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When boys want to be girls: effects of mating system and dispersal on parent–offspring sex ratio conflict

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ABSTRACT

Question: How is parent–offspring conflict over the sex ratio affected by mating system and sex-specific dispersal?

Methods: Inclusive fitness maximization models and dynamic simulations.

Life cycle: Patch-structured diploid population, fixed number of adult females per patch, sex-specific dispersal of offspring, mating after dispersal, competition for breeding sites. The mating system is monogamous, polygynous or polyandrous.

Results: In geographically structured populations, offspring can prefer a sex ratio more biased than that preferred by parents if the mating system is polygynous and dispersal is female-biased. This can be understood from an inclusive fitness perspective: offspring have to balance the benefits of belonging to the minority sex – which enjoys a higher reproductive success than the majority sex – with the cost of increased competition between relatives. Simulations confirm these results and show that mating system and dispersal regime can determine the invasion prospects of feminizing or masculinizing genes, and hence may be important for the evolution of sex-determining systems.

Keywords: inbreeding, inclusive fitness, kin selection, monogamy, parent–offspring conflict, polyandry, polygyny, sex allocation, sex determination, sex-specific dispersal.

INTRODUCTION

Trivers (1974) was the first to note that there may be a conflict of interest between parents and their offspring regarding parental allocation of resources to the offspring. Parental genes are selected to maximize the parents' inclusive fitness, while genes acting in the offspring are selected to maximize the offspring's inclusive fitness. Due to relatedness asymmetries between parents and offspring, these selection pressures may act in opposite directions. The most obvious parent–offspring conflict concerns the amount of resources provided by the parents to the offspring. From an inclusive fitness point of view, it is easy to see why

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parental genes are selected to provide fewer resources than the offspring's genes are attempting to extract: parents are more closely related to themselves than to their offspring, and vice versa.

Trivers also pointed out a more subtle parent–offspring conflict over sex allocation. If one sex is more costly to rear than the other, then parental genes will be selected to ultimately achieve equal parental investment in sons and daughters (Fisher, 1930). In this equilibrium, an excess of the 'cheap' sex will be produced, and as a result members of the 'expensive' minority sex will enjoy a higher average reproductive success than their cheap counterparts. In other words, some offspring get lucky and others do not, but for the parents the loss of one offspring is exactly compensated by the gain of other offspring who are equally related to the parents. However, an offspring is more closely related to itself than to its siblings and parents, hence an offspring would prefer to have a greater share of the benefits and shift the costs to others. Genes acting in offspring will therefore be selected to increase the odds of residing in the minority sex, even if doing so harms the inclusive fitness of their siblings and parents. As Trivers (1974) showed with an inclusive fitness model, the 'optimal' sex ratio under offspring control is still biased towards the cheaper sex, but less so than under parental control.

Cost differences between sons and daughters are not the only ultimate cause of biased sex ratios. Hamilton (1967) showed that in geographically structured populations, biased sex ratios can be a way to reduce competition between related individuals. Local competition between brothers over mating opportunities induces selection for female-biased sex ratios, whereas competition between sisters over breeding opportunities induces selection for male-biased sex ratios (Clark, 1978; Frank, 1986). On balance, the sex ratio tends to be biased towards the sex least likely to compete with relatives (Wild and Taylor, 2004). Just like in the sex-specific rearing cost-scenario of Trivers, selection in geographical populations also gives rise to parent–offspring conflict over the sex ratio. Werren and Hatcher (2000) studied a model of a patch-structured diploid population where offspring mate at random in their natal patch, after which mated females disperse to other patches to produce the next generation. Just like Trivers, they found that offspring prefer a sex ratio which is less biased than that preferred by the parents.

These results suggest that there may be a general rule which states that offspring always prefer a sex ratio that is less biased than that preferred by the parents, simply because the minority sex has a reproductive advantage over the majority sex, which can be exploited by genes acting in the offspring. However, it turns out that such an attractively simple universal principle does not hold. Instead, I show here that offspring sometimes prefer a sex ratio that is more biased than that preferred by the parents. I explore a number of kin selection models of patch-structured populations with sex-specific dispersal occurring before mating. A crucial ingredient of the models is that mating systems can vary between monogamy, polygyny and polyandry. In the case of polygynous populations with female-biased dispersal, the relatively high relatedness between offspring that share the same father but that were born to different mothers causes the offspring to prefer a more biased sex ratio than the mothers, who have a relatively low relatedness to offspring born to other mothers in the same patch.

