

**A kin-selection approach to the resolution of sex-ratio conflict
between mates**

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Abstract.— We investigate an instance of conflict between mates over the sex ratio of their brood. We construct a kin-selection model for the evolution of the sex ratio assuming local resource competition (LRC) among females. We explore two basic scenarios: (a) the case where parents contribute to the brood sex ratio in an additive fashion (the additive effects model); and (b) the case where parental contributions are multiplicative (the multiplicative effects model). In the additive effects model, resolution of the conflict between mates depends on the extent to which relative paternal contribution influences the brood sex ratio. Our multiplicative effects model is mechanistic. Males determine primary sex-ratio through fertilization bias; then females modify the male's sex-ratio decision by adjusting the level of investment of some resource that contributes to offspring survival. Under multiplicative effects, a compromise is always achieved; however this compromise favours one perspective or the other, depending on the extent to which maternal investment influences offspring survival.

Keywords: Conflict; Direct fitness; Kin selection; Sex ratio; LRC

1 Introduction

Fisher (1930) argued that parents who bias their production of offspring toward the rarer sex enjoy a selective advantage. This frequency-dependent advantage means that, on average, parents should invest equally in sons and daughters, producing brood sex-ratios that are unbiased.

It has long been known that Fisher's argument for the evolution of unbiased sex ratios relies on a few tacit assumptions (Hamilton, 1967). In particular, Fisher assumed that competition for the resources necessary for reproduction does not occur among same-sex relatives. When this assumption is violated we say there exists *local competition for reproductive resources* (LCRR); and in this case some form of sex-ratio bias is often advantageous. For example, selection favours female-biased sex ratios when related males compete with one another for mates (called *local mate competition*, LMC; Hamilton, 1967; Taylor and Bulmer, 1980); whereas selection favours male-biased sex ratios when related females compete with one another for nesting sites (called *local resource competition*, LRC; Clark, 1978; Silk, 1984; Taylor, 1994). In general, sex-ratio bias under LCRR favours the sex that is less likely to engage in local competition, i.e. the 'less competitive sex' (Wild and Taylor, 2004).

Sex-ratio evolution under LCRR is easily understood using the related notions of kin selection and inclusive fitness (Hamilton, 1964). From a parent's perspective, over-production of the less competitive sex provides a net benefit to relatives (e.g. sons/daughters, nieces/nephews). In other words, sex-ratio bias toward the less competitive sex will add to an individual's inclusive fitness, and

so is favoured by kin-selection.

The extent of sex-ratio bias under LCRR will depend on the level of relatedness between a parent and its social group; and sometimes, the level of relatedness is different between members of a mated pair. In these cases, the optimal level of sex-ratio bias depends on which parental perspective (mom or dad) is considered; and we say that parents are in *conflict* over the sex ratio.

Sex-ratio conflict between mates, at least for LMC models, has been discussed extensively in the literature (see Courteau and Lessard, 2000, and references therein). Still, the manner by which such conflicts come to be resolved remains to be seen. Using a simple model of LRC, Lessells (1998) has argued that the end result of these sex-ratio conflicts must be investment in only one sex of offspring by one mate, with compensatory investment in offspring of the opposite sex by its partner. Lessells' model, however, falls short of a careful inclusive fitness account of the problem.

In this paper we investigate the sex-ratio conflict that exists between mates under LRC. We choose LRC models of sex-ratio evolution because they involve an outbreeding population. Relative to other LMC models, then, LRC models appear straightforward. We adopt the *direct fitness approach* to constructing kin-selection models, introduced by Taylor and Frank (1996). This approach approximates the evolutionary dynamics described by the famous Price equation (Price, 1970), under the assumption that selection is weak (Taylor, 1988).

Our main findings describe the resolution of sex-ratio conflict (a) when parents make additive contributions to brood sex-ratios (the additive effects

model); and (b) when parental contributions to brood sex-ratios are multiplicative (the multiplicative effects model). Under the additive effects model, resolution of the conflict depends on the extent to which relative paternal contribution influences the brood sex ratio. Under the multiplicative effects model, a compromise is always achieved, and this compromise favours one perspective or the other, depending on the extent to which parental investment influence offspring survival. The contrast between additive effects and multiplicative effects models highlights the importance of accounting for the biological details of conflict resolution in a theoretical setting.

2 Models

2.1 A framework

Our main interest is the co-evolution of two *sex-ratio behaviours* (phenotypes). The proportion of paternal investment made in sons, we call the *paternal sex-ratio behaviour*. Similarly, the proportion of maternal investment made in sons, we call the *maternal sex-ratio behaviour*.

We consider a diploid organism, and we suppose that sex-ratio behaviours are separate quantitative traits—controlled by separate autosomal loci. We will assume that both males and females possess the genetic information coding for both paternal and maternal sex-ratio behaviour. Later, we assume that this information is silent in one sex or the other. In addition, our phenotypic approach to the problem will assume that the genetic covariance between

paternal and maternal sex-ratio behaviours is zero.

We assume an infinite population undergoing discrete, non-overlapping generations. We assume further that the population is divided into many patches of finite size, with each patch able to support N mated pairs. In order to set up the direct fitness argument presented in a later section, the model will be described with reference to one particular offspring (male or female, chosen at random). We call this offspring the *focal offspring*.

