Cooperative interactions among females and even more extraordinary sex ratios

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Abstract

Hamilton's local mate competition theory provided an explanation for extraordinary female biased sex ratios in a range of organisms. When mating takes place locally, in structured populations, a female biased sex ratio is favoured to reduce competition between related males, and to provide more mates for males. However, there are a number of wasp species where the sex ratios appear to more female biased than predicted by Hamilton's theory. We investigated theoretically the extent to which cooperative interactions between related females can interact with local mate competition to favour even more female biased sex ratios. We found that: (i) cooperative interactions between females can lead to sex ratios that are more female biased than predicted by local competition theory alone; (ii) sex ratios can be more female biased when the cooperative interactions are offspring helping parents, rather than cooperation between siblings. Our results can be applied to a range of organisms, and provide an explanation for the extreme sex ratio biases that have been observed in *Sclerodemus* and *Melittobia* wasps.

Key words:

- Kin selection;
- Local resource competition;
- Local mate competition;
- Local resource enhancement;
- Population structure;

Introduction

Sex ratio theory has provided one of the most productive and successful areas of evolutionary biology [1–3]. Theory predicts a number of situations in which individuals are expected to adjust the sex of their offspring in response to local conditions [1, 4]. This theory has been applied to explain variation in the offspring sex ratio (proportion males) across a range of taxa, from malaria parasites to ants to birds [2, 3, 5].

One of the major challenges is to explain when sex ratios are biased away equal investment in the sexes. Hamilton's [6] local mate competition (LMC) theory provides an explanation for female biased sex ratios observed in fig wasps (e.g., *Scelionidae* [7], *Alfonsiella* [8], *Apanteles* [9, 10] and *Nasonia* [11–13]), aphids (e.g., *Prociphilus oriens*; [14]), and a number of fig wasps [15]. Specifically, Hamilton showed that if n haplodiploid females lay eggs in a patch, and that mating occurs before females disperse, then the evolutionarily stable strategy (ESS; [16]) is to produce an offspring sex ratio of $(n-1)/(2n)$ (Fig 1), which predicts female biased offspring sex ratios (smaller than 1/2) and becomes less biased as more females lay eggs in a patch. Succeeding work [4, 17–21] made it clear that in Hamilton's LMC theory, selection on the female bias is mediated by the balance among three factors: (i) a benefit for reduced competition between sons, (ii) a benefit for production of more mates (daughters) for those sons ("mating bonus"; [4]), and (iii) a cost for stronger local resource competition among females (LRC; [22]). Hamilton's LMC theory has been extremely successful in explaining variation in the offspring sex ratio, both across species and between individuals [3, 12, 17, 23–28].

However, there are a number of cases where females produce extremely female biased offspring sex ratios, which do not appear to be completely explained by LMC theory. One example is provided by *Melittobia* wasps, where females of several species produce approximately 2 % male offspring when ovipositing alone ($n = 1$), and hardly change their offspring sex ratio when more females lay eggs on a patch (Fig 1A; [29, 30]). Another example is provided by *Sclerodemus* wasps, in which multiple females can lay eggs on a host but the females still only produce 7% males Fig 1B; [31–33]). These cases therefore suggest that identifying additional factors that favour female-biased sex ratio is required.

A possible explanation for the observed female-biases is that there is the potential for mutually beneficial cooperative interactions between females [31, 34–41].For example, in presocial, allodapine bee *Exoneura bicolor*, cooperative nesting occurs among related females, which result in higher per capita reproductive outputs [34, 37]. In this case, a more female biased offspring sex ratio can be favoured, to increase these beneficial interactions between related females, as a form of local resource enhancement (LRE; in this literature we focus on LRE provided by females). Cooperative interactions beetween females have been suggested to be important in both *Melittobia* and

Sclerodemus wasps either [29–32], but the extremely female-biased sex ratios under LRE in these species remain to be formally explained.

We expand existing theory to examine whether LRE can explain the extremely female biased sex ratios that have been observed in *Melittobia* and *Sclerodemus* wasps. We examine three factors that may be especially relevant to the biology of these species: (1) competitions between sons and between daughters; (2) the cooperative interactions that can occur at different times, either when laying eggs (intra-generational LRE) as in Pen & Weissing [42] and Wild [43], or when colonizing females help each other before competition (trans-generational LRE); (3) both females and males may disperse to different extents, hence varying the degree to which these competitive and cooperative interactions occur locally We specifically look at how sex-specific dispersal rates, the number of foundresses, and fecundity effect of LRE influence the evolution of sex ratios.