Genetic conflicts are thought to be of major importance for the evolution of sex-determining mechanisms (Hurst *et al.*, 1996; Werren and Beukeboom, 1998; Beukeboom *et al.*, 2001). In particular, it has been postulated that co-evolution of parental genes and offspring genes, fuelled by sex ratio conflict, might underlie the apparently rapid evolution of sex-determining mechanisms and transitions between them (Werren and Beukeboom, 1998; Werren and Hatcher, 2000; Werren *et al.*, 2002). I use individual-based simulations to show that this co-evolution can be affected by the mating system and dispersal regime of the parents.

THE MODELS

Life cycle and mating system

The population is subdivided into infinitely many identical patches, each containing N breeding females that die after reproduction. A proportion d_f of female offspring and d_m of male offspring disperse to random patches (island model), while the rest remain in their natal patch. Mating occurs after dispersal. Females compete for the N breeding slots, either before or after mating, and the cycle is complete.

I consider three basic mating systems:

1. *Monogamy*: each female has a single mate; different females have different mates.
2. *Polygyny*: a single male monopolizes all females in a patch.
3. *Polyandry*: each female has multiple mates.

For polyandrous mating systems, I assume that each offspring has a different father. This simplifies some calculations (see Appendix). Eva Kisdi pointed out to me that there cannot be enough males to accomplish this, but if a female mates with a large number of males and she has many offspring compared with N, then two random surviving offspring are quite unlikely to have the same father.

The kin selection model

I use the direct fitness approach (Taylor and Frank, 1996) to obtain equilibrium conditions for the sex ratio under maternal or offspring control. The same results can be obtained using a ‘classical’ inclusive fitness approach (e.g. Wild and Taylor, 2004). The inclusive fitness approach has the advantage that a careful biological accounting is made of all inclusive fitness effects of a change in the phenotypic trait under study. However, it can be quite difficult to identify from scratch all such effects and one therefore easily overlooks important biological consequences. The direct fitness approach yields all the inclusive fitness effects ‘automatically’ without obscuring their biological interpretation.

A single gene locus is assumed to affect the sex ratio. If the gene is active in a mother, it determines the sex ratio among her offspring; if the gene is active in an offspring, it determines the probability that the offspring develops into a male or a female. Let x denote the sex ratio (proportion sons) of a focal female or the probability that a focal offspring develops into a male. Let $\bar{x}$ be the corresponding patch average and $\hat{x}$ the population average. The expected number of competitors of a female who remains in her natal patch is given by $(1 - d_f)(1 - \bar{x}) + d_f(1 - \hat{x})$, and the expected number of competitors of a dispersing female by $(1 - d_f)(1 - \hat{x}) + d_f(1 - \hat{x}) = 1 - \hat{x}$. The relative fitness via the ‘female pathway’ of a focal individual with ‘behaviour’ x is therefore given by

$$W_f = (1 - x)\left[\frac{1 - d_f}{(1 - d_f)(1 - \bar{x}) + d_f(1 - \hat{x})} + \frac{d_f}{1 - \hat{x}}\right] \tag{1}$$

Similar reasoning leads to the relative fitness via the 'male pathway':

$$W_{\mathrm{m}} = x\left[\frac{1-d_{\mathrm{m}}}{(1-d_{\mathrm{m}})\bar{x}+d_{\mathrm{m}}\hat{x}}+\frac{d_{\mathrm{m}}}{\hat{x}}\right] \tag{2}$$

The inclusive fitness effect ΔW of a small change in behaviour x can now be calculated as (Taylor and Frank, 1996):

$$\Delta W = r\left[\frac{\partial W_{\mathrm{f}}}{\partial x}+\frac{\partial W_{\mathrm{m}}}{\partial x}\right]+R\left[\frac{\partial W_{\mathrm{f}}}{\partial \bar{x}}+\frac{\partial W_{\mathrm{m}}}{\partial \bar{x}}\right] \tag{3}$$

The parameters r and R are coefficients of relatedness, the interpretation of which depends on the party in control of the sex ratio. By giving the mother control, r refers to her relatedness to her own offspring, and R her relatedness to a random offspring born in the same patch. By giving control to the offspring, $r = 1$ is the offspring's relatedness to itself, and R its relatedness to a random patch-offspring.