We will need the following notation:

- x_m , the paternal sex-ratio behaviour exhibited by the father of the focal offspring;
- x_f , the maternal sex-ratio behaviour exhibited by the mother of the focal offspring;
- y_m , the average paternal sex-ratio behaviour exhibited on the focal offspring's natal patch (i.e. the *focal patch*);
- y_f , the average maternal sex-ratio behaviour exhibited on the *focal patch*;
- z_m , the *resident* paternal sex-ratio behaviour;
- z_f , the *resident* maternal sex-ratio behaviour.

Our approach is rooted in game theory. We will allow x_m and x_f – and so y_m and y_f also – to describe deviant or ‘mutant’ behaviour. However, we assume that mutants are rare, and that the population is otherwise fixed at the resident behaviours z_m and z_f .

We explore three separate cases, each defined by who controls the parental

sex-ratio behaviours. In the first case, a father controls both his behaviour and that of his mate (i.e. paternal control of the sex ratio). In the second case, a mother controls both her behaviour and that of her mate (i.e. maternal control of the sex ratio). The final case assumes that a father controls paternal sex-ratio behaviour, and that a mother controls maternal sex-ratio behaviour. Conflict occurs in this last case only.

2.2 *Life cycle*

The hypothetical life cycle is outlined below. All notation we introduce can be found in Table 1.

(a) *Parental investment period.*— Our first model assumes that the realized sex ratio of a brood is determined by parental sex-ratio behaviours in an additive fashion. This model corresponds to a situation in which both parents provide the same type of parental investment; e.g. both parents provide nutrients to ensure the survival of a developing zygote.

We begin by assuming that each mated pair produces K sons and K daughters, where K is large, and parental sex-ratio behaviours contribute to the viability of offspring. If the focal offspring is male, we express his viability (or the viability of any of his brothers) as

$$\text{Add. effects: } M(x_m, x_f) = a x_m + (1 - a) x_f \quad (1)$$

where $0 \leq a \leq 1$. The viability of a focal female offspring, we express as

$$\text{Add. effects: } F(x_m, x_f) = a(1 - x_m) + (1 - a)(1 - x_f). \quad (2)$$

Note that $M(x_m, x_f)$ and $F(x_m, x_f)$ describe the proportions of viable brood that are male and female, respectively. We can interpret the products KM and KF , with arguments suppressed, as numbers of sons and daughters, respectively. This interpretation holds throughout the paper.

Our second model assumes that the brood sex-ratio is determined by parental sex ratio behaviour in a multiplicative fashion. Now, each mated pair produces K offspring, and paternal sex-ratio behaviour determines the primary sex ratio of the brood (e.g. which oocytes are fertilized X sperm, and which are fertilized with Y sperm), so that there are Kx_m sons and $K(1 - x_m)$ daughters born to a pair. Maternal sex-ratio behaviour, by contrast, is assumed to determine the survival of offspring. We suppose a mother has a fixed amount of parental resource, T to offer to her offspring. We then interpret maternal sex-ratio behaviour as the proportion of the maternal resource given to sons.

Now, suppose that each unit of maternal resource given to an offspring (son or daughter) reduces the probability of its mortality by a proportion p . It follows that an offspring given u units of maternal resource survives with probability, $1 - (1 - p)^u$. If the focal offspring is male, he expects Tx_f/Kx_m units of maternal resource, and we express his survival as

$$s(x_f/x_m) = 1 - (1 - p)^{Tx_f/Kx_m} = 1 - \exp(-bx_f/x_m) \quad (3)$$

where $b = \ln\{(1 - p)^{-1}\}(T/K) > 0$ is a constant. Similarly, if the focal offspring

is female, her survival is given by $s((1 - x_f)/(1 - x_m))$. It follows that

$$\text{Mult. effects: } M(x_m, x_f) = x_m s(x_f/x_m), \quad (4)$$

gives the realized male proportion of the brood, and

$$\text{Mult. effects: } F(x_m, x_f) = (1 - x_m) s((1 - x_f)/(1 - x_m)) \quad (5)$$

gives the realized female proportion of the brood. Note that, unlike the case of additive effects, $M + F$ under multiplicative effects does not equal one.

(b) *Dispersal*.—All male offspring disperse, but female offspring remain on their natal patch. We assume that males arrive safely on a new patch, where they encounter no relatives. We assume further that each patch receives an equal share of the dispersing males.

(c) *Mating*.—We assume that each female is mated exactly once, but that males compete at random on each patch for access to females. When mating takes place on the focal patch, we find $NKM(z_m, z_f)$ males competing for access to $NKF(y_m, y_f)$ females. It follows that each male expects

$$\# \text{ females}/\# \text{ males} = F(y_m, y_f)/M(z_m, z_f) \quad (6)$$

matings.

(d) *LRC*.—A total of $NKF(y_m, y_f)$ fertilized females compete at random for one of N breeding sites on the focal patch. The probability that a given fertilized female wins a breeding site, then, is given by

$$\# \text{ sites}/\# \text{ females} = 1/KF(y_m, y_f). \quad (7)$$

3 A direct fitness argument

3.1 Recipient fitness

The direct fitness approach begins by assigning different roles to different individuals in the population. Parental sex-ratio behaviour involves some form investment in offspring, and so we cast the focal offspring in the role of ‘recipient,’ i.e. recipient of the parental investment ‘gift.’ Using the same reasoning we cast parents in the role of ‘donor.’

