally determined, for example through sex-differences in juvenile mortality (Clutton-Brock et al., 1985; Kokko and Monaghan, 2001; Kokko and Jennions, 2008; Pongou, 2013), differences in resource demand (Bateman, 1948; Ruckstuhl, 2007; Elliott Smith et al., 2015) or other ecological differences between the sexes (Slatkin, 1984; Shine, 1989) that determine the effective number of territories. However, future studies should consider scenarios where the primary sex ratio indeed affects the number of competing adults of each sex, as we would then predict that biases in the sex ratio affect sex differences in life-history traits like parental care or other life history traits. Note however, that all this assumes that parents are actually able to bias the sex ratio, whereas this is not a certainty given constraints like chromosomal sex determination (West et al., 2005).

This assumption of a fixed number of female and male breeding positions is frequently used to show how competition among relatives of each sex shapes sex-differences in social behavior (Johnstone and Cant, 2008; Gardner, 2010; Johnstone et al., 2012) and life-history traits (e.g., Wild and Taylor, 2005; Úbeda and Gardner, 2010; Rankin, 2011; Úbeda and Gardner, 2011, 2012; Van Cleve et al., 2010; Johnstone and Kuijper, 2014; Faria et al., 2015). However, in reality, it may not be the case that habitats are always saturated. It would thus be interesting to assess the evolution of parental care in populations that are less limited by the available amount of resources. Models on the evolution of social traits that assume a more elastic population structure find, for example, that elasticity reduces the negative effect of local competition (e.g., Lehmann et al., 2006; Alizon and Taylor, 2008; Lion and Gandon, 2010; Lion, 2010). As a consequence, we would predict that elastic population sizes would likely diminish the evolution of sex differences in parental care. Nonetheless, as habitat saturation has been repeatedly associated with the evolution of extended parental care (e.g., Emlen, 1982, 1995; Russell et al., 2004; Brown et al., 2010), we think that fixed population sizes are a real and interesting ecological feature in many populations.

Another assumption in most life-history models that consider overlapping generations (e.g., Kokko and Monaghan, 2001; Kokko and Johnstone, 2002; Wild, 2006; Johnstone and Cant, 2008; Van Cleve et al., 2010; Úbeda and Gardner, 2012; Kokko and Jennions, 2008) is that once adults have established themselves as breeders, they do not experience any competition from juveniles. To give an example of why such adult-juvenile competitive interactions can be important, consider the result in Figure 3A-C, in which we show that the rarer sex provides less care and lives longer. In the presence of adult-juvenile interactions, however, any longer-living adult will experience more competitive attempts from juveniles during its lifetime, which reduces the reproductive value of an adult of the rare sex. In addition, when primary sex ratios are equal, there will be more juveniles competing for each breeding position occupied by the rare sex relative to those of the common sex, again reducing the reproductive value of an adult of the rarer sex. In section S1 of the online supplement, we therefore analyze an extension of the current model that includes the effect of such adult-juvenile interactions on the mortality rates of each sex. Importantly, including adult-juvenile interactions does not alter our conclusion that sex-specific care increases with the degree of philopatry of that sex (see Figure S1). However, adult-juvenile interactions indeed weaken the effect of the ASR on sex-differences in care relative to Figure 3 (see Figure S1A-C). Moreover, in the presence of communal care (in which the

effect of the ASR is already weakened, as set out in the main text in Figure 3D-F), juvenile-adult interactions can lead to scenarios where the rarer sex provides more care than the commoner sex, which is opposite to well-established predictions (see Figure S1D-F). Hence, direct competition between adults and juveniles can potentially reduce (or even reverse) the effect of the ASR. Consequently, our model shows that adult-juvenile interactions are a hitherto overlooked aspect of competition in overlapping generations that should be included in future studies. In essence, adult-juvenile interactions are analogous to a ‘birth-death’ model in continuous time (Ohtsuki and Nowak, 2006; Taylor, 2010), where the occurrence of new births result in a mortality pressure on adults. The model considered in the main text, however, is analogous to a ‘death-birth’ model (Ohtsuki and Nowak, 2006; Taylor, 2010), where mortalities are the driving demographical force, and births occur after breeding positions are vacated by mortality. We believe, however, that both demographical descriptions apply to different taxa and that neither can be said to be more general than the other. Therefore, more studies that place demography central to the evolution of family conflict are necessary to make sense of the great variation in family life histories in nature.

Acknowledgements

We thank the associate editor, Peter Taylor, and three anonymous reviewers for their comments which substantially improved the manuscript. BK has been funded by an EPSRC 2020 Science fellowship (grant number EP/I017909/1) and a Leverhulme Trust Early Career Research Fellowship (ECF 2015-273). RAJ has been funded by a EPSRC grant number EP/H031928/1. This work has made use of the Carson computing cluster at the Environment and Sustainability Institute at the University of Exeter. In addition, the authors acknowledge the use of the UCL Legion High Performance Computing Facility (Legion@UCL) and associated support services in the completion of this work. The Dutch Academy of Arts and Sciences (KNAW) and the Lorentz Centre at the University of Leiden, the Netherlands funded a workshop on nongenetic effects that contributed to this article.

Appendix: analytical results

Baseline scenario: optimal effort in well-mixed populations

To fix ideas, 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: Brown, 1978; Cant, 2012), so that the survival of an individual offspring depends only upon the efforts of its own father and mother. Later on, we relax these assumptions.

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:

$$\frac{\mu'_m(u_m^*)}{\mu_m(u_m^*)} = \frac{b'_{u_m}(u_f^* + u_m^*)}{b(u_f^* + u_m^*)} \quad (\text{A1})$$

$$\frac{\mu'_f(u_f^*)}{\mu_f(u_f^*)} = \frac{b'_{u_f}(u_f^* + u_m^*)}{b(u_f^* + u_m^*)}, \quad (\text{A2})$$

where $\mu'_x(u_x)$ reflects the derivative of mortality cost $\mu_x(u_x^*)$ of parental care to sex x and $b'_{u_x}(u_f^* + u_m^*)$ reflects the partial derivatives of parental effort with respect to the variable u_x . Although results below are phrased in terms of mortality and fecundity, note that we can also derive our results in terms of reproductive value. For example, the denominator on the left hand side can be written in terms of adult reproductive value, with $v_m = 1/\mu_m$ and $v_f = 1/\mu_f$ (see the Supplementary Information, section S2.3 for a derivation). The respective left hand sides can then be written as v'_m/v_m and v'_f/v_f , reflecting the marginal costs of reproduction in units of each sex’s reproductive value. Similarly, $v_j = 1/b(u_f^* + u_m^*)$ reflects the reproductive value of a surviving offspring, so that the right-hand side can be written as v'_j/v_j , representing the marginal benefit of reproduction in terms of reproductive value (see also Pen, 2000). The question then becomes whether sex-differences in dispersal affect the marginal benefits and costs of reproduction, which is what we assess below.

Optimal effort in viscous populations

To assess the effect of limited dispersal, let $h_f = 1 - d_f$ (and $h_m = 1 - d_m$) be the probabilities that a female (and male) remains at the natal patch. To assess the effect of mating skew, we note that males can possibly 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 $b(\cdot)$ 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 $b(u_f + u_m/n_f)$. We then obtain (see section S2 of the Supplementary Information):

$$\left[r_{\text{self}} - r_{f \rightarrow \text{locally competing juv}} \right] \frac{\mu'_f(u_f^*)}{\mu_f(u_f^*)} = 2 \left[r_{f \rightarrow \text{own juv}} - r_{f \rightarrow \text{competing juv}} \right] \frac{b'_{u_f}\left(u_f^* + \frac{n_m}{n_f} u_m^*\right)}{b\left(u_f^* + \frac{n_m}{n_f} u_m^*\right)} \quad (\text{A3})$$

$$\frac{n_f}{n_m} \left[r_{\text{self}} - r_{m \rightarrow \text{locally competing juv}} \right] \frac{\mu'_m(u_m^*)}{\mu_m(u_m^*)} = 2 \left[r_{m \rightarrow \text{own juv}} - r_{m \rightarrow \text{competing juv}} \right] \frac{b'_{u_m}\left(u_f^* + \frac{n_m}{n_f} u_m^*\right)}{b\left(u_f^* + \frac{n_m}{n_f} u_m^*\right)}. \quad (\text{A4})$$

The left-hand side shows 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 $r_{x \rightarrow \text{locally competing juv}}$, 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 $r_{x \rightarrow \text{own juv}}$, which denotes the relatedness of a focal to its own juvenile offspring and $r_{x \rightarrow \text{competing juv}}$, 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 numbers n_m, n_f of adult males and females in the patch (see Supplementary Information, section S2.4). In addition, mating skew affects the equilibrium balance also directly, given that the left-hand side of eq. (A4) is multiplied by n_f/n_m .

Note that the equations (A3,A4) above reduce to those of a well-mixed population (eqns. [A1,A2]) when there is no philopatry ($h_f = h_m = 0$) and mating skew is absent ($n_f = n_m$). In this case, $r_{f \rightarrow \text{own juv}} = r_{m \rightarrow \text{own juv}} = \frac{1}{2}$, $r_{f \rightarrow \text{locally competing juv}} = r_{m \rightarrow \text{locally competing juv}} = r_{f \rightarrow \text{competing juv}} = r_{m \rightarrow \text{competing juv}} = 0$, so that coefficients on both sides are equal to 1.

Effect of sex differences in dispersal What happens, however, when $h_m, h_f > 0$? In line with Figure 1, we consider a scenario in which males are more philopatric than are females ($h_m > h_f$). Now, a male's average relatedness $r_{m \rightarrow \text{locally competing juv}}$ to locally competing juveniles of his own sex increases compared to a female's average relatedness $r_{f \rightarrow \text{locally competing juv}}$ to juveniles of her own sex. The left-hand side in eq. (A4) therefore becomes smaller relative to the left-hand side in eq. (A3). 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. (A4), $h_m > h_f$ also entails a decrease in the marginal benefits of increased male effort. This is because the term $r_{m \rightarrow \text{competing juv}}$ 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, favors greater parental effort by the more philopatric sex (here males), because it can be shown that $r_{m \rightarrow \text{competing juv}}$ on the right-hand side is smaller to an order $(h_f^2 + h_m^2)/h_m$ relative to the coefficient $r_{m \rightarrow \text{local juv}}$ on the left-hand side (see eqns. S28, S30). As a result, male-biased philopatry leads males to increase their level of parental effort, while females reduce theirs.

Effect of mating skew

When males are the more common sex, the left hand side in eq. (A4) is reduced relative to that in eq. (A3), so that an increase in male parental effort has a smaller effective mortality cost relative to an increase in female effort. Selection thus favors greater caring effort by males when they are the more common sex (and a lower caring effort when they are the rarer sex).

In addition, mating skew has a more subtle, indirect effect on parental effort, by modulating the relatedness coefficients. 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 $r_{m \rightarrow \text{locally competing juv}}$ to any locally competing juveniles. Vice versa, the coefficient $r_{f \rightarrow \text{locally competing juv}}$ 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, $r_{m \rightarrow \text{competing juv}}$ on the right-hand side of eq. (A4) is also reduced when males are the common sex, reducing the fecundity benefit of increased care for the more common sex. However, $r_{m \rightarrow \text{competing juv}}$ is smaller than $r_{m \rightarrow \text{locally competing juv}}$ on the left hand side (compare eqns. [S30, S28]), so overall these indirect effects through relatedness suggest the more common sex should provide less care relative to the rare sex. Overall however, Figure 3A-C shows that the direct effect of mating skew (via the coefficient n_f/n_m) favoring more effort by the common sex overrides the indirect effect via relatedness.

Effect of communal care

In the case of communal care, parents care for all locally born offspring, so coefficients $r_{f \rightarrow \text{own juv}}$ and $r_{m \rightarrow \text{own juv}}$ in equations (A3,A4) for the case of individual care are now replaced by the coefficients $r_{f \rightarrow \text{locally born juv}}$ and $r_{m \rightarrow \text{locally born juv}}$. 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 ($n_m > n_f$), 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 $r_{m \rightarrow \text{locally born juv}}$ becomes smaller relative to $r_{f \rightarrow \text{locally born juv}}$ as n_m increases. Going back to eqns. (A3,A4), 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).