The equilibrium sex ratio x^* is obtained by evaluating the right-hand side of (3) in $x = \bar{x} = \hat{x} = x^*$, setting that to zero and solving for x^*. The result is:

$$\frac{x^*}{1-x^*} = \frac{r-h_{\mathrm{m}}^2 R}{r-h_{\mathrm{f}}^2 R} \tag{4}$$

The $h_i = 1 - d_i$ are the probabilities that sex-i individuals ($i = \mathrm{m}, \mathrm{f}$) are native to the patch (h as in 'home'). Clearly, the equilibrium sex ratio is biased towards the sex with the lowest h-value. Another way of saying this is that the sex ratio is biased towards the sex least likely to compete with relatives, since the model assumes that dispersing individuals never encounter relatives. Frank (1986) and Wild and Taylor (2004) found a sex ratio formula equivalent to (4) by slightly different means.

The crucial part of the model is to let the relatedness coefficients r and R vary according to mating system and the party in control of the sex ratio. In the Appendix, I show how equilibrium values of the relatedness coefficients are obtained from population genetic recursion equations that reflect the assumptions about control and mating system. These equilibrium coefficients are then plugged in (4) to arrive at the equilibrium sex ratios.

I did not check mathematically for stability of the equilibria, but the individual-based simulations described below strongly suggest that all equilibria are indeed stable endpoints of the evolutionary dynamics.

Individual-based simulations

I simulated a population of 1000 patches containing individual males and females. Each individual carried two 'alleles' that took values between 0 and 1. The average value of the alleles determined the proportion of sons in the case of maternal control and the probability of developing as a male in the case of offspring control. In each generation, every allele had a 2% probability of 'mutating' by adding to its value a random number drawn from a normal distribution with mean of zero and standard deviation of 0.005. At the start of each simulation, every allele was set at a value of 0.5. The C++ code is available upon request.

In addition to simulating the evolution of the sex ratio gene under maternal or offspring control separately, I also simulated co-evolution of maternal genes and offspring genes.

Specifically, I followed the scenario of Werren and Hatcher (2000), who investigated analytically/numerically whether a population in maternal sex ratio equilibrium can be invaded by rare genes that have a tendency to turn an offspring into a male or female regardless of the maternal sex ratio genes. An analytic approach has certain advantages of course, but the simulations allowed me to look beyond initial invasion prospects and check whether feminizing or masculinizing genes can go to fixation and how this affects the ultimate sex ratio.

In the co-evolutionary simulations, every individual has two unlinked loci – one maternal sex ratio locus and one 'sex-determining' (SD) locus. Every individual is either homozygous 0/0 for a neutral 'null-allele' at the SD locus, or heterozygous $0/z$ or homozygous z/z. The latter two genotypes have the same phenotypic effect due to dominance. In every simulation only a single value of z is used – that is, the SD locus does not mutate. The SD locus can be a 'feminizing' locus, in which case the value of z determines the probability that the individual becomes female, or it is a 'masculinizing' locus that determines the probability that the individual becomes a male. The maternal sex ratio locus can affect the offspring sex ratio, but the SD locus can 'override' the maternal locus. An example will clarify this. Suppose an individual offspring has one or two z-alleles with a value of 0.6 at a masculinizing SD locus and its mother has sex ratio genes coding for a 0.4 sex ratio. Two random numbers u_1 and u_2 are drawn from the unit interval. If $u_1 < 0.6$, the offspring becomes male; if $u_1 \geq 0.6$, then u_2 is compared with 0.4 to determine whether the offspring becomes male ($u_2 < 0.4$) or female ($u_2 \geq 0.4$).