Once roles are assigned, a direct fitness argument proceeds by identifying expressions for recipient fitness. Given that the recipient is female, recipient fitness is given by

$$W_f(x_m, x_f, y_m, y_f, z_m, z_f) = F(x_m, x_f)/F(y_m, y_f); \quad (8)$$

i.e. she survives to mate with probability $F(x_m, x_f)$, is mated once, obtains one of N breeding sites with probability $1/KF(y_m, y_f)$, and has a total of K offspring. When the recipient is male, a similar argument gives

$$W_m(x_m, x_f, y_m, y_f, z_m, z_f) = M(x_m, x_f)/M(z_m, z_f). \quad (9)$$

To calculate an average recipient fitness we must devise a method of weighting W_f and W_m . The correct method weights males and females in proportion to their total reproductive value, respectively (Taylor, 1990; Taylor and Frank, 1996). In our model, the total reproductive value of males equals

that of females, and so expected recipient fitness is

$$(1/2)F(x_m, x_f)/F(y_m, y_f) + (1/2)M(x_m, x_f)/M(z_m, z_f). \quad (10)$$

Readers familiar with the evolutionary theory of sex-ratio behaviour will recognize the previous line as a variation of the *Shaw-Mohler* expression for parental fitness (Shaw and Mohler, 1953; Charnov, 1982).

3.2 *Direct fitness effects*

Let g_m and g_f be the genotypic value of the focal individual (i.e. recipient) at the locus coding for paternal and maternal sex-ratio behaviour, respectively. Direct fitness effects describe the consequences of altering g_m or g_f . The positive genetic covariance that exists between relatives tells us that changes to g_m or g_f in the recipient will also occur in his/her relatives. A direct fitness argument captures this idea by treating x_m and y_m as functions of g_m , and x_f and y_f as functions of g_f . It should be understood, however, that these functional relationships are more properly understood as covariances. The functional notation is simply a device that provides us with the correct approximate of Price's (1970) formula under weak selection.

Supposing the recipient is female, the direct fitness effect of increasing g_m is

$$\text{Add. effects: } \partial W_f / \partial g_m |_{x_m=y_m=z_m, x_f=y_f=z_f} = a(y'_m - x'_m) / F(z_m, z_f) \quad (11)$$

under the additive effects model, and

$$\begin{aligned} \text{Mult. effects: } \partial W_f / \partial g_m |_{x_m=y_m=z_m, x_f=y_f=z_f} &= [(y'_m - x'_m) / F(z_m, z_f)] \\ &\times [s((1 - z_f) / (1 - z_m)) - s'((1 - z_f) / (1 - z_m))(1 - z_f) / (1 - z_m)] \end{aligned} \quad (12)$$

under multiplicative effects. Similarly, supposing the recipient is a male,

$$\text{Add. effects: } \partial W_m / \partial g_m |_{x_m=y_m=z_m, x_f=y_f=z_f} = ax'_m / M(z_m, z_f), \quad (13)$$

and

$$\begin{aligned} \text{Mult. effects: } \partial W_m / \partial g_m |_{x_m=y_m=z_m, x_f=y_f=z_f} &= \\ &[x'_m / M(z_m, z_f)] \times [s(z_f / z_m) - s'(z_f / z_m)z_f / z_m]. \end{aligned} \quad (14)$$

Following Taylor and Frank (1996) we replace x'_m in (11-14) with r , the relatedness between the focal male offspring (the recipient) and his parent—the one that controls x_m . In addition, we replace y'_m in (11-14) with \bar{r} , the relatedness between the recipient and a random parent breeding on the focal patch. We want to emphasize that the genotype of the parents considered by the relatedness coefficients r and \bar{r} is that parent who controls paternal sex ratio behaviour, and is not necessarily the parent who expresses the behaviour (the donor).

The overall direct fitness effect of increasing g_m we denote by, ΔW_{g_m} ; and this is obtained by averaging eqns (11) and (13) (or eqns 12 and 14) using total reproductive values as weights. Under the additive effects model,

$$\text{Add. effects: } \Delta W_{g_m} = (1/2) a(\bar{r} - r) / F(z_m, z_f) + (1/2) ar / M(z_m, z_f); \quad (15)$$

and under the multiplicative effects model

$$\begin{aligned} \text{Mult. effects: } \Delta W_{g_m} = & \\ (1/2)[(\bar{r} - r)/F(z_m, z_f)][s((1 - z_f)/(1 - z_m)) - s'((1 - z_f)/(1 - z_m))(1 - z_f)/(1 - z_m)] & \\ + (1/2)[r/M(z_m, z_f)][s(z_f/z_m) - s'(z_f/z_m)z_f/z_m]. & \quad (16) \end{aligned}$$

We compute the direct fitness effect of increasing g_f , call it ΔW_{g_f} , in a similar fashion:

$$\text{Add. effects: } \Delta W_{g_f} = (1/2)(1 - a)(\bar{r} - r)/F(z_m, z_f) + (1/2)(1 - a)r/M(z_m, z_f), \quad (17)$$

and

$$\begin{aligned} \text{Mult. effects: } \Delta W_{g_f} = & \\ (1/2)s'((1 - z_f)/(1 - z_m))(\bar{r} - r)/F(z_m, z_f) + (1/2)s'(z_f/z_m)r/M(z_m, z_f). & \quad (18) \end{aligned}$$

In Appendix A we demonstrate that $r = 1/2$, and

$$\bar{r} = \begin{cases} 1/2N & \text{between offspring and a random father,} \\ (5N - 1)/2N(3N + 1) & \text{between offspring and a random mother.} \end{cases} \quad (19)$$

Notice that $1/2N \leq (5N - 1)/2N(3N + 1)$ with equality if and only if $N = 1$.