References

- Alizon, S., and P. Taylor. 2008. Empty sites can promote altruistic behavior. *Evolution* 62:1335–1344.
- Alonzo, S. H. 2010. Social and coevolutionary feedbacks between mating and parental investment. *Trends Ecol. Evol.* 25:99–108.
- . 2012. Sexual selection favours male parental care, when females can choose. *Proc. R. Soc. Lond. B Biol. Sci.* 279:1784–1790.
- Arnqvist, G., and L. Rowe. 2005. *Sexual Conflict*. Princeton University Press, Princeton.
- Balshine, S. 2012. Patterns of parental care in vertebrates. *In* N. Royle, P. T. Smiseth, and M. Kölliker, eds., *The Evolution of Parental Care*. Oxford University Press, Oxford.
- Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2:349–368.
- Brown, J. L. 1978. Avian communal breeding systems. *Annu. Rev. Ecol. Evol. Syst.* 9:123–155.
- . 1987. *Helping and Communal Breeding in Birds*. Princeton University Press, Princeton, NJ.
- Brown, J. L., V. Morales, and K. Summers. 2010. A key ecological trait drove the evolution of biparental care and monogamy in an amphibian. *Am. Nat.* 175:436–446.
- Bulmer, M. G., and P. D. Taylor. 1980. Dispersal and the sex ratio. *Nature* 284:448–449.
- Cant, M. A. 2012. Cooperative breeding systems. Pages 206–225 *in* N. J. Royle, P. T. Smiseth, and M. Kölliker, eds. *The Evolution of Parental Care*. Oxford University Press, Oxford.
- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* 313:131–133.
- Cockburn, A. 1998. Evolution of helping behavior in cooperatively breeding birds. *Annu. Rev. Ecol. Syst.* 29:141–177.
- Dercole, F., and S. Rinaldi. 2008. *Analysis of Evolutionary Processes: the Adaptive Dynamics Approach and its Applications*. Princeton University Press, Princeton.
- Donald, P. F. 2007. Adult sex ratios in wild bird populations. *Ibis* 149:671–692.
- Eikenaar, C., D. S. Richardson, L. Brouwer, and J. Komdeur. 2008. Sex biased natal dispersal in a closed, saturated population of Seychelles warblers *Acrocephalus sechellensis*. *J. Avian Biol.* 39:73–80.
- Elliott Smith, E. A., S. D. Newsome, J. A. Estes, and M. T. Tinker. 2015. The cost of reproduction: differential resource specialization in female and male california sea otters. *Oecologia* 178:17–29.
- Emlen, S. T. 1982. The evolution of helping. I. An ecological constraints model. *Am. Nat.* 119:29–39.
- . 1995. An evolutionary theory of the family. *Proc. Natl. Acad. Sci. U.S.A.* 92:8092–8099.
- Faria, G. S., S. A. M. Varela, and A. Gardner. 2015. Sex-biased dispersal, kin selection and the evolution of sexual conflict. *J. Evol. Biol.* 28:1901–1910.
- Frank, S. A. 1986. The genetic value of sons and daughters. *Heredity* 56:351–354.

- Gardner, A. 2010. Sex-biased dispersal of adults mediates the evolution of altruism among juveniles. *J. Theor. Biol.* 262:339–345.
- Gardner, A., and S. A. West. 2006. Demography, altruism, and the benefits of budding. *J. Evol. Biol.* 19:1707–1716.
- Gardner, A., S. A. West, and G. Wild. 2011. The genetical theory of kin selection. *J. Evol. Biol.* 24:1020–1043.
- Goodwin, N. B., S. Balshine-Earn, and J. D. Reynolds. 1998. Evolutionary transitions in parental care in cichlid fish. *Proc. R. Soc. Lond. B Biol. Sci.* 265:2265–2272.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28:1140–1162.
- Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Evol. Syst.* 13:1–21.
- Gros, A., T. Hovestadt, and H. J. Poethke. 2008. Evolution of sex-biased dispersal: the role of sex-specific dispersal costs, demographic stochasticity, and inbreeding. *Ecol. Model.* 219:226–233.
- Gross, M. R., and R. C. Sargent. 1985. The evolution of male and female parental care in fishes. *Am. Zool.* 25:807–822.
- Haig, D. 2000. Genomic imprinting, sex-biased dispersal, and social behavior. *Ann. NY. Acad. Sci.* 907:149–163.
- Hamilton, W. D. 1964a. The genetical evolution of social behaviour. I. *J. Theor. Biol.* 7:1–16.
- . 1964b. The genetical evolution of social behaviour. II. *J. Theor. Biol.* 7:17–52.
- . 1967. Extraordinary sex ratios. *Science* 156:477–488.
- Hausfather, G., and S. B. Hrdy, eds. 1984. *Infanticide: Comparative and Evolutionary Perspectives*. Aldine, New York.
- Hildén, O., and S. Vuolanto. 1972. Breeding biology of the red-necked phalarope *Phalaropus lobatus* in Finland. *Ornis Fenn.* 49:57–85.
- Hinde, C. A., and R. M. Kilner. 2007. Negotiations within the family over the supply of parental care. *Proc. R. Soc. Lond. B Biol. Sci.* 274:53–60.
- Houston, A. I., and N. B. Davies. 1985. The evolution of cooperation and life history in the dunnock, *Prunella modularis*. Pages 471–487 in R. M. Sibley and R. H. Smith, eds. *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour*. Blackwell Publishing Inc, Oxford, UK.
- Houston, A. I., T. Székely, and J. M. McNamara. 2005. Conflict between parents over care. *Trends Ecol. Evol.* 20:33–38.
- 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.
- Hutchings, J. A. 2003. Sex-biased dispersal in a salmonid fish: implications for growth rate and survival. *J. Fish. Biol.* 63:233–233.

- Irwin, A. J., and P. D. Taylor. 2001. Evolution of altruism in stepping-stone populations with overlapping generations. *Theor. Popul. Biol.* 60:315–325.
- Johnstone, R. A. 2011. Load lightening and negotiation over offspring care in cooperative breeders. *Behav. Ecol.* 22:436–444.
- Johnstone, R. A., and M. A. Cant. 2008. Sex differences in dispersal and the evolution of helping and harming. *Am. Nat.* 172:318–330.
- Johnstone, R. A., M. A. Cant, and J. Field. 2012. Sex-biased dispersal, haplodiploidy and the evolution of helping in social insects. *Proc. R. Soc. Lond. B Biol. Sci.* 279:787–793.
- Johnstone, R. A., and C. A. Hinde. 2006. Negotiation over offspring care – how should parents respond to each other’s efforts? *Behav. Ecol.* 17:818–827.
- Johnstone, R. A., and B. Kuijper. 2014. Kin competition and the evolution of sex differences in development time and body size. *Am. Nat.* 183:537–546.
- Johnstone, R. A., A. Manica, A. L. Fayet, M. C. Stoddard, M. A. Rodriguez-Gironés, and C. A. Hinde. 2014. Reciprocity and conditional cooperation between great tit parents. *Behav. Ecol.* 25:216–222.
- Kappeler, P. 1993. Female dominance in primates and other mammals. Pages 143–158 in P. P. G. Bateson, P. H. Klopfer, and N. S. Thompson, eds. *Perspectives in Ethology*. Vol. 10: Behavior and Evolution. Plenum Press, New York.
- Kitchen, D., and J. Beehner. 2007. Factors affecting individual participation in group-level aggression among non-human primates. *Behaviour* 144:1551–1581.
- Koenig, W. D., P. N. Hooge, M. T. Stanback, and J. Haydock. 2000. Natal dispersal in the cooperatively breeding acorn woodpecker. *Condor* 102:492–502.
- Kokko, and Monaghan. 2001. Predicting the direction of sexual selection. *Ecol. Lett.* 4:159–165.
- Kokko, H., and M. D. Jennions. 2008. Parental investment, sexual selection and sex ratios. *J. Evol. Biol.* 21:919–948.
- Kokko, H., and R. A. Johnstone. 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.
- Kuijper, B., and R. A. Johnstone. 2012. How dispersal influences parent-offspring conflict over investment. *Behav. Ecol.* 23:898–906.
- Lawson Handley, L. J., and N. Perrin. 2007. Advances in our understanding of mammalian sex-biased dispersal. *Mol. Ecol.* 16:1559–1578.
- Lehmann, L., and N. Perrin. 2003. Inbreeding avoidance through kin recognition: choosy females boost male dispersal. *Am. Nat.* 162:638–652.
- Lehmann, L., N. Perrin, and F. Rousset. 2006. Population demography and the evolution of helping behaviors. *Evolution* 60:1137–1151.
- 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.

- . 2012. Sexual conflict. Pages 150–170 in N. J. Royle, P. T. Smiseth, and M. Kolliker, eds. *The Evolution of Parental Care*. Oxford University Press, Oxford, UK.
- Lessells, C. M., and J. M. McNamara. 2012. Sexual conflict over parental investment in repeated bouts: negotiation reduces overall care. *Proc. R. Soc. Lond. B Biol. Sci.* 279:1506–1514.
- Liebgold, E. B., E. D. Brodie, III, and P. R. Cabe. 2011. Female philopatry and male-biased dispersal in a direct-developing salamander, *Plethodon cinereus*. *Mol. Ecol.* 20:249–257.
- Liker, A., R. P. Freckleton, and T. Székely. 2013. The evolution of sex roles in birds is related to adult sex ratio. *Nat. Commun.* 4:1587.
- Liker, A., and T. Székely. 2005. Mortality costs of sexual selection and parental care in natural populations of birds. *Evolution* 59:890–897.
- Lion, S. 2010. Evolution of reproductive effort in viscous populations: the importance of population dynamics. *J. Evol. Biol.* 23:866–874.
- Lion, S., and S. Gandon. 2010. Life history, habitat saturation and the evolution of fecundity and survival altruism. *Evolution* 64:1594–1606.
- Lion, S., V. A. A. Jansen, and T. Day. 2011. Evolution in structured populations: beyond the kin versus group debate. *Trends Ecol. Evol.* 26:193–201.
- Lion, S., and M. Van Baalen. 2007. From infanticide to parental care: why spatial structure can help adults be good parents. *Am. Nat.* 170:E26–E46.
- McGill, B. J., and J. S. Brown. 2007. Evolutionary game theory and adaptive dynamics of continuous traits. *Annu. Rev. Ecol. Evol. Syst.* 38:403–435.
- McNamara, J. M. 2013. Towards a richer evolutionary game theory. *J. Roy. Soc. Interface* 10:20130544.
- McNamara, J. M., C. E. Gasson, and A. I. Houston. 1999. Incorporating rules for responding into evolutionary games. *Nature* 401:368–371.
- McNamara, J. M., A. I. Houston, Z. Barta, and J.-L. Osorno. 2003. Should young ever be better off with one parent than with two? *Behav. Ecol.* 14:301–310.
- McNamara, J. M., T. Székely, J. N. Webb, and A. I. Houston. 2000. A dynamic game-theoretic model of parental care. *J. Theor. Biol.* 205:605–623.
- Mock, D. W., and G. A. Parker. 1997. *The Evolution of Sibling Rivalry*. Oxford University Press, Oxford, UK.
- Nol, E., and M. S. Blanken. 2000. Semipalmated plover (*Charadrius semipalmatus*). In A. Poole, ed., *The Birds of North America Online*. Cornell Lab of Ornithology, Ithaca.
- Nol, E., S. Williams, and B. K. Sandercock. 2010. Natal philopatry and apparent survival of juvenile semipalmated plovers. *Wilson J. Ornithol.* 122:23–28.
- Ohtsuki, H., and M. A. Nowak. 2006. Evolutionary games on cycles. *Proc. R. Soc. Lond. B Biol. Sci.* 273:2249–2256.
- Olson, V., A. Liker, R. Freckleton, and T. Székely. 2008. Parental conflict in birds: comparative analyses of offspring development, ecology and mating opportunities. *Proc. R. Soc. Lond. B Biol. Sci.* 275:301–307.