RESULTS

Analytical results

Table 1 and Fig. 1 show examples of equilibrium sex ratios under maternal control and offspring control for varying dispersal regimes and mating systems. In the examples, one sex

Table 1. Equilibrium sex ratios (proportion sons) under maternal or offspring control for different mating systems and dispersal scenarios (one sex complete dispersal, the other sex zero dispersal), expressed in terms of the number of breeding females (N) per patch

Dispersal	Control	Monogamy	Polygyny	Polyandry
♀ dispersal	Mother	$\frac{N-1}{2N-1}$	$\frac{N-1}{2N-1}$	$\frac{N-1}{2N-1}$
	Offspring	$\frac{3N-1}{6N}$	$\frac{3N-1}{7N-1}$	$\frac{3N-1}{6N-1}$
♂ dispersal	Mother	$\frac{N(3N+1)}{6N^2-3N+1}$	$\frac{3N+1}{5N-1}$	$\frac{3N+1}{6N-2}$
	Offspring	$\frac{3N+1}{6N}$	$\frac{3N+1}{5N+1}$	$\frac{3N+1}{6N+1}$

Note: The graphs of these formulas are plotted in Fig. 1.

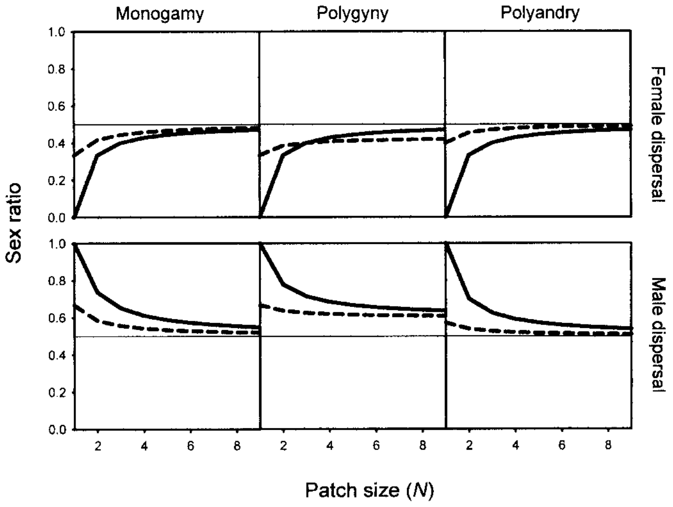

Fig. 1. Equilibrium sex ratios (proportion sons) under maternal control (solid lines) or offspring control (dashed lines) for different mating systems and dispersal scenarios, expressed in terms of the number of breeding females (N) per patch. Note that sex ratios under offspring control are less biased than those under maternal control, except when dispersal is female-biased and mating is polygynous.

has complete dispersal, the other sex no dispersal. As a result, there is absolutely no inbreeding. As expected, sex ratios are always biased towards the dispersing sex. The striking result is that in polygynous populations with female dispersal, offspring prefer a sex ratio more biased than the mother. In all other cases, the offspring prefer a less biased sex ratio.

The formulas in Table 1 for the case of maternal control and monogamy were also found by Frank (1986), who assumed haploid genetics. Interestingly, the formula $(N-1)/(2N-1)$ for the case of female dispersal and maternal control was also obtained by Werren and Hatcher (2000), but they assumed offspring control of the sex ratio and mating before instead of after dispersal.

In three cases of polygyny (Table 1), the sex ratio does not go to 1/2 as N goes to infinity. This is because a single male fathers all offspring in a patch and relatedness between individuals controlling the sex ratio does not go to zero as N grows without bound.

Simulation results

The simulations confirm the results of the analytical model quite closely (Fig. 2), suggesting that all equilibria are stable endpoints of evolution. Whenever female-biased sex ratios are selectively favoured, feminizing factors can invade and go to fixation when offspring prefer a more female-biased sex ratio than the mother (Fig. 3) and masculinizing factors can invade and go to fixation when offspring prefer a less female-biased sex ratio than the mother (Fig. 4). When male-biased sex ratios are selectively favoured, offspring always prefer a less male-biased sex ratio than the mother (Fig. 1) and feminizing factors but not masculinizing factors can invade. Completely feminizing or masculinizing factors ($z = 1$) can never invade; a similar result was found by Werren and Hatcher (2000). It is interesting to note that in all