Models and Analyses

Life cycle

We assume Wright's [44] island model of dispersal, in which the metapopulation is subdivided into an infinite number of patches each fostering n mated females [27]. We focus on a particular female, and we denote her proportional investment of reproductive resource into sons ('sex ratio') by $x_\bullet$, the average sex ratio of the adult females in her patch in the same generation by y_0, and the average sex ratio of adult females in the metapopulation by z. Immediately upon birth, juvenile males may disperse to an alternative patch at a rate d_m each, or else stay in the natal patch $(1 - d_\mathrm{m})$, followed by random mating on the patch, with each female mating only once but each male potentially mating many times. Males die after mating and females disperse with a probability of d_f each. After dispersal, breeding females compete for the limited number of breeding sites on the patch (n), after which the metapopulation is returned back to its original size and a new cycle starts (Fig 2A).

We consider two types of LRE. In the first, LRE occurs due to helping behaviors among juvenile females (before dispersal) that promotes the survival rate of all juveniles born in the same patch. We refer to this as 'intra-generational LRE' ("intra-" indicates that survival rate depends on the sex ratio, y_0, of the focal generation, $\tau = 0$). Intra-generational LRE may be relevant in species where juvenile females engage in helping behaviors before dispersal (at the latest), or equivalently, where juvenile females assist reproduction of the reproductive adults (survivorship and fecundity interpretations are mathematically equivalent). In the second, we posit that LRE occurs due to mutual helping at the colonization stage (before competition for breeding spots), namely 'trans-generational

LRE' ("trans-" indicates that the fecundity depends on the sex ratio, y_1, of the previous generation, $\tau = 1$). This applies to species where females communally colonize common patches, as in *Sclerodemus*.

LRE by natal juvenile females: intra-generational LRE

We start with our analyses for intra-generational LRE, where offspring can help members of their parents generation. We assume that, for a patch with the average sex ratio X, the per capita fecundity (which is the number of offspring born times their survival rate) is given by $\beta(X)$. Turning our attention to the focal patch with its inhabitants' average sex ratio y_0 (including her own sex ratio), the fecundity of the females in the patch is given by $\beta_0 := \beta\big(y_0\big)$, and the average fecundity (the total number of offspring produced per capita times their survival rate) in the metapopulation assuming that the mutants are vanishingly rare is given by $\beta^\circ := \beta(z)$, where we use ':=' to define a quantity henceforth. Using a parameter α (with $0 \leq \alpha \leq 1$) which tunes the strength of LRE on fecundity (β_0), we formulate β by:

$$\beta\big(y_0\big) = K + \alpha\big(1 - y_0\big)\beta\big(y_0\big) = \frac{K}{1 - \alpha\big(1 - y_0\big)}, \tag{1}$$

(see Appendix A for derivation). In this formalism, per capita fecundity (β_0 higher) is higher when neighboring individuals produce more females (y_0 lower). The fecundity $\beta\big(y_0\big)$ decreases from $K/(1-\alpha)$ to K as y_0 varies from 0 to 1, and grows from $\beta_0 \equiv K$ to K/y_0 as α varies from 0 to 1 (for $y_0 > 0$ fixed).

LRE by colonizing females after dispersal: trans-generational LRE

We now turn our attention to trans-generational LRE, where juvenile females of the same generation can cooperate after dispersal. We use the same symbol (β_0) to designate the fecundity of individuals in the focal patch, to keep the consistency between the two models. Let $\tau \geq 0$ be a generic symbol to count the generations backwards ordinally in time: $\tau = 0$ for the present, $\tau = 1$ for the parental generation, and generally τ for τ-generations prior ('τ-th generation' henceforth). We write y_τ for the average sex ratio of adult females in the focal patch in the τ-th generation, and β_τ for their fecundity (Fig 2B). We recursively define β_τ by:

$$\begin{aligned} \beta_\tau &= B\big(\beta_{\tau+1}, y_{\tau+1}\big) \\ &= K + \alpha\Big((1 - d_\mathrm{f})\big(1 - y_{\tau+1}\big)\beta_{\tau+1} + d_\mathrm{f}(1 - z)\overline{\beta}\Big), \end{aligned} \tag{2}$$