- Palo, J. U., D. Lesbarrères, D. S. Schmeller, C. R. Primmer, and J. Merilä. 2004. Microsatellite marker data suggest sex-biased dispersal in the common frog *Rana temporaria*. *Mol. Ecol.* 13:2865–2869.
- Parker, G. A. 1979. Sexual selection and sexual conflict. Pages 123–166 in N. S. Blum and N. B. Blum, eds. *Sexual selection and Reproductive Competition in the Insects*. Academic Press, New York.
- Parker, G. A., and M. R. Macnair. 1978. Models of parent–offspring conflict. I. Monogamy. *Anim. Behav.* 26:97–110.
- Parker, G. A., N. J. Royle, and I. R. Hartley. 2002. Intrafamilial conflict and parental investment: a synthesis. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 357:295–307.
- Parker, G. A., and L. W. Simmons. 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.
- Pen, I. 2000. Reproductive effort in viscous populations. *Evolution* 54:293–297.
- . 2006. When boys want to be girls: effects of mating system and dispersal on parent-offspring sex ratio conflict. *Evol. Ecol. Res.* 8:103–113.
- Perrin, N., and V. Mazalov. 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. *Am. Nat.* 155:116–127.
- Pongou, R. 2013. Why is infant mortality higher in boys than in girls? A new hypothesis based on pre-conception environment and evidence from a large sample of twins. *Demography* 50:421–444.
- Rankin, D. J. 2011. Kin selection and the evolution of sexual conflict. *J. Evol. Biol.* 24:71–81.
- Reynolds, J. D., M. A. Colwell, and F. Cooke. 1986. Sexual selection and spring arrival times of red-necked and Wilson’s phalaropes. *Behav. Ecol. Sociobiol.* 18:303–310.
- Reynolds, J. D., and F. Cooke. 1988. The influence of mating systems on philopatry: a test with polyandrous red-necked phalaropes. *Anim. Behav.* 36:1788–1795.
- Ronce, O., and D. Promislow. 2010. Kin competition, natal dispersal and the moulding of senescence by natural selection. *Proc. R. Soc. Lond. B Biol. Sci.* 277:3659–3667.
- Rousset, F. 2004. *Genetic Structure in Subdivided Populations*. Princeton University Press, Princeton.
- Rubega, M. A., D. Schamel, and D. M. Tracey. 2000. Red-necked phalarope. In A. Poole, ed., *The Birds of North America Online*. Cornell Lab of Ornithology, Ithaca.
- Ruckstuhl, K. E. 2007. Sexual segregation in vertebrates: proximate and ultimate causes. *Integr. Comp. Biol.* 47:245–257.
- Russell, E. M., Y. Yom-Tov, and E. Geffen. 2004. Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. *Behav. Ecol.* 15:831–838.
- Sankamethawee, W., B. D. Hardesty, and G. A. Gale. 2010. Sex-bias and timing of natal dispersal in cooperatively breeding puff-throated bulbuls *Alophoixus pallidus*. *J. Ornithol.* 151:779–789.
- Savage, J. L., A. F. Russell, and R. A. Johnstone. 2013. Maternal costs in offspring production affect investment rules in joint rearing. *Behav. Ecol.* 24:750–758.

- Schamel, D., and D. M. Tracy. 1991. Breeding site fidelity and natal philopatry in the sex role-reversed red and red-necked phalaropes. *J. Field. Ornithol.* 62:390–398.
- Schwagmeyer, P. L., D. W. Mock, and G. A. Parker. 2002. Biparental care in house sparrows: negotiation or sealed bid? *Behav. Ecol.* 13:713–721.
- Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q. Rev. Biol.* 64:419–461.
- Slatkin, M. 1984. Ecological causes of sexual dimorphism. *Evolution* 38:622–630.
- Smiseth, P. T., and A. J. Moore. 2004. Behavioral dynamics between caring males and females in a beetle with facultative biparental care. *Behav. Ecol.* 15:621–628.
- Sullivan Blanken, M., and E. Nol. 1998. Factors affecting parental behavior in semipalmated plovers. *Auk* 115:166–174.
- Székely, T., J. N. Webb, A. I. Houston, and J. M. McNamara. 1996. An evolutionary approach to offspring desertion in birds. *Curr. Ornithol.* 13:271–330.
- Taylor, P. 2010. Birth-death symmetry in the evolution of a social trait. *J. Evol. Biol.* 23:2569–2578.
- Taylor, P. D. 1981. Intra-sex and inter-sex sibling interactions as sex ratio determinants. *Nature* 291:64–66.
- . 1988. An inclusive fitness model for dispersal of offspring. *J. Theor. Biol.* 130:363–378.
- . 1992. Inclusive fitness in a homogeneous environment. *Proc. R. Soc. Lond. B Biol. Sci.* 249:299–302.
- . 1994. Sex ratio in a stepping-stone population with sex-specific dispersal. *Theor. Pop. Biol.* 45:203–218.
- Taylor, P. D., and S. A. Frank. 1996. How to make a kin selection model. *J. Theor. Biol.* 180:27–37.
- Taylor, P. D., G. Wild, and A. Gardner. 2007. Direct fitness or inclusive fitness: how shall we model kin selection? *J. Evol. Biol.* 20:301–309.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136–179 in B. Campbell, ed. *Sexual Selection and the Descent of Man*. Aldine Publishing Company, Chicago.
- . 1974. Parent-offspring conflict. *Am. Zool.* 14:249–264.
- Úbeda, F., and A. Gardner. 2010. A model for genomic imprinting in the social brain: juveniles. *Evolution* 64:2587–2600.
- . 2011. A model for genomic imprinting in the social brain: adults. *Evolution* 65:462–475.
- . 2012. A model for genomic imprinting in the social brain: elders. *Evolution* 66:1567–1581.
- Valera, F., H. Hoi, and B. Schleicher. 1997. Egg burial in penduline tits, *Remiz pendulinus*: its role in mate desertion and female polyandry. *Behav. Ecol.* 8:20–27.
- Van Cleve, J., M. W. Feldman, and L. Lehmann. 2010. How demography, life history, and kinship shape the evolution of genomic imprinting. *Am. Nat.* 176:440–455.

- Van Dijk, R. E., I. Szentirmai, J. Komdeur, and T. Székely. 2007. Sexual conflict over parental care in penduline tits *Remiz pendulinus*: the process of clutch desertion. *Ibis* 149:530–534.
- Vehrencamp, S. L., and J. S. Quinn. 2004. Joint laying systems. Pages 177–196 in W. D. Koenig and J. L. Dickinson, eds. *Ecology and Evolution of Cooperative Breeding in Birds*. Cambridge University Press, Cambridge UK. Cambridge Books Online.
- Verzijden, M. N., C. ten Cate, M. R. Servedio, G. M. Kozak, J. W. Boughman, and E. I. Svensson. 2012. The impact of learning on sexual selection and speciation. *Trends Ecol. Evol.* 27:511–519.
- Wang, Y., A. Lane, and P. Ding. 2012. Sex-biased dispersal of a frog (*Odorrana schmackeri*) is affected by patch isolation and resource limitation in a fragmented landscape. *PLoS One* 7:e47683.
- Wedell, N., C. Kvarnemo, C. M. Lessells, and T. Tregenza. 2006. Sexual conflict and life histories. *Anim. Behav.* 71:999–1011.
- West, S. A., D. M. Shuker, and B. C. Sheldon. 2005. Sex-ratio adjustment when relatives interact: a test of constraints on adaptation. *Evolution* 59:1211–1228.
- Whitfield, D. P. 1990. Male choice and sperm competition as constraints on polyandry in the red-necked phalarope *Phalaropus lobatus*. *Behav. Ecol. Sociobiol.* 27:247–254.
- Wild, G. 2006. Sex ratios when helpers stay at the nest. *Evolution* 60:2012–2022.
- Wild, G., T. Pizzari, and S. A. West. 2011. Sexual conflict in viscous populations: The effect of the timing of dispersal. *Theor. Pop. Biol.* 80:298–316.
- Wild, G., and P. D. Taylor. 2004. Kin selection models for the co-evolution of the sex ratio and sex-specific dispersal. *Evol. Ecol. Res.* 6:481–502.
- . 2005. A kin-selection approach to the resolution of sex-ratio conflict between mates. *J. Theor. Biol.* 236:126–136.
- Wright, S. 1931. Evolution in Mendelian populations. *Genetics* 16:97–159.
- . 1951. The genetical structure of populations. *Annals Eugen.* 15:323–354.

Figure captions

Figure 1 Three examples highlighting how sex biases in dispersal can affect sex differences in care, and possibly even lead to uniparental care (e.g., panel C). Each panel depicts how female effort u_f and male effort u_m coevolve towards a stable equilibrium, for different combinations of male h_m and female philopatry h_f . To assess the course of evolution, start by taking a certain value of male effort u_m (fixed height on the graph). Then evolution acting on the level of female effort will tend to decrease it if male effort is too high or increase it if male effort is too low (the direction of evolution is indicated by the vertical, thick grey arrows). Evolution of u_f in response to this fixed level of male care stops at the corresponding point on the u_f isocline (solid black line), which reflects the evolutionarily stable u_f level. A corresponding description applies to the u_m isocline, where horizontal, thick grey arrows indicate the direction of selection on u_m towards the isocline (dashed black line). The intersection of the isoclines provides a stable level of both efforts, u_f^* and u_m^* (black dots). 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 favors males to provide almost all care to young, whereas the amount of female care is negligible. Parameters: $n_m = n_f = 1$, $k_f = k_m = 0.1$. Light grey lines: individual-based simulations.

Figure 2 The equilibrium amount of total male effort as a proportion of total effort by both sexes $u_m^*/(u_m^* + u_f^*)$, for different combinations of philopatry in each sex. At the dashed black contour line, males and females have identical levels of effort ($u_f^* = u_m^*$). 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 favors 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 provides the majority of care to young. Parameters: $k_f = k_m = 0.1$. See Supplementary Figure S2 for corresponding absolute levels of u_f^* and u_m^* .

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) provides the majority of care, regardless of the level of dispersal. Nonetheless, amount of care by a particular sex 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: $k_m = k_f = 0.1$. See Supplementary Figure S3 for the corresponding absolute levels of u_f^* and u_m^* .

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). The black line indicates where both males and females provide identical amounts of care to their young. 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: $n_m = n_f = 1$, $d_f = 0.2$, $k_f = 0.5$.