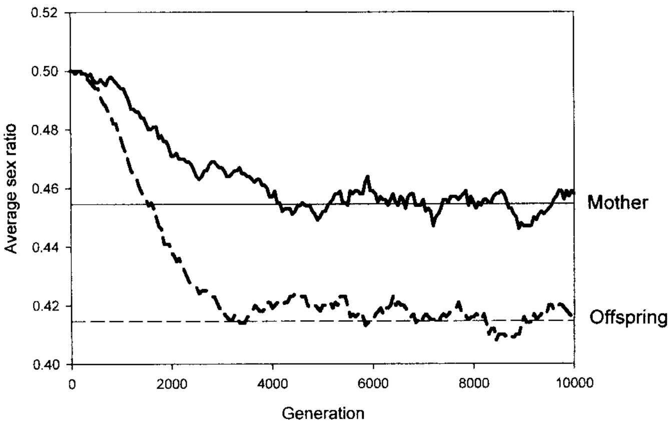

Fig. 2. Typical examples of individual-based simulations. The mating system is polygynous, females disperse and there are six females per patch. The bold lines are the evolving average sex ratios as they evolve under maternal control (solid line) and offspring control (dashed line). The thin lines are the corresponding equilibrium sex ratios predicted by the kin selection model (from Table 1). Note that the sex ratio under offspring control evolves towards a greater bias.

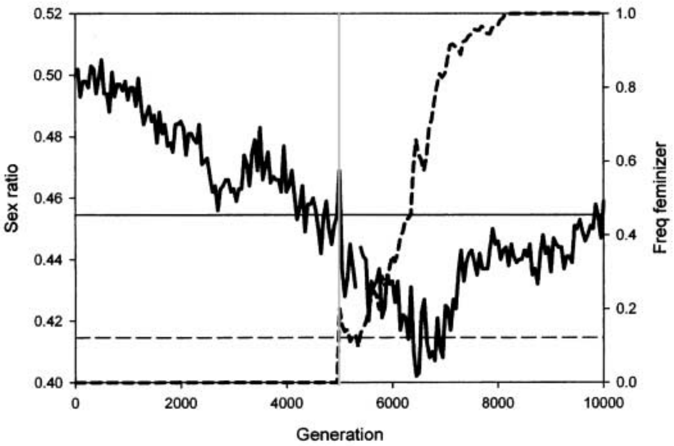

Fig. 3. A feminizing gene invades and goes to fixation in a polygynous population with maternal sex ratio control (same scenario as in Fig. 2). The sex ratio (bold solid line) first evolves towards the maternal optimum (thin solid line). After 5000 generations, a dominant feminizing gene (30% female; bold dashed line) is introduced and the sex ratio temporarily fluctuates around the offspring optimum (thin dashed line). When the feminizing gene fixates, the sex ratio returns to the maternal optimum.

cases evolution ends up at the maternal optimum, even though the offspring genes can override the maternal genes in a sense. As long as the feminizing or masculinizing genes are sufficiently rare, the sex ratio evolves temporarily towards the offspring optimum, but as soon as they reach sufficiently high frequencies, the sex ratio evolves back to the maternal optimum. This return to the maternal optimum can only happen when z is sufficiently small. For example, if a masculinizing gene z is fixed, then a maternal gene y can achieve any

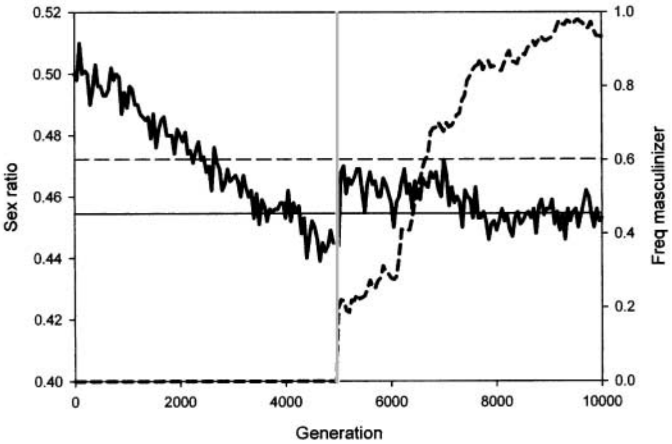

Fig. 4. A masculinizing gene invades and goes towards fixation in a monogamous population with maternal sex ratio control (except for the mating system, same scenario as Figs. 2 and 3). The sex ratio (bold solid line) first evolves towards the maternal optimum (thin solid line). After 5000 generations, a dominant masculinizing gene (10% male; bold dashed line) is introduced and the sex ratio evolves closer to the offspring optimum (thin dashed line). When the masculinizing gene reaches a high frequency, the sex ratio returns to the maternal optimum.

proportion of sons x such that $y + (1 - y)z = x$, which is bounded by z and 1. Therefore, a maternal optimum below z is not feasible.