This relatedness asymmetry exists in both the additive effects and multiplicative effects models.

Our analysis will focus on the signs of ΔW_{g_m} and ΔW_{g_f} , respectively. The sign of ΔW_{g_m} determines whether normal sex-ratio behaviour z_m is increasing or decreasing over evolutionary time. When $\Delta W_{g_m} > 0$ normal sex-ratio behaviour

z_m is increasing (i.e. selection favours increasing paternal care given to sons). When $\Delta W_{g_m} < 0$ normal sex-ratio behaviour z_m is decreasing (i.e. selection favours less paternal care given to sons). When $\Delta W_{g_m} = 0$, z_m is not changing over time (i.e. the level of paternal care given to sons does not change). The sign of ΔW_{g_f} determines the evolution of z_f in a similar fashion.

Because the signs of the direct fitness effects, respectively, are central to the analysis, we will often be interested in the *equilibrium condition*

$$\Delta W_{g_m} = 0, \quad \Delta W_{g_f} = 0. \quad (20)$$

We will use z_m^0 , and z_f^0 to denote the solution to system (20).

4 Conflict under additive effects

Let us first determine what sex-ratio each member of a mated pair considers to be optimal. We do this by giving control of both sex-ratio behaviours to one parent only. To give the father control, we set $\bar{r} = 1/2N$ (see 19) in both ΔW_{g_m} and ΔW_{g_f} ; and we identify optimal parental sex-ratio behaviours (from dad's perspective) by solving system (20). Doing so yields an infinite number of solutions, defined by a relation between z_m^0 and z_f^0 . Straightforward algebra tells us that (z_m^0, z_f^0) , satisfies

$$M_{\text{dad}}^* = M(z_m^0, z_f^0) = N/(2N - 1) > 1/2. \quad (21)$$

The optimal proportion of female offspring from dad's perspective is

$F_{\text{dad}}^* = 1 - M_{\text{dad}}^*$. That an infinite number of pairs, (z_m^0, z_f^0) can all be considered

‘optimal’ is not surprising. Selection only requires that sex-ratio behaviours maintain $M(z_m, z_f) = M_{\text{dad}}^*$ —and there are an infinite number of ways to do this.

Now we give control of sex-ratio behaviours to mothers. We set $\bar{r} = (5N - 1)/2N(3N + 1)$ in both ΔW_{g_m} and ΔW_{g_f} . We determine the optimal parental sex-ratio behaviours (from mom’s perspective) by solving (20). Again, we find an infinite number of possibilities for (z_m^0, z_f^0) . In this case, however, a solution (z_m^0, z_f^0) satisfies

$$M_{\text{mom}}^* = M(z_m^0, z_f^0) = N(3N + 1)/[3N(2N - 1) + 1] \geq M_{\text{dad}}^*, \quad (22)$$

with equality if and only if $N = 1$. Again we have $F_{\text{mom}}^* = 1 - M_{\text{mom}}^*$.

Eqns (21) and (22) show that both parents prefer a male-biased sex ratio. However, (22) makes the key observation that, in most cases, dad prefers less male bias than does mom. This establishes the existence of male-female conflict over the sex ratio under the additive effects model. If we adopt interpretation of male-biased sex-ratio behaviour as a form of altruism, we see that females, being more closely related to members of their social group, opt for a more altruistic strategy than males.

Now we allow a father to control paternal sex-ratio behaviour set (set $\bar{r} = 1/2N$ in ΔW_{g_m}), and a mother to control maternal sex-ratio behaviour (set $\bar{r} = (5N - 1)/2N(3N + 1)$ in ΔW_{g_f}). In this case, mates are in conflict over the sex ratio, and we ask: how is this conflict resolved?

Observe that, under the additive effects model, there does not exist a pair of resident sex-ratio behaviours, (z_m^0, z_f^0) for which both ΔW_{g_m} and ΔW_{g_f} are zero.

This follows from the fact that

$$\Delta W_{g_m} = 0 \text{ gives } z_f = -z_m a / (1 - a) + M_{\text{dad}}^* / (1 - a), \quad (23)$$

$$\Delta W_{g_f} = 0 \text{ gives } z_f = -z_m a / (1 - a) + M_{\text{mom}}^* / (1 - a). \quad (24)$$

These are parallel lines when $N \geq 2$, i.e. they do not intersect.

The resolution of the sex-ratio conflict that exists between mates ultimately depends on the relationship between the parameter a – the contribution of paternal sex ratio behaviour to the determination of realized brood sex ratio – and the sex-specific optima, M_{dad}^* and M_{mom}^* themselves.

Consider (23) and (24). As mentioned above, these equations describe parallel lines of negative slope (Fig. 1). Since $M_{\text{dad}}^* \leq M_{\text{mom}}^*$, we can assert that the vertical intercept of (23) will never lie above that of (24) on the z_f -axis. Whenever $N \geq 2$, then, we are able to divide the unit square in the z_m, z_f -plane into three regions:

- (I) $\Delta W_{g_m}, \Delta W_{g_f} > 0$, and so selection favours fathers and mothers that increase allocation to sons;
- (II) $\Delta W_{g_m} < 0$ and $\Delta W_{g_f} > 0$, and so selection favours fathers that reduce their allocation to sons, whereas selection favours mothers that increase their allocation to sons;
- (III) $\Delta W_{g_m}, \Delta W_{g_f} < 0$, and so selection favours fathers and mothers that reduce allocation to sons.