Figures

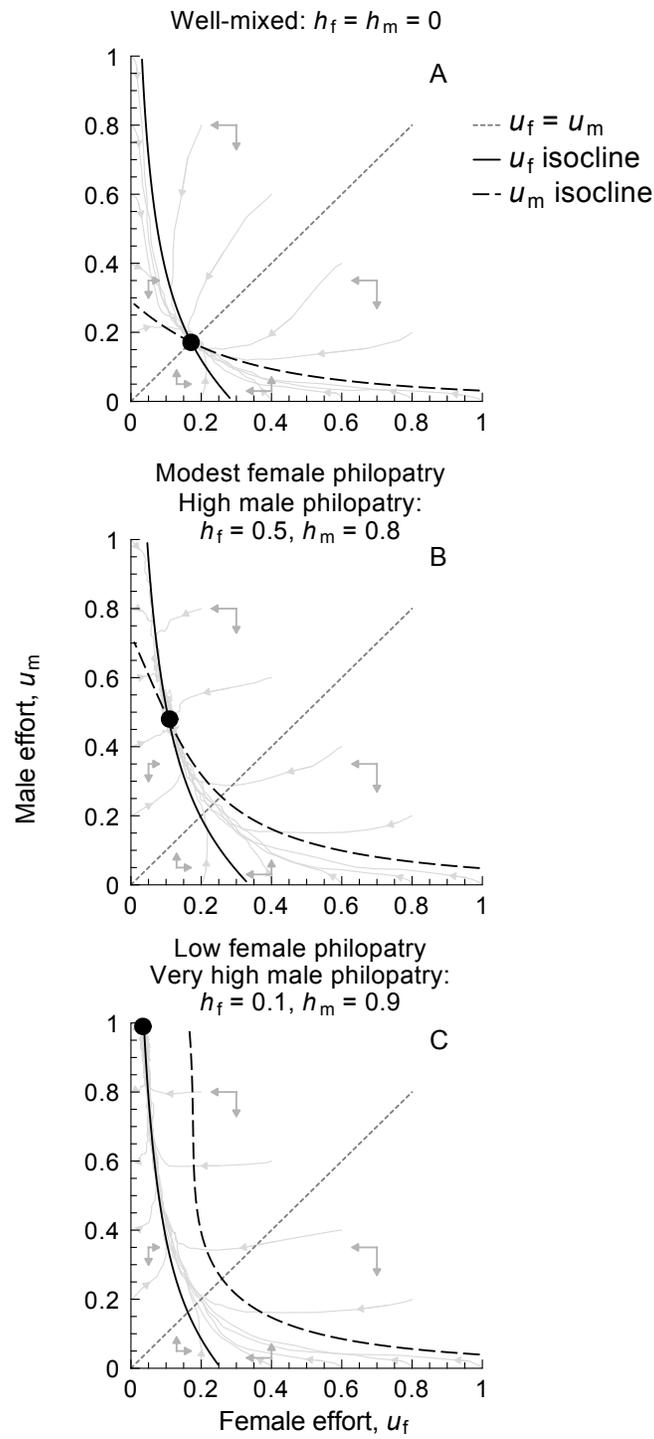


Figure 1:

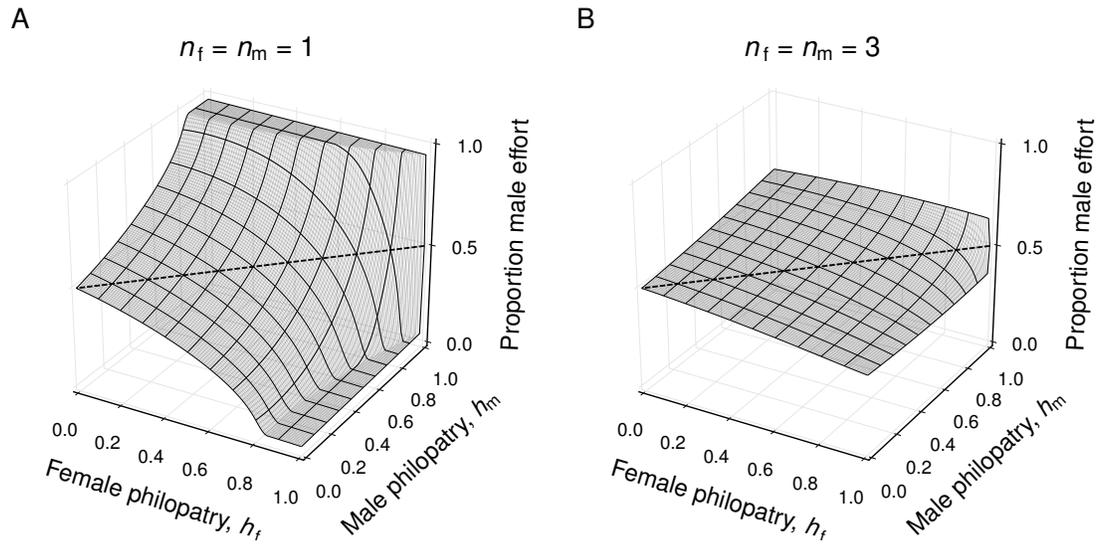


Figure 2:

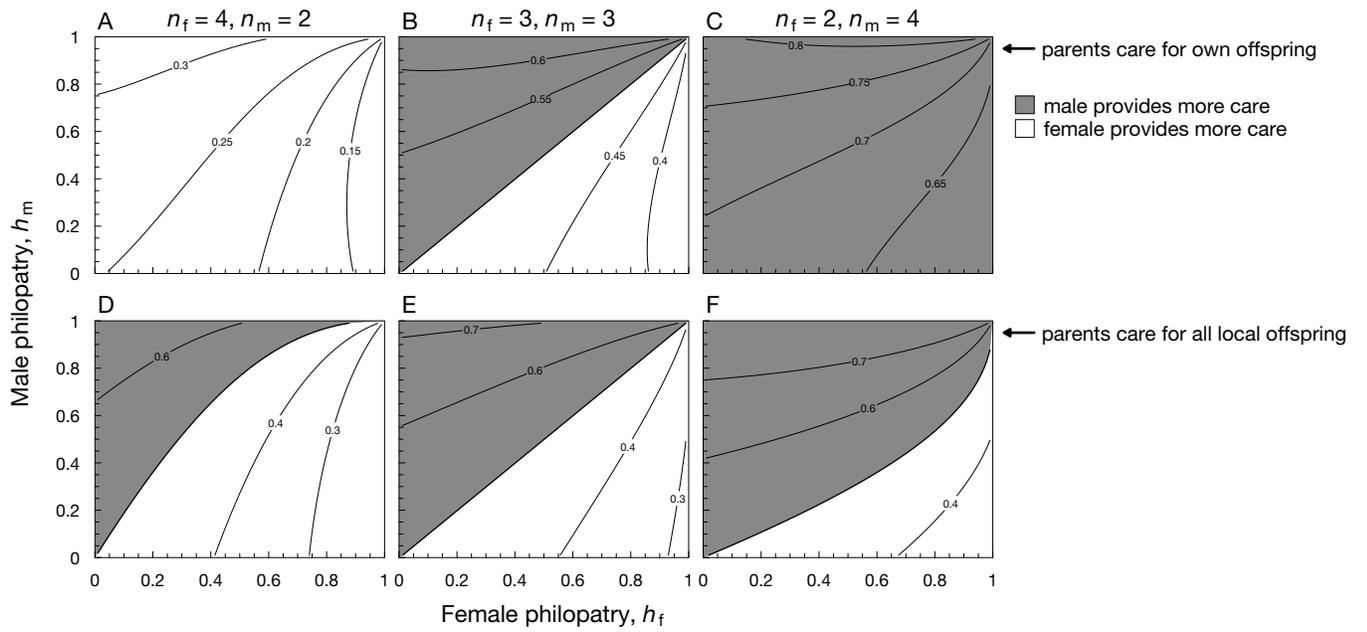


Figure 3:

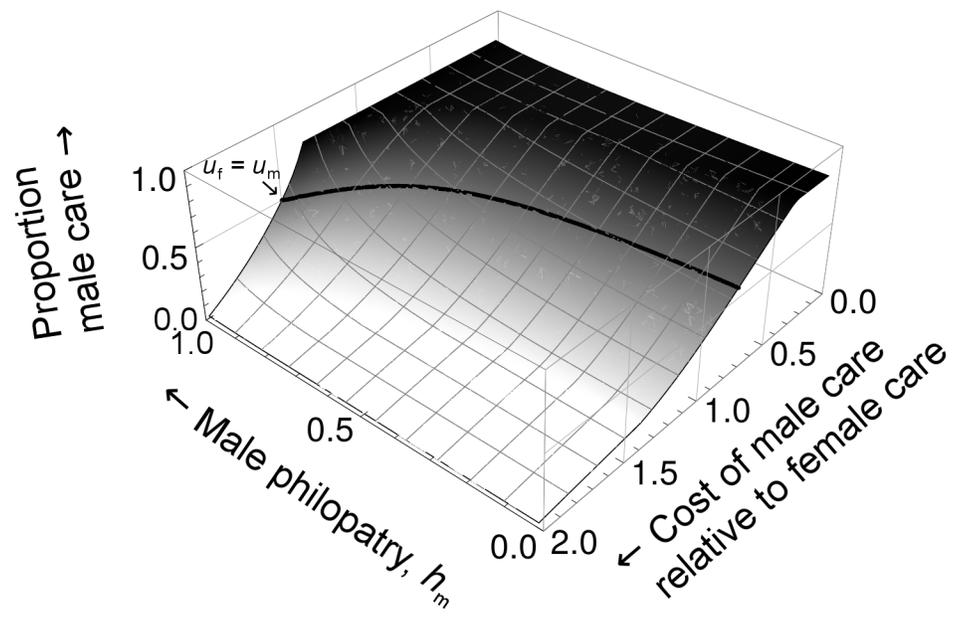


Figure 4:

How sex-biased dispersal affects sexual conflict over care: supplementary information

The American Naturalist

Bram Kuijper^{1,*} & Rufus A. Johnstone²

¹) Environment and Sustainability Institute, University of Exeter, Penryn Campus, TR10 9EZ Penryn, United Kingdom

²) Department of Zoology, University of Cambridge, Downing Street, CB2 3EJ Cambridge, United Kingdom

*) Corresponding author: a.l.w.kuijper@exeter.ac.uk

S1 Supplementary Figures

Figure S1: additional adult mortality due to competition between adults and juveniles The model in the main text assumed that adults, once they occupy a breeding position, are unaffected by competition with juveniles. As we raised this issue in the discussion, we relax this assumption by assuming that adult breeders have to compete with juveniles during every timestep, resulting in an adult mortality cost proportional to the number of juveniles with which the adult competes. Accounting for such adult-juvenile interactions may be important in the context of mating skew: as juveniles are born at a 1:1 sex ratio, the rarer sex would experience relatively more competition by juveniles than the commoner sex, which could potentially reduce selection for increased survival (and lower care) in the rarer sex. To this end, male and female mortalities are now given by $\mu_m(u_m) = u_m^2 + 1 - \exp[-gn_f/n_m]$ and $\mu_f(u_f) = u_f^2 + 1 - \exp[-g]$: here, g is a constant reflecting the effective amount of competing juveniles of a particular sex in a local patch born from a single female, so $g \cdot n_f$ reflects the total amount of competing juveniles of each sex. Hence, each breeding male experiences an effective amount of $g \cdot n_f/n_m$ of competition from juveniles, while each adult female experiences $g \cdot n_f/n_f = g$ competing juveniles. Throughout, we assume $g = 0.8$ to prevent mortality from exceeding 1 when u_m or u_f become large.

Panels A-C: when parents only care for their own offspring, the effect of adult-juvenile interactions is limited, as it is still the commoner sex that provides most of the care. However, relative to Figure 3A-C, the effect of the adult sex ratio (ASR) on sex differences in care is much less pronounced.

Panels D-F: the effect of juvenile-adult interactions become more striking when parents care communally: Figure 3D, F already showed that communal care reduces selection for care in the commoner sex (as its care is diluted over an increased number of offspring). In addition, adult-juvenile interactions cause the commoner sex to experience fewer competitive interactions with juveniles relative to the rarer sex, selecting for increased survival (and hence reduced care) in the commoner sex. Overall, adult-juvenile interactions thus further reduce the effect of mating skew.