DISCUSSION

The main result of this study is that in geographically structured diploid populations, offspring sometimes prefer more biased sex ratios than parents. This result should not be confused with the well-known result that in haplodiploid social insects, workers usually prefer a more biased sex ratio among their siblings than preferred by their mother, the queen (Trivers and Hare, 1976). In my model, the offspring are in a position to determine their own sex, whereas in the social insect scenario the workers do not determine their own sex but rather control the sex ratio of a subset of their siblings, namely those that are targeted for reproduction. Both types of conflict arise from relatedness asymmetries between different carriers of genes that control the sex ratio. In the case of social insects, the workers are more closely related to their sisters than to their brothers, whereas the queen is equally related to sons and daughters. In the model presented here, offspring and parent may differ in their relatedness to the individual males and females whose intensity of local competition is affected by the sex ratio. For certain mating systems (polygyny) and dispersal regimes (female dispersal), offspring are more closely related than their mother to those affected by local competition, and in that case they may prefer a more strongly biased sex ratio in order to reduce the intensity of competition between relatives. This effect of reducing competition between relatives has to be balanced against the benefit of being a member of the minority sex, the mechanism that explains why offspring prefer a less biased sex ratio in well-mixed populations (Trivers, 1974; Werren *et al.*, 2002).

Other situations are conceivable in which offspring prefer a more extreme sex ratio than the parents. In the scenario of Trivers' (1974) original paper, mothers are assumed to raise the offspring and pay the sex-specific rearing costs. If the father contributes nothing but sperm, then under the simplest of assumptions (autosomal genes, no long-term pair bond, etc.) paternal genes will be selected to produce a 50 : 50 sex ratio regardless of the cost difference between sons and daughters, in which case offspring prefer a more biased sex ratio than the father.

It is difficult to test directly whether empirical sex ratios in diploid organisms conform more closely to the maternal optima rather than the offspring's optima, or vice versa, since the different optima are often quite close to each other (see Fig. 1). However, the consequences of sex-ratio conflict may vary quite a lot and may be open to empirical investigation. Specifically, I am thinking about the role of sex-ratio conflict in the evolution of sex-determining mechanisms (Werren and Beukeboom, 1998). It has been shown before (Werren and Hatcher, 2000; Werren *et al.*, 2002) that whether masculinizing or feminizing factors can invade in a population can be decided by sex ratio conflict. In particular, Werren and Hatcher (2000) showed that in geographically structured populations with selection for female-biased sex ratios, offspring prefer a less female-biased sex ratio than the mother, thus paving the way for the invasion of zygotic masculinizing factors. My simulations go a step further and show that such factors can actually go to fixation and that the ultimate sex ratio returns to the maternal optimum (see Figs. 3 and 4). This is a bit surprising, since the offspring's genes are assumed to override the maternal sex ratio genes. A similar 'paradox' was found by Pen and Taylor (2005), who showed that in the worker–queen sex ratio conflict, the queen may 'win', even though the workers have the ability to observe the queen's actions and are in a position to adjust sex allocation afterwards. In contrast, Werren *et al.* (2002) found that in well-mixed diploid populations with sex-specific rearing costs, after invasion of feminizing or masculinizing genes, an ultimate sex ratio of 50 : 50 is established, which is neither the maternal optimum nor the offspring's optimum. The reason appears to be that in well-mixed populations, completely masculinizing or feminizing genes can invade and result in a population with a heterogametic sex-determining system. In geographically structured populations, such as in my simulations and the model of Werren and Hatcher (2000), only partially feminizing or masculinizing genes can invade. Presumably, this is because fully masculinizing or feminizing genes have a relatively large effect on the patch sex ratio when patches are sufficiently small. Apparently, geographic population structure *per se* can have important effects on the evolutionary dynamics of sex-determining systems.