From the way in which Regions I-III are characterized, it is clear that selective pressure will force normal sex-ratio behaviours into Region II, and onto

the boundary of the unit square (Fig. 1). However, the level of behaviour resulting from the long-term action of selection depends entirely on the placement of the vertical intercepts of (23) and (24).

Fig. 1A illustrates the case $M_{\text{mom}}^* \leq 1 - a$. In this case, both nullclines intersect the face $z_m = 0$, and we observe z_m approaches zero, while z_f approaches $M_{\text{mom}}^*/(1 - a)$. It follows that the realized proportion of males in a brood,

$$a z_m + (1 - a) z_f \rightarrow M_{\text{mom}}^*. \quad (25)$$

The conflict is resolved in favour of a mother. Notice that in order for $M_{\text{mom}}^* \leq 1 - a$ to hold, $a < 1/2$.

In Fig. 1B we assume $M_{\text{dad}}^* \leq 1 - a < M_{\text{mom}}^*$, and so we require $a < 1/2$. In this case the nullcline $\Delta W_{g_m} = 0$ intersects the face $z_m = 0$, whereas the nullcline $\Delta W_{g_f} = 0$ intersects $z_f = 1$. Over time, then, z_m approaches zero, z_f approaches one, and the realized proportion of males in a brood approaches $1 - a$. This outcome corresponds to neither sex-specific optimum. Instead, it represents a compromise: greater than M_{dad}^* , but less than M_{mom}^* .

Fig. 1C assumes $M_{\text{dad}}^* > 1 - a$, and so we require $a \geq 1/2$. In this case both nullclines intersect the face $z_f = 1$. Over time we observe that z_m approaches $(M_{\text{dad}}^* - (1 - a))/a$, z_f approaches one, and so

$$a z_m + (1 - a) z_f \rightarrow M_{\text{dad}}^*. \quad (26)$$

The conflict is resolved in favour of the father.

One consistent feature of the additive effects model – found for any a – is that

selection leads one parent to always provide care to offspring of only one sex; while selection leads the other parent to compensate by investing, at least to some degree, in offspring of the opposite sex. However, the latter parent does not always *bias* its sex-ratio toward the sex overlooked by its mate, as suggested elsewhere (see Lessells, 1998, p. 402). To see why, consider the additive effects model with $N = 2$ and $a = 5/6$. This case is depicted in Fig. 1C. Our analysis above tells us that selection encourages a mother to invest only in sons, but encourages fathers to use sex-ratio behaviour,

$$(M_{\text{dad}}^* - (1 - a))/a = 6/10 > 1/2. \quad (27)$$

Parents are in conflict, but both bias effort toward sons.

5 Conflict under multiplicative effects

As before, let us begin by establishing the sex-ratio behaviour each parent considers optimal. Assuming paternal control, and following the same recipe outlined in the previous section we find that $z_m^0 = z_f^0 = N/(2N - 1)$ (see Appendix B). Unlike the additive effects case, the equilibrium solution is unique; however, the realized brood sex ratio are the unchanged. Under paternal control we find

$$M_{\text{dad}}^*/F_{\text{dad}}^* = [N/(N - 1)]/[1 - N/(N - 1)] = N/(N - 1). \quad (28)$$

Assuming maternal control of sex-ratio behaviours the unique equilibrium

solution is $z_m^0 = z_f^0 = N(3N + 1)/[3N(2N - 1) + 1]$ (Appendix B). It follows that

$$M_{\text{mom}}^*/F_{\text{mom}}^* = N(3N + 1)/(N - 1)(3N - 1), \quad (29)$$

which is again unchanged from the additive effects model.

The conflict over the sex ratio is clearly maintained in the multiplicative effects model. The main result of this section states that, when parents are allowed to control only their own sex-ratio behaviour, a compromise is always established—in the sense that solution pairs (z_m^0, z_f^0) are readily found using numerical methods. The stability of these solutions, under a multidimensional version of the convergence stability concept – originally proposed by Christiansen (1991) (see Appendix B) – was also verified numerically.

Table 2 presents numerical approximates for z_m^0 and z_f^0 , under various combinations of parameters N and b , and found using the Maple software package (Waterloo Maple, 2002). In each case investigated, we found $M_{\text{dad}}^* < z_m^0 < z_f^0 < M_{\text{mom}}^*$, i.e. the stable joint equilibrium represented a sort of compromise between male and female perspectives. The same pattern can be observed in the realized brood sex-ratio, M/F (Table 2).

Reading down the rows of Table 2 we see also a shift in which perspective dominates the compromise. When the parameter b is small the female’s perspective carries more weight; and when b is large the male perspective prevails. Why might this pattern be expected? To answer this, let us fix attention on a single value of p (= the proportion by which offspring mortality is reduced with one unit of maternal investment). In order for b to be small, then,

T (= total maternal resource) must small relative to K (= brood size). That is to say, when b is small a mother is unable to provide resources to all her offspring. It follows that offspring survival is low, and so maternal investment is able to alter the primary sex ratio significantly. It is instructive to observe that in the limit as b approaches zero, the multiplicative effects model for ΔW_{g_f} approaches the additive effects ΔW_{g_f} with maternal control.

When b is large, T must be large relative to K . In other words, a mother has an abundance of resources to distribute among her offspring. In this case the survival of offspring is almost assured, and so manipulation of maternal investment does little to change the primary sex ratio set out by a father. Observe that in the limit as b approaches ∞ , the multiplicative effects model for ΔW_{g_m} approaches the additive effects ΔW_{g_m} with paternal control.