where α (with $0 \leq \alpha \leq 1$) measures the strength of LRE as before, $(1 - d_\mathrm{f})\big(1 - y_{\tau+1}\big)\beta_{\tau+1} + d_\mathrm{f}(1 - z)\overline{\beta}$ is proportional to the density of females after female dispersal (before competition), and $\overline{\beta}$ is the metapopulation-wide

average of β to be determined by assuming that it has reached an equilibrium value for a phenotypically monomorphic population with z. The equilibrium value for $\beta = \overline{\beta} = \beta^\circ$ is given as the solution to $\beta^\circ = B\big(\beta^\circ, z\big)$; that is:

$$\beta^\circ = \beta(z) = \frac{K}{1-\alpha(1-z)} \tag{3}$$

(see Eqn (1)). Specifically, the fecundity of the focal female in the present generation $\tau = 0$ is given by:

$$\begin{aligned} \beta_0 &= B\big(\beta_1, y_1\big) \\ &= B\Big(B\big(\beta_2, y_2\big), y_1\Big) \\ &= B\Bigg(B\Big(B\big(\beta_3, y_3\big), y_2\Big), y_1\Bigg) \\ &= \dots \end{aligned} \tag{4}$$

(see Appendix A for more details), which implies that to determine (the effect of selection on) β_0, we need to consider a sequence of retrospective, expected sex ratios in the focal patch, $\big(y_1, y_2, y_3, \dots\big)$, in addition to the focal's and neighbors' sex ratios in the present generation, $\big(x_\bullet, y_0\big)$ [45]. LRE supplied by founding females hence generates the trans-generational kin selection effects in viscous populations, by which the impacts of biased sex ratios in the patch descend down to reproductive success of individuals (including the focal's offspring) living in future generations, which thus in turn induces selection on the sex ratios.

Notably, Eqns (1) and (3) assume that LRE occurs in an additive way, but we can also consider multiplicativity, which turns out to exhibit a similar but stronger effect than the additive effect (i.e., female-bias is much more likely when LRE is of multiplicativity). For demonstration purpose, however, we restrict our attention to the additive effects in the main text.

Invasion fitness and the selection gradient

We can write the invasion fitness of the focal female through daughters and sons (respectively) as:

$$W_\bullet^{\mathbf{f}} := W^{\mathbf{f}}\big(x_\bullet, y_0, \beta_0\big) := \frac{(1-d_{\mathrm{f}})(1-x_\bullet)\beta_0}{(1-d_{\mathrm{f}})\big(1-y_0\big)\beta_0 + d_{\mathrm{f}}(1-z)\beta^\circ} + \frac{d_{\mathrm{f}}(1-x_\bullet)\beta_0}{(1-z)\beta^\circ}, \tag{5}$$

$$W_\bullet^{\mathbf{m}} := W^{\mathbf{m}}\Big(x_\bullet, y_0, W_0^{\mathbf{f}}, \beta_0\Big) := \frac{(1-d_{\mathrm{m}})x_\bullet\beta_0}{(1-d_{\mathrm{m}})y_0\beta_0 + d_{\mathrm{m}}z\beta^\circ}\underbrace{W^{\mathbf{f}}\big(y_0, y_0, \beta_0\big)}_{=:W_0^{\mathbf{f}}} + \frac{d_{\mathrm{m}}x_\bullet\beta_0}{z\beta^\circ} \tag{6}$$

(see [27, 45]), where the invasion subcomponent for sons (Eqn (6)) is envisioned as a function of the focal adult female's sex ratio $x_\bullet$, patch-average sex ratio y_0, the survival rate of a random female as a mate for local males $W_0^{\mathbf{f}}$

(local mating bonus; see [4], pp.199), and the average fecundity of the focal adult female β_0. Note that β_0 depends on model assumptions (intra- and trans-generational LRE). See Appendix B for derivation.