The simplest testable prediction from my model is that in species with female dispersal, feminizing factors are more likely to invade in polygynous species than in species with other mating systems. In species with male dispersal, no such correlation is expected. One way to test this prediction is by means of a comparative analysis, superimposing evolutionary trees of dispersal behaviour and mating systems on top of a tree of sex-determining mechanisms (such as in Kraak and Pen, 2002; Janzen and Krenz, 2004). Alternatively, this prediction could be tested by means of experimental evolution. One could set up laboratory populations of an appropriate organism with a known variety of maternal control and offspring control genes, such as the housefly (Dübendorfer *et al.*, 2002), impose different dispersal regimes and mating systems, and see what happens.

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APPENDIX: CALCULATION OF RELATEDNESS COEFFICIENTS

The relatedness coefficients in the equilibrium sex ratio formula can be expressed in terms of a single coefficient of relatedness r_{xy} between two random offspring x and y born in the same patch. This coefficient can be defined as

$$r_{xy} = \frac{g_{xy}}{g_{xx}} \tag{A1}$$

Here g_{xy} is the coefficient of consanguinity (CC) between x and y (Michod and Hamilton, 1980; Taylor, 1996), the probability that two random alleles drawn with replacement from x and y are identical by descent. These CCs can be calculated with population genetic recursion equations, which I set up at the end of this Appendix.

In the case of offspring control, $r = 1$ and $R = r_{xy}$ and we are done. In the case of maternal control, the relatedness r between a mother and her own offspring can be written as

$$r = \frac{1}{2} + \frac{1}{2} h_{\mathrm{f}} h_{\mathrm{m}} r_{xy} \tag{A2}$$

Here $h_i = 1 - d_i$ is the probability that a sex-i individual is native to the patch. The relatedness R between a mother and a random native offspring can be written as

$$R = \frac{1}{N} r + \frac{N-1}{2N} (h_{\mathrm{f}}^2 + h_{\mathrm{f}} h_{\mathrm{m}}) r_{xy} \tag{A3}$$

Let α be the probability that two random offspring are full sibs, β the probability that two random offspring are half-sibs that have the same mother, and γ the probability that two random offspring are half-sibs that have the same father. Different mating systems can be modelled by varying α, β and γ. A fully monogamous mating system corresponds to the parameter values $\alpha = 1/N$, $\beta = 0$, $\gamma = 0$; a polygynous mating system with a single male per patch corresponds to the parameter values $\alpha = 1/N$, $\beta = 0$, $\gamma = 1 - 1/N$; a polyandrous mating system, where each offspring has a different father, has $\alpha = 0$, $\beta = 1/N$, $\gamma = 0$. These three sets of parameter values were used to generate the examples in Fig. 1.

The CCs obey the recursions

$$\begin{aligned} g'_{xx} &= \frac{1}{2} + \frac{1}{2} h_{\mathrm{f}} h_{\mathrm{m}} g_{xy} \\ g'_{xy} &= \frac{\alpha}{2} (g_{xx} + h_{\mathrm{f}} h_{\mathrm{m}} g_{xy}) \\ &\quad + \frac{\beta}{4} (g_{xx} + h_{\mathrm{m}}^2 g_{xy} + 2 h_{\mathrm{f}} h_{\mathrm{m}} g_{xy}) \\ &\quad + \frac{\gamma}{4} (g_{xx} + h_{\mathrm{f}}^2 g_{xy} + 2 h_{\mathrm{f}} h_{\mathrm{m}} g_{xy}) \\ &\quad + \frac{\delta}{4} (h_{\mathrm{f}} + h_{\mathrm{m}})^2 g_{xy} \end{aligned} \tag{A4}$$

where $\delta = 1 - \alpha - \beta - \gamma$. It turns out that the equilibrium value of g_{xy} computes as

$$\hat{g}_{xy} = \frac{2\alpha + \beta + \gamma}{8 - (2\alpha + \beta + \gamma) h_{\mathrm{f}} h_{\mathrm{m}} + 2(\alpha + \beta) h_{\mathrm{f}}^2 + 2(\alpha + \gamma) h_{\mathrm{m}}^2 - 2(h_{\mathrm{f}} + h_{\mathrm{m}})^2} \tag{A5}$$

This is plugged into (A1)–(A3) to obtain equilibrium values of the relatedness coefficients, which in turn are plugged into (4) to obtain the equilibrium sex ratios.