6 Conclusions

Not surprisingly, the resolution of sex-ratio conflict between mates under LRC depends on how parental efforts are combined to determine the realized sex-ratio of a brood. When efforts are combined in an additive fashion the relative weights assigned to sex-specific levels of care tells the story. If the weight assigned to paternal care is sufficiently large (i.e. $a \geq 1/2$), the brood sex-ratio is optimum from the perspective of the father. In contrast to this, we see that $a < 1/2$ is not sufficient to guarantee that mother's optimal sex is achieved. Setting $a < 1/2$ can, at best, assure a compromise between mates—in the sense that neither sex-specific optimum 'wins' (Fig. 1A, B). In order for the mother's optimum to

prevail, we need $a \leq 1 - M_{\text{mom}}^* < 1/2$. All else being equal, the resolution of sex-ratio conflict under LRC – and under the additive effects model – appears to be biased in favour of the father’s perspective.

In nature, the coefficient a will certainly vary across species; and likely vary according to some non-uniform distribution, respectively. Birds, for instance, tend to exhibit bi-parental care (perhaps a nearer to $1/2$), whereas sole maternal care is common in many mammals (perhaps a near zero).

The multiplicative effects model we present here provides an interesting contrast to the previous case. Our numerical investigations suggest that an equilibrium compromise is always achieved. In this case the perspective that receives greater weight is determined by the parameter b . When b is small, the offspring are resource-limited and the parent responsible for distributing the resource (in our model, the mother) has greater degree of control over the realized brood sex-ratio. When b is large offspring thrive and the realized sex-ratio is closer to the optimum from the perspective of the parent controlling the primary sex-ratio (in our model, the father).

One might wonder why it is that, under the multiplicative effects model, the mother’s perspective does not always prevail. After all, it is the mother who makes the final adjustment to the brood sex ratio. At first glance this logic is appealing. Nevertheless, ‘winning the conflict’ would require a mother to make an investment in sons that, because of diminishing returns on offspring survival, would have been better spent on daughters. In short, a mother does not try to win because it is unprofitable to do so.

As a final comment on the multiplicative effects model, we note that we have assumed that a mother divides her investment evenly among all same-sex individuals in a brood. This assumption is valid because of the ‘diminishing returns’ form of the survival function, s . The assumption will not be reasonable for other forms of s , e.g. forms whose graphs are concave up.

The idea that parents are in conflict over parental investment is not new (e.g. see Trivers, 1972). Usually, this conflict is centred around the overall level of parental care given, rather than the manner in which care is divided between sons and daughters. For instance, one mate in a pair might choose to either care for offspring, or desert—providing no parental care whatsoever (Maynard Smith, 1977). The decision to care comes at the expense of future reproduction, and so there exists a tradeoff (Williams, 1966). Incorporating such tradeoffs into a model of sex-ratio conflict could suggest how likely it is that male perspective wins out.

Our model assumes that selection is the only way in which conflict can be resolved. There may, however, be other factors that either contribute to conflict resolution, or at least, reduce the intensity of the conflict. One noteworthy factor is patch size, N . We can see that larger N reduces the size of the disparity between sex-specific behavioural optima. In these situations, then, being on the ‘losing end’ of a sex-ratio conflict may not be that bad; and this may actually represent a benefit of such behaviours as communal nesting sites. In general, any factor that brings \bar{r} closer to one half should be relevant to the resolution of sex-ratio conflict in geographically structured populations.

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Appendices

A Relatedness calculations

In this appendix, we compute expressions for the relatedness coefficients used in the main text. Let H_{IJ} denote the *coefficient of consanguinity* (CC) between two individuals, I and J , i.e. the probability that a random allele from I and a random allele from J are identical-by-descent. Following Michod and Hamilton (1980), we define the *relatedness between I and J* as

$$H_{IJ}/H_{II} = H_{IJ}/H_{JJ}. \quad (\text{A.1})$$

We define H_{ff} as the CC between two females breeding on the same patch, taken with replacement. We define H_{mm} and H_{fm} in a similar way. Since no male breeds on his natal patch (i.e. outbreeding population), $H_{mm} = 1/2N$, and $H_{fm} = 0$. To compute H_{ff} we use a recursive equation. We suppose that, in generation t , $H_{ff}(t)$ is known, and we compute its value one generation in the future, $H_{ff}(t+1)$. A conditional probability argument yields

$$\begin{aligned} H_{ff}(t+1) &= 1/2N + (N-1)/N (H_{ff}(t)/4 + H_{fm}/2 + H_{mm}/4) \\ &= 1/2N + (N-1)/N (H_{ff}(t)/4 + 1/8N). \end{aligned} \quad (\text{A.2})$$

At equilibrium $H_{ff}(t+1) = H_{ff}(t)$. Making this substitution in (A.2) and solving for H_{ff} we get

$$H_{ff} = (5N-1)/2N(3N+1). \quad (\text{A.3})$$

Since there is no inbreeding, parent-offspring relatedness, r is simply $1/2$. To compute \bar{r} we note that we are effectively comparing an allele from an adult with an allele drawn either from an adult female (probability = $1/2$), or an adult male (probability = $1/2$). It follows that the relatedness between a recipient offspring and a random adult female donor is given by

$$\bar{r} = (H_{fm}/2 + H_{ff}/2)/(1/2) = H_{ff}. \quad (\text{A.4})$$

Similarly, the relatedness between a recipient offspring and a random adult male donor is given by

$$\bar{r} = (H_{fm}/2 + H_{mm}/2)/(1/2) = H_{mm}. \quad (\text{A.5})$$

Observe that $H_{ff} \geq H_{mm}$ with equality if and only if $N = 1$.