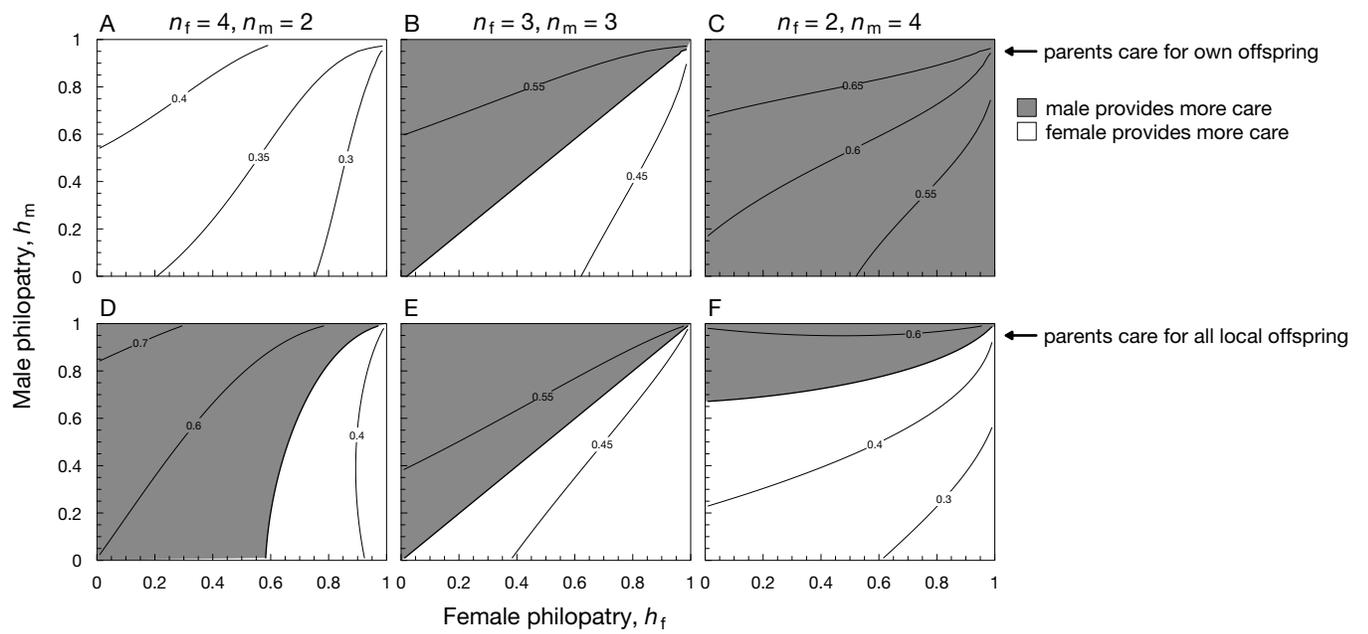


Figure S1:

Figure S2: sex differences in philopatry and absolute levels of male and female effort Absolute values for the amount of total female (panels A, B) and male effort (panels C, D) for different combinations of philopatry in each sex, corresponding to Figure 2 in the main text. First column: 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 viscous populations, kin competition among adults is intense, leading the more philopatric sex to value reproductive effort over survival, as the production of a few dispersing offspring is the only way to escape kin competition in viscous populations (Pen, 2000). Hence, large values of reproductive effort are selectively favored in the more philopatric sex, while levels of care are slight in the dispersing sex. Second column: in populations with a higher number of individuals per patch, viscosity is reduced, so sex differences are less pronounced. Nonetheless, the most philopatric sex still provides the majority of care to its young. Parameters: $k_f = k_m = 0.1$.

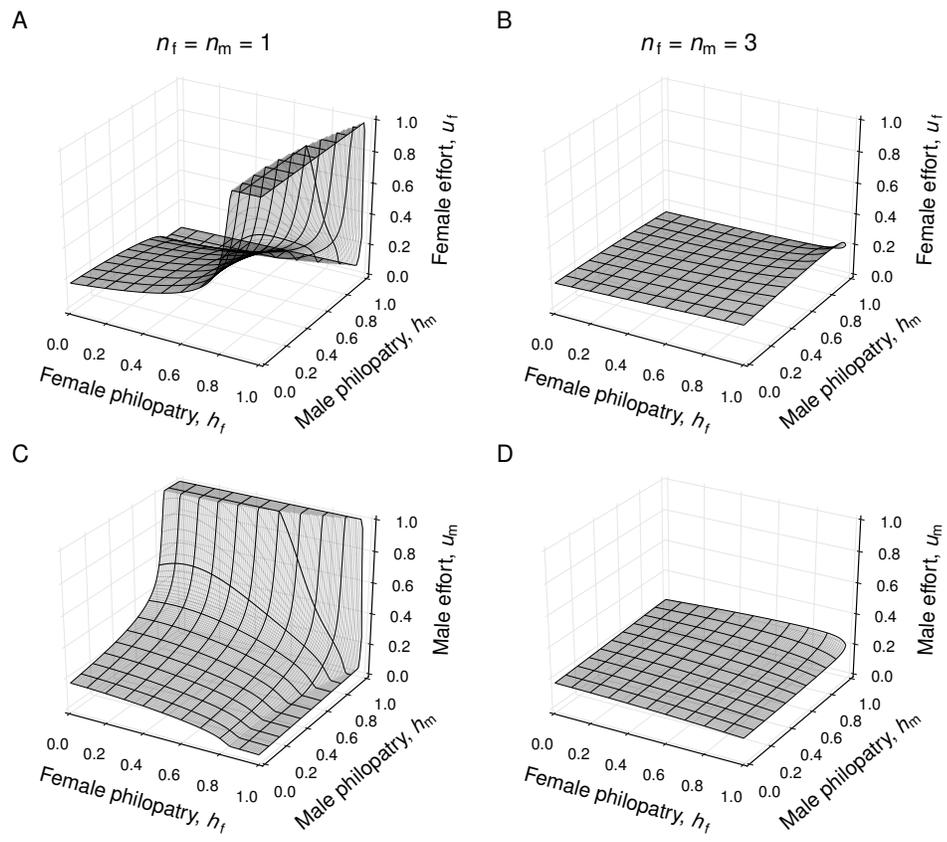


Figure S2:

Figure S3: absolute levels of male and female effort when parents care for own young or care communally Absolute values for the amount of total female (panels A-C, G-I) and male effort (panels D-F, J-L) corresponding to Figure 3 in the main text. When parents only care for their own offspring (panels A-I), note that the common sex provides more effort to the brood than the rare sex (e.g., panels A and F), as it values reproductive effort more than survival (see main text). Note that female effort u_f is higher when females are the more common sex than male effort u_m is when males are the more common sex (compare panel A with panel F). This asymmetry stems from our assumption (see section “A demographical model of parental care” in the main text) that offspring in a brood all have the same genetic mother, whereas a male’s genetic share in a brood to whom he provides care is given by n_f/n_m . Hence, when males are the more common sex, the returns on male effort are diluted by a lower average relatedness to their brood. By contrast, when females are the common sex, female relatedness to her brood is unchanged, resulting in higher relative returns on maternal care. When parents care for all locally born offspring (communal care, panels G-L), we find that effort of the more common sex is strongly reduced relative to a scenario where parents only care for their own offspring (e.g., compare panels A with panel G and panel F with panel L). By contrast, the level of effort of the rarer sex is less affected by communal care. The reason why the value of effort is particularly reduced in the common sex is that an individual of the more common sex has a much lower genetic share in any offspring born in the local patch, relative to the rare sex parent. As a consequence, the value of parental effort by parents belonging of the more common sex is disproportionately reduced relative to the value of care by parents belonging to the rarer sex. By contrast, care levels in the rarer sex are much less affected, as any randomly chosen locally born offspring is much more likely to be one of its own offspring. Moreover, the rarer sex is already selected to provide a minimum level of effort, as it faces reduced competition for breeding opportunities relative to the commoner sex (see main text). Parameters: $k_f = k_m = 0.1$.

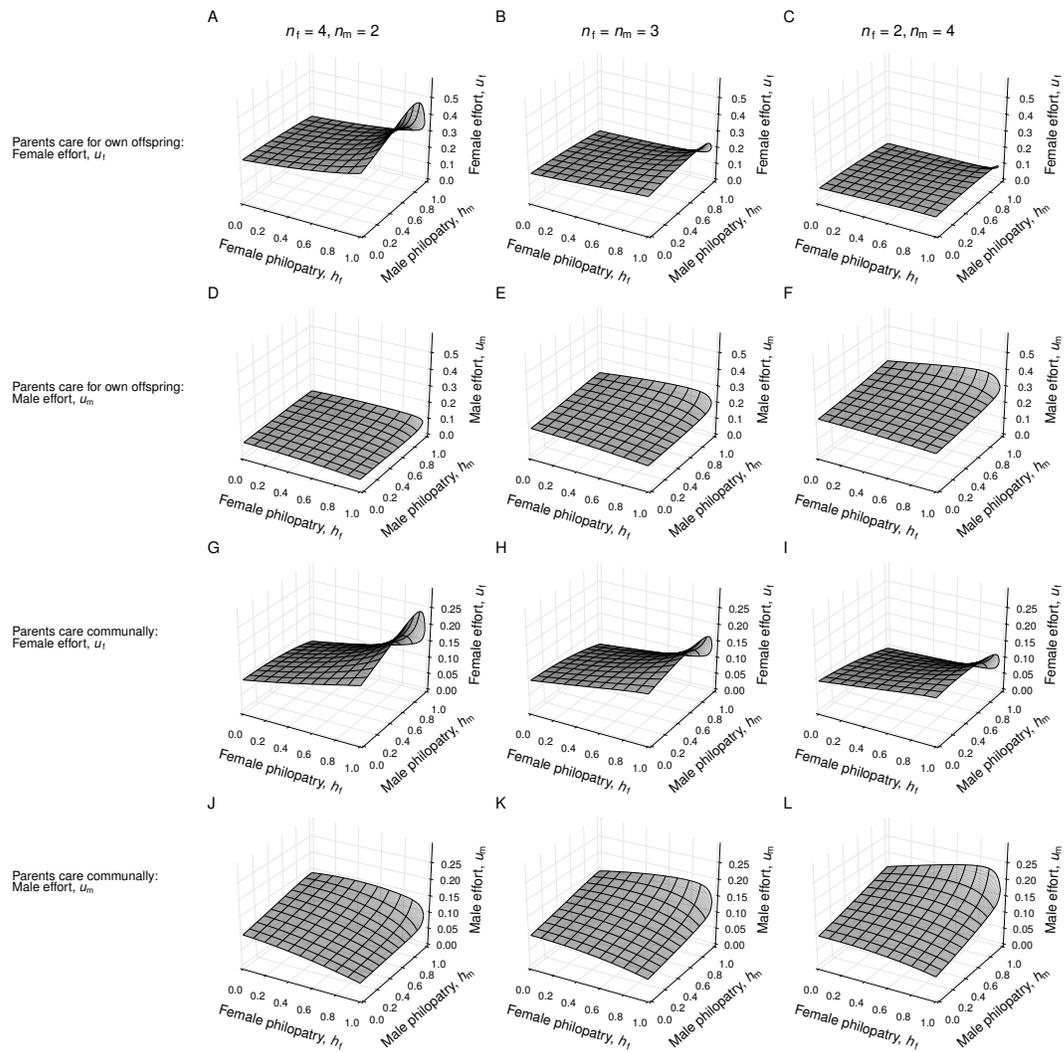


Figure S3:

Figure S4: absolute levels of male and female effort when varying the costs of care Absolute values for the amount of total male (panels A) and female effort (panel B) corresponding to Figure 4 in the main text, when female philopatry is $h_f = 0.8$. The relative cost of male versus female care is given by $(1 - k_m)/(1 - k_f)$. For low levels of male philopatry h_m , male care (female care) rapidly decreases (increases) with increasing relative costs of male care. By contrast, for high levels of male philopatry, we find that male effort is sustained at relatively high levels despite high relative costs of male care. Only when relative costs of male care are very high (e.g., $(1 - k_m)/(1 - k_f) \approx 2$), do we find that male care evolves to $u_m = 0$. Interestingly, however, for the combination of high costs of male care and high levels of male philopatry (specifically when $h_m \geq 0.8 \iff d_m \leq 0.2$), we find that female care only evolves to modest values, resulting in lower levels of overall care given to the brood. For this combination of parameters, female care only evolves to modest values because females become the more dispersing sex when $h_m \geq 0.8$. Consequently, females are more likely than males to share demes with unrelated individuals, selecting females to reduce levels of effort (as in dying, a female would be relatively more likely to be replaced by a non-relative). Parameters: $n_f = n_m = 1$, $k_f = 0.5$.