We perform the neighbor-modulated fitness approach to kin selection methodology [4, 46–49], particularly for sex-structured populations [27, 49, 50] with trans-generational effects of kin selection [45, 51]. We take a random juvenile female and male in the present generation each as a recipient, and adult females breeding in the τ-th generation (with $\tau = 0, 1, 2 \ldots$, including the focal juveniles' mother) each as an actor. As postulated by Lehmann [45, 51], the condition for which a slightly larger sex ratio (i.e., producing more sons than does the metapopulation average) is favoured by selection is captured by Hamilton's rule:

$$c_{\mathrm{f}}\left(\underbrace{\frac{\partial W_{\bullet}^{\mathbf{f}}}{\partial x_{\bullet}} R_{\bullet}^{\mathbf{f}}}_{\text{daughters}} + \underbrace{\frac{\partial W_{\bullet}^{\mathbf{f}}}{\partial y_0} R_0^{\mathbf{f}}}_{\text{LRC effect}} + \underbrace{\sum_{\tau=0}^{+\infty} \frac{\partial W_{\bullet}^{\mathbf{f}}}{\partial \beta_0} \cdot \frac{\partial \beta_0}{\partial y_\tau} R_\tau^{\mathbf{f}}}_{\text{LRE on females \& LRC}}\right)$$
$$+c_{\mathrm{m}}\left(\underbrace{\frac{\partial W_{\bullet}^{\mathbf{m}}}{\partial x_{\bullet}} R_{\bullet}^{\mathbf{m}}}_{\text{sons}} + \underbrace{\frac{\partial W_{\bullet}^{\mathbf{m}}}{\partial y_0} R_0^{\mathbf{m}}}_{\text{LMC}} + \underbrace{\frac{\partial W_{\bullet}^{\mathbf{m}}}{\partial W_0^{\mathbf{f}}} \cdot \frac{\partial W_0^{\mathbf{f}}}{\partial y_0} R_0^{\mathbf{m}}}_{\text{Mating bonus (MB)}} + \underbrace{\sum_{\tau=0}^{+\infty} \frac{\partial W_{\bullet}^{\mathbf{m}}}{\partial \beta_0} \cdot \frac{\partial \beta_0}{\partial y_\tau} R_\tau^{\mathbf{m}}}_{\text{LRE on males \& LMC}} + \underbrace{\sum_{\tau=0}^{+\infty} \frac{\partial W_{\bullet}^{\mathbf{m}}}{\partial W_0^{\mathbf{f}}} \cdot \frac{\partial W_0^{\mathbf{f}}}{\partial \beta_0} \cdot \frac{\partial \beta_0}{\partial y_\tau} R_\tau^{\mathbf{m}}}_{\text{LRE on MB}}\right) > 0 \tag{7}$$

(see Appendix B for derivation), where each derivative is evaluated at phenotypic neutrality ($x_\bullet = y_0 = y_1 = \cdots = z$). $R_\bullet^{\mathbf{f}}$ (or $R_\bullet^{\mathbf{m}}$) represents the regression coefficient of relatedness ('relatedness' hereafter; [52, 53]) for a juvenile female (or juvenile male) from the perspective of their mother each in the present generation; $R_0^{\mathbf{f}}$ (or $R_0^{\mathbf{m}}$) represents the relatedness for a random juvenile female (or juvenile male) from the perspective of a random adult female in the same patch each in the present generation; and $R_\tau^{\mathbf{f}}$ (or $R_\tau^{\mathbf{m}}$) represents the relatedness for a random juvenile female (or juvenile male) in the present from the perspective of an adult female in the τ-th generation [20, 54]; c_{f} (or c_{m}) represents the class reproductive value of female (or male; [50, 55]).

In Eqn (7), we explicitly separated the selective forces, to ease biological interpretation. The intensity of LRC is proportional to $\ell_{\mathrm{RC}} := (1 - d_{\mathrm{f}})^2$, which is the proportion of focal adult female's daughters (or sons) competing for resources (or for mates) with a juvenile female (or juvenile male) born in the same patch (respectively), as in previous studies [56]. Similarly, the intensity of LMC is proportional to $\ell_{\mathrm{MC}} := (1 - d_{\mathrm{m}})^2$, the proportion of focal adult female's sons competing for mates with a juvenile male born in the same patch. Increasing ℓ_{RC} (or ℓ_{MC}) favours less (or more) female-biased sex ratios (respectively). The effect of extra daughters born locally on males' reproductive success is given by $\ell_{\mathrm{MB}} := (1 - d_{\mathrm{m}})(1 - \ell_{\mathrm{RC}})$ (i.e., local mating bonus; see [3, 4, 57], pp.199), which

reads as the probability that males mate locally $(1-d_{\mathrm{m}})$ times the probability that the mated female(s) do not encounter local resource competition with a juvenile female born in the same patch $1-(1-d_{\mathrm{f}})^2 = 1-\ell_{\mathrm{RC}}$.