B Sex-specific optima under multiplicative effects model

Here we show that, under multiplicative effects,

$$M_{\text{dad}}^*/F_{\text{dad}} = N/(N - 1) \quad (\text{B.1})$$

is optimal from father's perspective, and

$$M_{\text{mom}}^*/F_{\text{mom}} = N(3N + 1)/(N - 1)(3N - 1) \quad (\text{B.2})$$

is optimal from mother's perspective.

We begin by defining two functions

$$\phi(x, y) = s'(y/x)/(s(y/x) - s'(y/x)y/x), \quad (\text{B.3})$$

$$\psi(x, y) = \phi(1 - x, 1 - y) \quad (\text{B.4})$$

restricted to the domain, $E = (0, 1) \times (0, 1)$. We observe the following:

- $\partial\phi/\partial x > 0$ and $\partial\phi/\partial y < 0$;
- $\partial\psi/\partial x < 0$ and $\partial\psi/\partial y > 0$;
- $\phi = \psi$ on the set $\{(x, y) \in E \mid x = y\}$.

Suppose sex-ratio behaviour is controlled by only one parent. We seek a solution to equilibrium condition (20). One can easily verify that $z_m^0 = z_f^0 = N/(2N - 1)$ is a solution under paternal control, and that $z_m^0 = z_f^0 = N(3N + 1)/[3N(2N - 1) + 1]$ is a solution under maternal control; but are these the only solutions for the respective cases? We claim that they are.

To prove the claim, suppose that we have found a solution to (20), (z_m^0, z_f^0) . A simple rearrangement of (20) shows that $\phi(z_m^0, z_f^0) = \psi(z_m^0, z_f^0)$ must hold. By the observations made above, $\phi(z_m^0, z_f^0) = \psi(z_m^0, z_f^0)$ holds if and only if $z_m^0 = z_f^0$. Since $z_m^0 = z_f^0$ condition (20), under multiplicative effects is

$$(r - \bar{r})/(1 - z_i^0) = r/z_i^0 \quad (i = m, f). \quad (\text{B.5})$$

We conclude that if (z_m^0, z_f^0) is a solution to (20) under multiplicative effects, then it must satisfy (B.5).

It follows from the preceding comments that $\bar{r} = 1/2N$ (paternal control) yields

$$z_m^0 = z_f^0 = N/(2N - 1), \quad (\text{B.6})$$

and we have (B.1). When $\bar{r} = (5N - 1)/2N(3N + 1)$ (maternal control)

$$z_m^0 = z_f^0 = N(3N + 1)/[3N(2N - 1) + 1], \quad (\text{B.7})$$

and we have (B.2).

To generalize Christiansen (1991), we say that a pair (z_m^0, z_f^0) is *convergence stable* provided

$$(\Delta W_{g_m}, \Delta W_{g_f})^T (z_m^0 - z_m, z_f^0 - z_f) > 0, \quad (\text{B.8})$$

for resident behaviours (z_m, z_f) sufficiently close to (z_m^0, z_f^0) . The standard derivative condition for convergence stability in this sense is that the eigenvalues of the matrix

$$(1/2) \begin{bmatrix} \partial \Delta W_{g_m} / \partial z_m & \partial \Delta W_{g_m} / \partial z_f \\ \partial \Delta W_{g_f} / \partial z_m & \partial \Delta W_{g_f} / \partial z_f \end{bmatrix} + (1/2) \begin{bmatrix} \partial \Delta W_{g_m} / \partial z_m & \partial \Delta W_{g_m} / \partial z_f \\ \partial \Delta W_{g_f} / \partial z_m & \partial \Delta W_{g_f} / \partial z_f \end{bmatrix}^T \quad (\text{B.9})$$

be strictly negative. We verified numerically that (B.1) and (B.2) correspond to convergence stable values of (z_m^0, z_f^0) .

Table 1. A summary of notation used in the main text.

Symbol	Explanation
a	additive paternal contribution to sex ratio
b	$= (1 - p)^{-1}T/K$, describes the extent to which maternal investment influences offspring survival in the multiplicative effects model
ΔW_{g_i}	direct fitness effect of increasing g_i
\bar{F}	prop'n of a brood devoted to daughters under additive effects; joint prob that an oocyte is fertilized female and survives parental investment period under multiplicative effects
F_{dad}^*	optimal \bar{F} from the perspective of a father
F_{mom}^*	optimal \bar{F} from the perspective of a mother
g_i	recipient's genotypic value for the locus controlling sex- i sex-ratio behaviour ($i = m, f$)

Table 1, continued.

Symbol	Explanation
K	total number of surviving offspring under additive effects; total number of fertilized oocytes under multiplicative effects
M	prop'n of a brood devoted to sons under additive effects; joint prob that an oocyte is fertilized male and survives parental investment period under multiplicative effects
M_{dad}^*	optimal M from the perspective of a father
M_{mom}^*	optimal M from the perspective of a mother
N	patch size
r	relatedness between offspring and parent
\bar{r}	relatedness between offspring and random parent breeding on the focal patch

Table 1, continued.