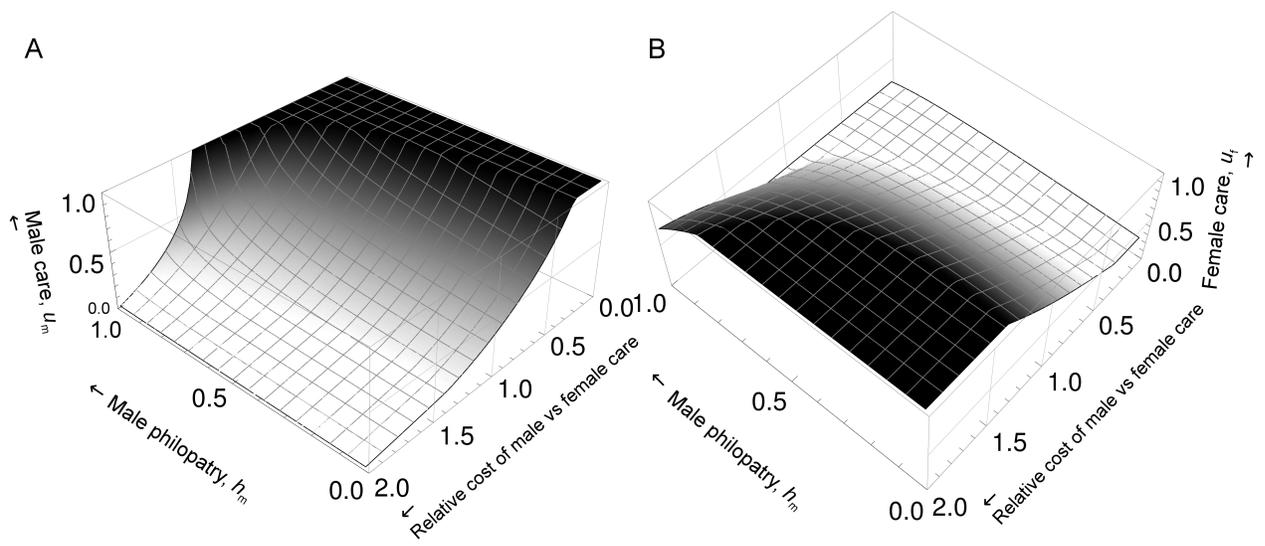


Figure S4:

S2 An evolutionary demographical model of biparental care

Below, we provide a formal description of a demographical model of biparental care for a scenario where both parents only provide care for their own offspring. In section S2.2 we then derive a version of this model where care occurs communally (i.e., where parents provide care to all locally born offspring).

S2.1 Fitness equations for u_f when parents care for their own offspring

Female fitness The fitness of a focal mutant allele u_f^i while residing in a breeding female is given by

$$W_f = 1 - \mu_f(u_f^i) + \frac{1}{2} w_{ff}(u_f^i, u_f^{ff}, u_f^{\text{pop}}) + \frac{1}{2} \frac{v_m}{v_f} w_{fm}(u_f^i, u_f^{ff}, u_f^{\text{pop}}), \quad (\text{S1})$$

where $1 - \mu_f(u_f^i)$ is the probability that the female breeder bearing the mutant allele survives, while w_{ff} and w_{fm} are the expected number of successfully established daughters and sons she produces (multiplied by $1/2$ to reflect the genetic contribution by each parent). The contribution through sons is weighed by the relative reproductive value of sons versus daughters, v_m/v_f . Expressions for the reproductive values are derived below. Expressions for w_{ff} and w_{fm} are

$$w_{ff}(u_f^i, u_f^{ff}, u_f^{\text{pop}}) = b \left(u_f^i + \frac{n_m}{n_f} u_m \right) \times \left[\frac{(1-d_f) \mu_f(u_f^{ff})}{b \left(u_f^{ff} + \frac{n_m}{n_f} u_m \right) (1-d_f) + b \left(u_f^{\text{pop}} + \frac{n_m}{n_f} u_m \right) d_f} + \frac{d_f \mu_f(u_f^{\text{pop}})}{b \left(u_f^{\text{pop}} + \frac{n_m}{n_f} u_m \right)} \right] \quad (\text{S2})$$

$$w_{fm}(u_f^i, u_f^{ff}, u_f^{\text{pop}}) = b \left(u_f^i + \frac{n_m}{n_f} u_m \right) \frac{n_m}{n_f} \times \left[\frac{(1-d_m) \mu_m(u_m)}{b \left(u_f^{ff} + \frac{n_m}{n_f} u_m \right) (1-d_m) + b \left(u_f^{\text{pop}} + \frac{n_m}{n_f} u_m \right) d_m} + \frac{d_m \mu_m(u_m)}{b \left(u_f^{\text{pop}} + \frac{n_m}{n_f} u_m \right)} \right], \quad (\text{S3})$$

where u_f^{ff} denotes the average investment level of a local female when the focal copy is borne by a female; and u_f^{pop} the population average female investment level. Male care is assumed to be evenly distributed over his female mates (the average of which is n_f/n_m), so that the per-brood contribution by a male is $u_m/(n_f/n_m)$. Taking w_{ff} as an example, note that any daughters the focal female produces will remain in the natal patch with probability $h_f = 1 - d_f$ or disperse to a remote patch with probability d_f . In case mortality of a local female breeder occurs (average number of local female mortality events per time step: $n_f \mu_f(u_f^{ff})$), juvenile females in the patch compete for a breeding position, which is reflected by the term in the denominator: the number of juvenile daughters produced by the n_f female breeders in the local patch is $n_f b(u_f^{ff} + \frac{n_m}{n_f} u_m)$, who remain at the natal patch with probability $1 - d_f$. In addition, with probability d_f immigrant juvenile females arrive from remote patches (in which fecundity is given by $n_f b(u_f^{\text{pop}} + \frac{n_m}{n_f} u_m)$). By contrast, the probability of establishment of a focal daughter that migrated to a remote patch (with probability d_f) is proportional to the average number of mortality events of female breeders in the remote patch $n_f \mu_f(u_f^{\text{pop}})$, and inversely proportional to the total fecundity of native and immigrant offspring in the remote patch $n_f b(u_f^{\text{pop}} + \frac{n_m}{n_f} u_m)$. The expression for $w_{fm}(u_f^i, u_f^{ff}, u_f^{\text{pop}})$ can be derived in a similar fashion.

Male fitness Similarly, fitness of the focal mutant allele u_f^i while residing in a breeding male is given by

$$W_m = 1 - \mu_m(u_m) + \frac{1}{2} w_{mm}(u_f^{fm}, u_f^{\text{pop}}) + \frac{1}{2} \frac{v_f}{v_m} w_{mf}(u_f^{fm}, u_f^{\text{pop}}), \quad (\text{S4})$$

where expressions for the expected number of copies of the u_f^i allele in successfully established sons and daughters are given by

$$w_{mm}(u_f^{fm}, u_f^{pop}) = \frac{n_f}{n_m} b \left(u_f^{fm} + \frac{n_m}{n_f} u_m \right) \frac{n_m}{n_f} \times \left[\frac{(1-d_m)\mu_m(u_m)}{b \left(u_f^{fm} + \frac{n_m}{n_f} u_m \right) (1-d_m) + b \left(u_f^{pop} + \frac{n_m}{n_f} u_m \right) d_m} + \frac{d_m \mu_m(u_m)}{b \left(u_f^{pop} + \frac{n_m}{n_f} u_m \right)} \right] \quad (S5)$$

$$w_{mf}(u_f^{fm}, u_f^{pop}) = \frac{n_f}{n_m} b \left(u_f^{fm} + \frac{n_m}{n_f} u_m \right) \times \left[\frac{(1-d_f)\mu_f(u_f^{fm})}{b \left(u_f^{fm} + \frac{n_m}{n_f} u_m \right) (1-d_f) + b \left(u_f^{pop} + \frac{n_m}{n_f} u_m \right) d_f} + \frac{d_f \mu_f(u_f^{pop})}{b \left(u_f^{pop} + \frac{n_m}{n_f} u_m \right)} \right], \quad (S6)$$

where u_f^{fm} denotes the average investment level of a local female when the focal gene copy is borne by a male. w_{mm} and w_{mf} can be derived in a similar fashion as eqns. (S2, S3), but note that $b(u_f^{fm} + \frac{n_m}{n_f} u_m)$ reflects a focal male's fecundity with a single female, which should thus be multiplied by a male's total number of mates n_f/n_m .

S2.1.1 Fitness equations for u_m when parents care for their own offspring

Similar to the equations in the main text, we have the following expressions for the fitness of a focal allele u_m^i that determines male parental investment:

$$W_f = 1 - \mu_f(u_f) + \frac{1}{2} w_{ff}(u_m^{mf}, u_m^{pop}) + \frac{1}{2} \frac{v_m}{v_f} w_{fm}(u_m^{mf}, u_m^{pop}) \quad (S7)$$

$$W_m = 1 - \mu_m(u_m^i) + \frac{1}{2} w_{mm}(u_m^i, u_m^{mm}, u_m^{pop}) + \frac{1}{2} \frac{v_f}{v_m} w_{mf}(u_m^i, u_m^{mm}, u_m^{pop}), \quad (S8)$$

where

$$w_{ff}(u_m^{mf}, u_m^{pop}) = b \left(u_f + \frac{n_m}{n_f} u_m^{mf} \right) \quad (S9)$$

$$\times \left[\frac{(1-d_f)\mu_f(u_f)}{b \left(u_f + \frac{n_m}{n_f} u_m^{mf} \right) (1-d_f) + b \left(u_f + \frac{n_m}{n_f} u_m^{pop} \right) d_f} + \frac{d_f \mu_f(u_f)}{b \left(u_f + \frac{n_m}{n_f} u_m^{pop} \right)} \right] \quad (S10)$$

$$w_{fm}(u_m^{mf}, u_m^{pop}) = b \left(u_f + \frac{n_m}{n_f} u_m^{mf} \right) \frac{n_m}{n_f} \times \left[\frac{(1-d_m)\mu_m(u_m^{mf})}{b \left(u_f + \frac{n_m}{n_f} u_m^{mf} \right) (1-d_m) + b \left(u_f + \frac{n_m}{n_f} u_m^{pop} \right) d_m} + \frac{d_m \mu_m(u_m^{pop})}{b \left(u_f + \frac{n_m}{n_f} u_m^{pop} \right)} \right] \quad (S11)$$

$$w_{mm}(u_m^i, u_m^{mm}, u_m^{pop}) = \frac{n_f}{n_m} b \left(u_f + \frac{n_m}{n_f} u_m^i \right) \frac{n_m}{n_f} \times \left[\frac{(1-d_m)\mu_m(u_m^{mm})}{b \left(u_f + \frac{n_m}{n_f} u_m^{mm} \right) (1-d_m) + b \left(u_f + \frac{n_m}{n_f} u_m^{pop} \right) d_m} + \frac{d_m \mu_m(u_m^{pop})}{b \left(u_f + \frac{n_m}{n_f} u_m^{pop} \right)} \right] \quad (S12)$$

$$w_{mf}(u_m^i, u_m^{mm}, u_m^{pop}) = \frac{n_f}{n_m} b \left(u_f + \frac{n_m}{n_f} u_m^i \right)$$

$$\times \left[\frac{(1-d_f)\mu_f(u_f)}{b\left(u_f + \frac{n_m}{n_f}u_m^{mm}\right)(1-d_f) + b\left(u_f + \frac{n_m}{n_f}u_m^{pop}\right)d_f} + \frac{d_f\mu_f(u_f)}{b\left(u_f + \frac{n_m}{n_f}u_m^{pop}\right)} \right]. \quad (S13)$$

S2.2 Fitness equations in case care is communal

In case parents care for all locally born offspring, a focal female's fecundity is now a function of the average female and male care levels in the local patch. Consequently, when a female bears the focal allele, her fecundity is given by $b(u_f^{ff} + \frac{n_m}{n_f}u_m)$, where u_f^{ff} denotes the parental effort averaged over all local female breeders, when the focal gene copy is borne by a female. Consequently, the same transition probabilities w_{ff} and w_{fm} from eqns. (S2,S3) apply here, with the difference that a focal's effort u_f^i is substituted by the average effort u_f^{ff} . Equations for w_{mm} and w_{mf} from eqns. (S5,S6) are unchanged.

Similarly, when considering expressions for the expected number of offspring bearing allele u_m , expressions for w_{ff} and w_{fm} are unaltered relative to eqns. (S11, S11). In the expressions for w_{mm} and w_{mf} (eqns. S12, S13) we replace u_m^i by u_m^{mm} , the level of effort averaged over all local male breeders when the focal gene copy is borne by a male.

S2.3 Reproductive values

We derive a 2×2 matrix \mathbf{P} , entries of which the probability p_{ij} that a gene copy present in an individual of sex i is derived (by survival or reproduction) from a gene copy in an individual of sex j in the previous time step. Hence,

$$\mathbf{P} = \begin{bmatrix} p_{ff} & p_{fm} \\ p_{mf} & p_{mm} \end{bmatrix} = \begin{bmatrix} 1 - \mu_f + \frac{1}{2}w_{ff} & \frac{1}{2}w_{mf} \\ \frac{1}{2}w_{fm} & 1 - \mu_m + \frac{1}{2}w_{mm} \end{bmatrix},$$

so we have (for a fully homogeneous population without mutant alleles)

$$\mathbf{P} = \begin{bmatrix} 1 - \mu_f + \frac{1}{2}\mu_f & \frac{1}{2}\mu_f \\ \frac{1}{2}\mu_m & 1 - \mu_m + \frac{1}{2}\mu_m \end{bmatrix}.$$

From the left eigenvalue of \mathbf{P} , we then obtain the class reproductive values $c_f = \mu_m/(\mu_m + \mu_f)$ and $c_m = \mu_f/(\mu_m + \mu_f)$. To obtain individual reproductive values for each sex, we use the relationship $v_i = c_i/u_i$ (?), we divide the class reproductive values c_i ($i \in [m, f]$) by the class frequencies $u_m = n_m/(n_m + n_f) + u_f = n_f/(n_m + n_f)$ so that we obtain

$$v_f = \frac{n_m + n_f}{n_f} \frac{\mu_m}{\mu_m + \mu_f} \quad (S14)$$

$$v_m = \frac{n_m + n_f}{n_m} \frac{\mu_f}{\mu_m + \mu_f}. \quad (S15)$$

As the total reproductive value is constant, we can scale values so that

$$v_m = \frac{1}{n_m \mu_m (u_m^*)}, \quad v_f = \frac{1}{n_f \mu_f (u_f^*)}, \quad (S16)$$

which facilitates the interpretation of the selection gradients in eqns. (A1-A4); see Appendix.

S2.4 Relatedness

Let Q_{ij} denote the average coefficient of relatedness among two randomly chosen adult breeders of sexes i and j . We then have the following recursions

$$\begin{aligned} Q_{ff,t+1} &= (1 - \mu_f(u_f))^2 Q_{ff,t} \\ &\quad + 2\mu_f(u_f)(1 - \mu_f(u_f))h_f \frac{1}{2} \left[\frac{1}{n_f} + \frac{n_f-1}{n_f} Q_{ff,t} + Q_{fm,t} \right] \\ &\quad + \mu_f(u_f)^2 h_f^2 \left(\frac{1}{4} \left[\frac{1}{n_f} + \frac{n_f-1}{n_f} Q_{ff,t} \right] + \frac{1}{2} Q_{fm,t} + \frac{1}{4} \left[\frac{1}{n_m} + \frac{n_m-1}{n_m} Q_{mm,t} \right] \right) \end{aligned} \quad (S17)$$

$$\begin{aligned} Q_{fm,t+1} &= (1 - \mu_m(u_m))(1 - \mu_f(u_f))Q_{fm,t} \\ &\quad + \mu_f(u_f)(1 - \mu_m(u_m))h_f \frac{1}{2} \left[\frac{1}{n_m} + \frac{n_m-1}{n_m} Q_{mm,t} + Q_{fm,t} \right] \\ &\quad + \mu_m(u_m)(1 - \mu_f(u_f))h_m \frac{1}{2} \left[\frac{1}{n_f} + \frac{n_f-1}{n_f} Q_{ff,t} + Q_{fm,t} \right] \\ &\quad + \mu_f(u_f)\mu_m(u_m)h_f h_m \\ &\quad \times \left(\frac{1}{4} \left[\frac{1}{n_f} + \frac{n_f-1}{n_f} Q_{ff,t} \right] + \frac{1}{2} Q_{fm,t} + \frac{1}{4} \left[\frac{1}{n_m} + \frac{n_m-1}{n_m} Q_{mm,t} \right] \right) \end{aligned} \quad (S18)$$

$$\begin{aligned} Q_{mm,t+1} &= (1 - \mu_m(u_m))^2 Q_{mm,t} \\ &\quad + 2\mu_m(u_m)(1 - \mu_m(u_m))h_m \frac{1}{2} \left[\frac{1}{n_m} + \frac{n_m-1}{n_m} Q_{mm,t} + Q_{fm,t} \right] \\ &\quad + \mu_m(u_m)^2 h_m^2 \left(\frac{1}{4} \left[\frac{1}{n_f} + \frac{n_f-1}{n_f} Q_{ff,t} \right] + \frac{1}{2} Q_{fm,t} + \frac{1}{4} \left[\frac{1}{n_m} + \frac{n_m-1}{n_m} Q_{mm,t} \right] \right). \end{aligned} \quad (S19)$$

The first equation reflects the coefficient of relatedness $Q_{ff,t+1}$ among two randomly sampled female breeders. With probability $(1 - \mu_f)^2$ both adult female breeders are survivors from the previous time step, in which case their expected relatedness is equal to $Q_{ff,t}$. With probability $2\mu_f(u_f)(1 - \mu_f(u_f))$ one female is a survivor from the previous time step, whereas the other female is newly born. In this case, both females are only related when the newborn female is native to the local patch, with probability h_f . With probability $1/2$ the newborn received its gene copy maternally and with probability $1/2$ paternally. In case of maternal inheritance, with probability $1/n_f$ the newborn female is a daughter of the sampled, surviving female. The probability that both gene copies are identical by descent is then 1. With probability $(n_f - 1)/n_f$, the newborn female is a daughter of one of the other breeding females in the local patch, so that the probability that both gene copies are identical by descent is given by $Q_{ff,t}$. In case the newborn received the gene copy from her father, the probability that the newborn's gene copy is identical by descent to the surviving female is r_{fm} . Finally, with probability $(1 - \mu_f(u_f))^2$, both sampled females are newly born and with probability h_f^2 to the local patch. With probability $1/4$, both females received their gene copies maternally. In case both females are born from the same mother (with probability $1/n_f$) the identity by descent is 1. By contrast, when both females are born from different mothers (with probability $(n_f - 1)/n_f$), the probability of identity by descent of both gene copies is given by $Q_{ff,t}$. Alternatively, with probability $1/2$ one gene copy is paternally inherited and one maternally inherited, in which case the identity by descent is given by $Q_{fm,t}$. Finally, with probability $1/4$ both gene copies are paternally inherited. With probability $1/n_m$ both females share the same father and hence the probability that both gene copies are identical by descent is 1. In case both are born from different fathers (with probability $(n_m - 1)/n_m$) the probability of identity by descent is given by $Q_{mm,t}$. The expressions for $Q_{fm,t+1}$ and $Q_{mm,t+1}$ can be derived in a similar fashion.

Equilibrium values \hat{Q}_{ff} , \hat{Q}_{fm} and \hat{Q}_{mm} can be easily obtained from the above equations. However, results are lengthy and not particularly insightful, so we do not display these equilibria here. We then use the

equilibrium values to calculate average values of relatedness r_{ff} , r_{fm} and r_{mm} that are used in the selection gradients below. Specifically, we have

$$r_{ff} = \frac{1}{n_f} + \frac{n_f - 1}{n_f} \hat{Q}_{ff} \quad (\text{S20})$$

$$r_{mm} = \frac{1}{n_m} + \frac{n_m - 1}{n_m} \hat{Q}_{mm} \quad (\text{S21})$$

$$r_{fm} = \hat{Q}_{fm}. \quad (\text{S22})$$

S2.5 Selection gradients

We derive selection differentials that determine the rate of evolutionary change in u_m and u_f using a direct fitness approach (Hamilton, 1964*b*; Taylor and Frank, 1996; Taylor et al., 2007)

$$\frac{dW}{du_f} = \left[c_f \left(\frac{\partial W_f}{\partial u_f^i} + r_{ff} \frac{\partial W_f}{\partial u_f^{ff}} \right) + r_{fm} c_m \frac{\partial W_m}{\partial u_f^{fm}} \right] \Big|_{u_f^{\text{pop}} = u_f^{fm} = u_f^{ff} = u_f^i} \quad (\text{S23})$$

$$\frac{dW}{du_m} = \left[c_m \left(\frac{\partial W_m}{\partial u_m^i} + r_{mm} \frac{\partial W_m}{\partial u_m^{mm}} \right) + r_{fm} c_f \frac{\partial W_f}{\partial u_m^{mf}} \right] \Big|_{u_m^{\text{pop}} = u_m^{fm} = u_m^{ff} = u_m^i}, \quad (\text{S24})$$

where the class reproductive values are $c_f = c_m = \frac{1}{2}$.

S2.6 Equilibrium condition when individuals care for their own offspring

Solving for the equilibrium condition where both selection gradients vanish ($dW/du_f = 0$, $dW/du_m = 0$), we have

$$\begin{aligned} & \left[1 - \frac{1}{2} h_f \left(\frac{1}{n_f} + \frac{n_f - 1}{n_f} r_{ff} + r_{fm} \right) \right] \frac{\mu'_f(u_f^*)}{\mu_f(u_f^*)} \\ &= \left[2 \left(\frac{1}{2} (1 + r_{fm}) - \frac{(h_f^2 + h_m^2)}{2} \frac{1}{2} \left(\frac{1}{n_f} + \frac{n_f - 1}{n_f} r_{ff} + r_{fm} \right) \right) \right] \frac{b'_{u_f} \left(u_f^* + \frac{n_m}{n_f} u_m^* \right)}{b \left(u_f^* + \frac{n_m}{n_f} u_m^* \right)} \end{aligned} \quad (\text{S25})$$

$$\begin{aligned} & \left[1 - \frac{1}{2} h_m \left(\frac{1}{n_m} + \frac{n_m - 1}{n_m} r_{mm} + r_{fm} \right) \right] \frac{\mu'_m(u_m^*)}{\mu_m(u_m^*)} \\ &= \frac{n_m}{n_f} \left[2 \left(\frac{1}{2} (1 + r_{fm}) - \frac{(h_f^2 + h_m^2)}{2} \frac{1}{2} \left(\frac{1}{n_m} + \frac{n_m - 1}{n_m} r_{mm} + r_{fm} \right) \right) \right] \frac{b'_{u_m} \left(u_f^* + \frac{n_m}{n_f} u_m^* \right)}{b \left(u_f^* + \frac{n_m}{n_f} u_m^* \right)}. \end{aligned} \quad (\text{S26})$$

Now substituting on the left-hand side $r_{\text{self}} = 1$ and

$$r_{f \rightarrow \text{locally competing juv}} = \frac{1}{2} h_f \left(\frac{1}{n_f} + \frac{n_f - 1}{n_f} r_{ff} + r_{fm} \right) \quad (\text{S27})$$

$$r_{m \rightarrow \text{locally competing juv}} = \frac{1}{2} h_m \left(\frac{1}{n_m} + \frac{n_m - 1}{n_m} r_{mm} + r_{fm} \right), \quad (\text{S28})$$

which denote the average relatedness of a focal female or focal male breeder to locally competing juveniles of the same sex, and on the right-hand side

$$r_{f \rightarrow \text{own juv}} = r_{m \rightarrow \text{own juv}} = \frac{1}{2} (1 + r_{fm}),$$

which denotes the average relatedness of a focal female (or male) breeder to its own offspring (averaging across both sexes of young), and

$$r_{f \rightarrow \text{competing juv}} = \frac{1}{2} \frac{(h_f^2 + h_m^2)}{2} \left(\frac{1}{n_f} + \frac{n_f - 1}{n_f} r_{ff} + r_{fm} \right) \quad (\text{S29})$$

$$r_{m \rightarrow \text{competing juv}} = \frac{1}{2} \frac{(h_f^2 + h_m^2)}{2} \left(\frac{1}{n_m} + \frac{n_m - 1}{n_m} r_{mm} + r_{fm} \right), \quad (\text{S30})$$

which denote the relatedness between a focal female (or male) breeder and any competing offspring of the same sex that are displaced by the focal's own offspring (again averaging over both sexes of young), we obtain equations (A3, A4) in the main text.