Symbol	Explanation
s	probability of offspring survival
T	total amount of maternal resource available for investment
W_i	fitness of a sex- i recipient ($i = m, f$)
u	an amount of maternal resource
x_i	sex-ratio behaviour exhibited by the sex- i parent of the focal offspring ($i = m, f$)
y_i	average sex-ratio behaviour exhibited by a sex- i parent on the focal patch ($i = m, f$)
z_i	resident sex- i sex-ratio behaviour ($i = m, f$)
z_m^0, z_f^0	solution to system (20)

Table 2. Approximate stable sex-ratio behaviours z_m^0 , z_f^0 and approximate value of the ratio M/F under various combinations of parameters N and b . Values corresponding to the optimum from a mother's perspective ($b \rightarrow 0$), and the optimum from a father's perspective ($b \rightarrow \infty$) are presented for comparison (na = not applicable).

		$N = 2$			$N = 4$		
b	z_m^0	z_f^0	M/F	z_m^0	z_f^0	M/F	
$\rightarrow 0$	na	$M_{\text{mom}}^* = .7368$	$M_{\text{mom}}^*/F_{\text{mom}}^* = 2.800$	na	$M_{\text{mom}}^* = .6118$	$M_{\text{mom}}^*/F_{\text{mom}}^* = 1.575$	
.01	.7028	.7367	2.795	.5917	.6117	1.574	
.1	.7018	.7353	2.756	.5911	.6108	1.563	
1	.6918	.7211	2.440	.5853	.6021	1.470	
10	.6667	.6742	2.000	.5714	.5755	1.333	
$\rightarrow \infty$	$M_{\text{dad}}^* = 0.66667$	na	$M_{\text{dad}}^*/F_{\text{dad}}^* = 2$	$M_{\text{dad}}^* = .5714$	na	$M_{\text{dad}}^*/F_{\text{dad}}^* = 1.333$	

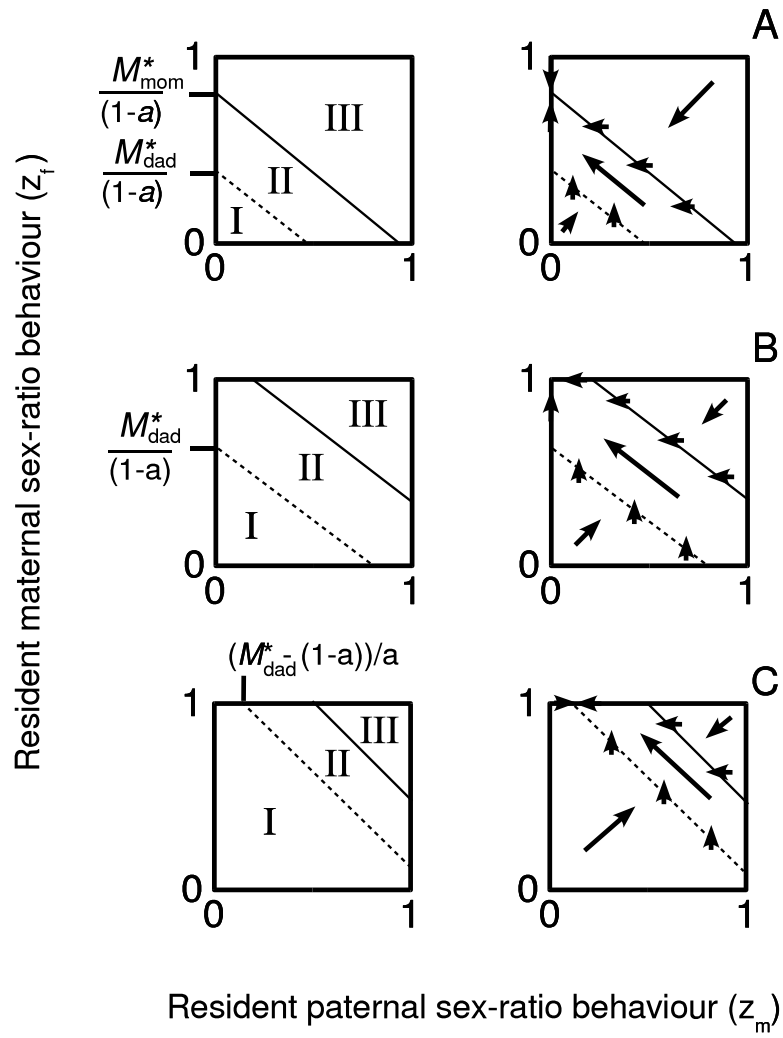


Fig. 1.

Figure legends

Fig. 1. The resolution of sex-ratio conflict under the additive effects model. The nullclines $\Delta W_{g_m} = 0$ and $\Delta W_{g_f} = 0$ are indicated with a dashed and solid line, respectively. Landmarks are indicated in panels on the left; the direction of evolution is indicated in panels on the right. Top row (A) describes the case $M_{\text{mom}}^* < 1 - a$; middle row (B) describes the case $M_{\text{dad}}^* < 1 - a \leq M_{\text{mom}}^*$; and bottom row (C) describes the case $M_{\text{dad}}^* \geq 1 - a$. Recall: in Region I $\Delta W_{g_m}, \Delta W_{g_f} > 0$; in Region II $\Delta W_{g_m} < 0$ and $\Delta W_{g_f} > 0$; and in Region III $\Delta W_{g_m}, \Delta W_{g_m} < 0$.