S2.7 Equilibrium condition when care is communal

For communal care we obtain a similar equilibrium condition as in eqns. (S25, S26):

$$\begin{aligned} & \left[1 - \frac{1}{2} h_f \left(\frac{1}{n_f} + \frac{n_f - 1}{n_f} r_{ff} + r_{fm} \right) \right] \frac{\mu'_f(u_f^*)}{\mu_f(u_f^*)} \\ &= \left[2 \left(\frac{1}{2} \left(\frac{1}{n_f} + \frac{n_f - 1}{n_f} r_{ff} + r_{fm} \right) - \frac{(h_f^2 + h_m^2)}{2} \frac{1}{2} \left(\frac{1}{n_f} + \frac{n_f - 1}{n_f} r_{ff} + r_{fm} \right) \right) \right] \frac{b'_{u_f} \left(u_f^* + \frac{n_m}{n_f} u_m^* \right)}{b \left(u_f^* + \frac{n_m}{n_f} u_m^* \right)} \end{aligned} \quad (\text{S31})$$

$$\begin{aligned} & \left[1 - \frac{1}{2} h_m \left(\frac{1}{n_m} + \frac{n_m - 1}{n_m} r_{mm} + r_{fm} \right) \right] \frac{\mu'_m(u_m^*)}{\mu_m(u_m^*)} \\ &= \left[2 \left(\frac{1}{2} \left(\frac{1}{n_m} + \frac{n_m - 1}{n_m} r_{mm} + r_{fm} \right) - \frac{(h_f^2 + h_m^2)}{2} \frac{1}{2} \left(\frac{1}{n_m} + \frac{n_m - 1}{n_m} r_{mm} + r_{fm} \right) \right) \right] \frac{b'_{u_m} \left(u_f^* + \frac{n_m}{n_f} u_m^* \right)}{b \left(u_f^* + \frac{n_m}{n_f} u_m^* \right)}. \end{aligned} \quad (\text{S32})$$

Hence, this leads to the same equilibrium condition as in eqns. (A3, A4), with the difference that $r_{f \rightarrow \text{own juv}}$ and $r_{m \rightarrow \text{own juv}}$ are replaced by

$$r_{f \rightarrow \text{locally born juv}} = \frac{1}{2} \left(\frac{1}{n_f} + \frac{n_f - 1}{n_f} r_{ff} + r_{fm} \right) \quad (\text{S33})$$

$$r_{m \rightarrow \text{locally born juv}} = \frac{1}{2} \left(\frac{1}{n_m} + \frac{n_m - 1}{n_m} r_{mm} + r_{fm} \right). \quad (\text{S34})$$

S3 Coevolution of parental care and the sex ratio

Below we provide a brief exploration of the evolutionary dynamics of parental care when allowing for the evolution of the sex ratio. We first ask how parental care affects previous results on equilibrium sex ratios in viscous populations, after which we consider how the sex ratio affects sex differences in care.

For the sake of simplicity, we consider the simplest possible scenario in which brood sex ratios are controlled by the mother rather than the individual offspring (Pen, 2006) and parents only care for their own young. Analogous to eqns. (S1, S4), we then have the following expressions for the fitness of a focal allele z^i that is present in a focal female (or male) and determines the proportion of sons in her (or his) offspring:

$$W_f = 1 - \mu_f(u_f) + \frac{1}{2} w_{ff}(z^i, z^{ff}, z^{\text{pop}}; u_f) + \frac{1}{2} \frac{v_m}{v_f} w_{fm}(z^i, z_f^{ff}, z_f^{\text{pop}}; u_m) \quad (\text{S35})$$

$$W_m = 1 - \mu_m(u_m) + \frac{1}{2} w_{mm}(z^{\text{mf}}, z^{\text{pop}}; u_m) + \frac{1}{2} \frac{v_f}{v_m} w_{mf}(z^{\text{mf}}, z^{\text{pop}}; u_f), \quad (\text{S36})$$

where z^{ff} (and z^{mf}) is the average proportion sons produced by all females in the local patch when the focal allele copy is borne by an adult female (male) and z^{pop} is the average proportion sons produced by the rest of the population. We then have

$$w_{ff}(z^i, z^{ff}, z^{\text{pop}}; u_f) = \frac{(1-d_f)(1-z^i)\mu_f(u_f)}{(1-d_f)(1-z^{ff}) + d_f(1-z^{\text{pop}})} + \frac{d_f(1-z^i)\mu_f(u_f)}{(1-z^{\text{pop}})} \quad (\text{S37})$$

$$w_{fm}(z^i, z_f^{ff}, z_f^{\text{pop}}; u_m) = \frac{n_m(1-d_m)z^i\mu_m(u_m)}{n_f[(1-d_m)z^{ff} + d_m z^{\text{pop}}]} + \frac{n_m d_m z^i \mu_m(u_m)}{n_f z^{\text{pop}}} \quad (\text{S38})$$

$$w_{mm}(z^{\text{mf}}, z^{\text{pop}}; u_m) = \frac{n_f}{n_m} \left(\frac{n_m(1-d_m)z^{\text{mf}}\mu_m(u_m)}{n_f[(1-d_m)z^{\text{mf}} + d_m z^{\text{pop}}]} + \frac{n_m d_m z^{\text{mf}} \mu_m(u_m)}{n_f z^{\text{pop}}} \right) \quad (\text{S39})$$

$$w_{mf}(z^{\text{mf}}, z^{\text{pop}}; u_f) = \frac{n_f}{n_m} \left(\frac{(1-d_f)(1-z^{\text{mf}})\mu_f(u_f)}{(1-d_f)(1-z^{\text{mf}}) + d_f(1-z^{\text{pop}})} + \frac{d_f(1-z^{\text{mf}})\mu_f(u_f)}{(1-z^{\text{pop}})} \right). \quad (\text{S40})$$

The evolutionary change in the proportion of sons z is then given by

$$\frac{dW}{dz} = \left[c_f \left(\frac{\partial W_f}{\partial z^i} + r_{ff} \frac{\partial W_f}{\partial z^{ff}} \right) + r_{fm} c_m \frac{\partial W_m}{\partial z^{\text{mf}}} \right] \Big|_{z^{\text{pop}}=z^{\text{fm}}=z^{\text{ff}}=z^i=z}, \quad (\text{S41})$$

with the relatedness coefficients given by eqns. (S20-S21) resulting in the equilibrium sex-ratio strategy

$$z^* = \frac{\frac{1}{2}(1+r_{fm}) - \frac{1}{2}(1-d_m)^2 \left(\frac{1}{n_f} + \frac{n_f-1}{n_f} r_{ff} + r_{fm} \right)}{\frac{1}{2}(1+r_{fm}) - \frac{1}{2}(1-d_f)^2 \left(\frac{1}{n_f} + \frac{n_f-1}{n_f} r_{ff} + r_{fm} \right)}. \quad (\text{S42})$$

When substituting for the values of r_{ff} and r_{fm} (eqns. [S20,S22]) and assuming that generations are non-overlapping, the above result is identical to previous expressions of equilibrium sex ratios in viscous populations (e.g., eq. [4] in Pen, 2006; see also Frank, 1986; Wild and Taylor, 2004). The expression above shows that the sex ratio is always biased towards the more dispersing sex, as it is least likely to compete with relatives relative to the philopatric sex. Figure S5 shows that sex ratios become even more biased towards the dispersing sex when the sex ratio coevolves with parental care. This is because our model on parental care necessarily assumes overlapping generations (as current reproductive success trades off with future reproduction: Trivers, 1972). Such overlapping generations increase relatedness among relatives, thus exacerbating the probability that the philopatric sex competes with relatives. Consequently, mothers are selectively favored to bias investment even more strongly towards the dispersing sex.

We then ask whether biased sex ratios have any effect on the equilibrium level of female u_f^* and male care u_m^* . However, it is straightforward to see that adding the equilibrium sex ratio z^* to eqns. (S2-S12) has no effect, because sex ratio terms in numerator and denominator cancel out against each other in each of the aforementioned equations.

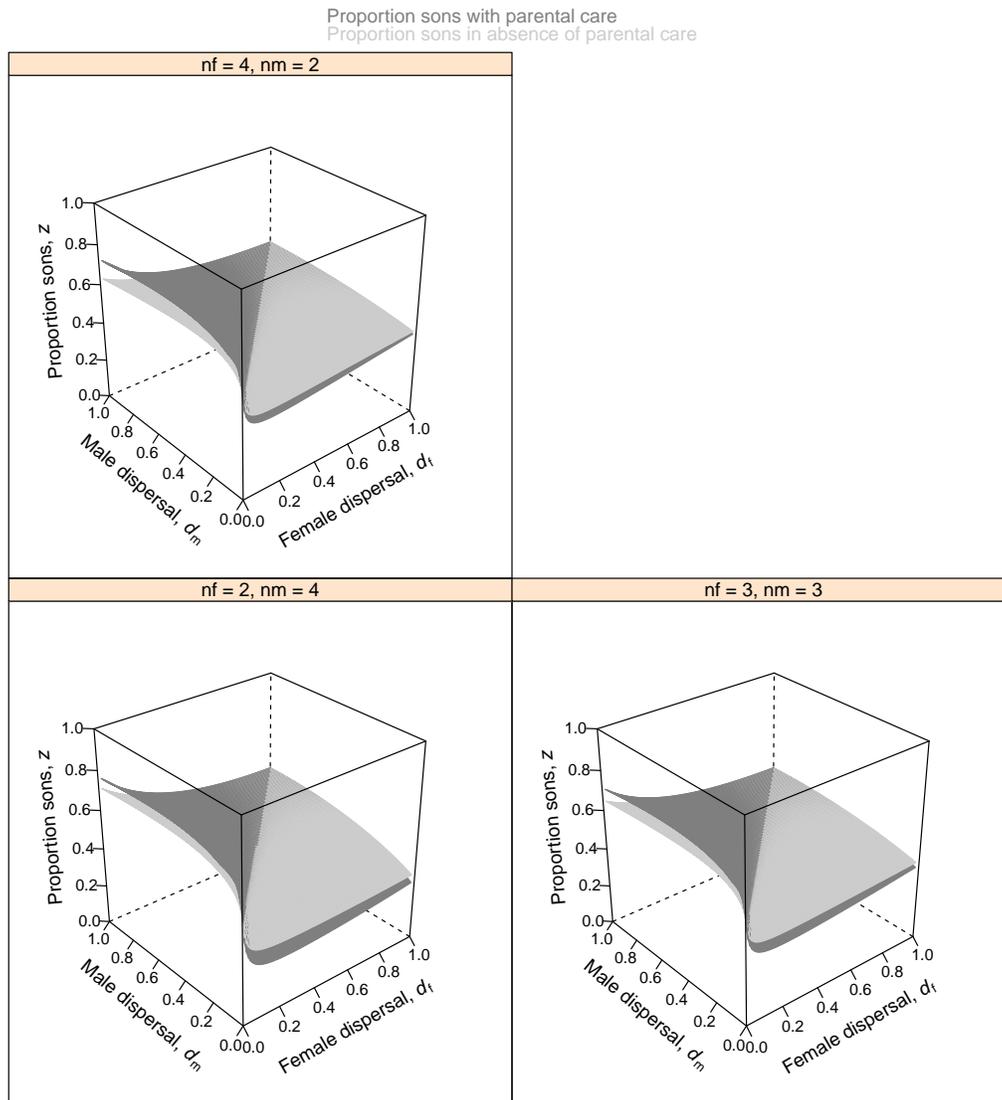


Figure S5: A comparison of the proportion sons z^* produced in the current model (dark grey) versus a model without parental care (Frank, 1986; Wild and Taylor, 2004; Pen, 2006) (light grey). Parameters: $k_m = k_f = 0.1$ when parental care is present and $k_m = k_f = 1.0$ when parental care is absent.