In the absence of LRE (thus no $\sum$ terms), investing maternal reproductive resources into sons has five consequences: the decrease in daughters' success, decrease in LRC, increase in sons' success, increase in LMC, and decrease in MB, as in the previous studies [17]. The summation ($\sum$) terms each capture the sum of LRE effects each supplied by the individuals having colonized the focal patch at time epochs $\tau = 0$ (for the intra-generational LRE), and $\tau = 1, 2, \ldots$ (for the trans-generational LRE), on the focal female's fitness (Fig 2B); this inclusive fitness effect occurs by which (i) LRE increases the number of sons and thus LMC, (ii) LRE increases the number of daughters and LRC, and (iii) LRE increases MB for sons.

Nullifying and solving Eqn (7) for z yields a candidate ESS of sex ratio (cESS henceforth; [58, 59]), which we generically designate with a hat ($\widehat{z}$).

Results

No LRE

We first assess the case for $\alpha = 0$ (no LRE). By nullifying Eqn (7) for $z = \widehat{Z_{\emptyset}}$ with $\alpha = 0$ gives:

$$\widehat{Z_{\emptyset}} = \frac{c_{\mathrm{m}}\left(R^{\mathbf{m}}_{\bullet} - \ell_{\mathrm{MC}} R^{\mathbf{m}}_{0}\right)}{c_{\mathrm{m}} R^{\mathbf{m}}_{\bullet}\left(-(\ell_{\mathrm{MC}} - \ell_{\mathrm{MB}}) R^{\mathbf{m}}_{0}\right) + c_{\mathrm{f}}\left(R^{\mathbf{f}}_{\bullet} - \ell_{\mathrm{RC}} R^{\mathbf{f}}_{0}\right)} \tag{8}$$

in agreement with [56]. This expression clarifies how the local interactions affect the adaptive value of sons and daughters, where remember that $\ell_{\mathrm{RC}} = (1-d_{\mathrm{f}})^2$, increases the value of $\widehat{Z_{\emptyset}}$, $\ell_{\mathrm{MC}} = (1-d_{\mathrm{m}})^2$, and $\ell_{\mathrm{MB}} = (1-d_{\mathrm{m}})(1-\ell_{\mathrm{RC}})$. Note that for males, the total scale of competition, which includes the effect of LRC among the males' mates (i.e., females that thus received males' gametes), reads $\ell_{\mathrm{MC}} - \ell_{\mathrm{MB}}$, which is negative when $(1-d_{\mathrm{f}})^2 < d_{\mathrm{m}} < 1$ (null for either $d_{\mathrm{m}} = 1$ or $d_{\mathrm{m}} = (1-d_{\mathrm{f}})^2$; otherwise positive). Eqn (8) is a general expression of cESS under LRC and LMC (but without LRE) when male dispersal precedes mating and subsequent female dispersal ('DMD model' in [56]). Substituting equilibrium values of the relatedness shows that $\widehat{Z_{\emptyset}}$ exhibits overall a female- or male-bias when d_{m} is small or large (respectively) and it approaches 1/2 (Fisherian sex ratio) as n increases (Fig 3A).

As in the classical LMC theory, inserting $d_{\mathrm{m}} = 0$ (no male dispersal as in *Melittobia*; [60]) yields $\ell_{\mathrm{MC}} = 1 (> \ell_{\mathrm{RC}})$ and $\ell_{\mathrm{MB}} = 1 - \ell_{\mathrm{RC}}$, meaning that $\ell_{\mathrm{MC}} - \ell_{\mathrm{MB}}$ equals ℓ_{RC} on the denominator of Eqn (8); this subsequently

supplies:

$$\widehat{Z_\emptyset}\Big|_{d_\mathrm{m}=0} = \frac{c_\mathrm{m}\left(R_\bullet^\mathbf{m} - R_0^\mathbf{m}\right)}{c_\mathrm{m}\left(R_\bullet^\mathbf{m} - \ell_\mathrm{RC} R_0^\mathbf{m}\right) + c_\mathrm{f}\left(R_\bullet^\mathbf{f} - \ell_\mathrm{RC} R_0^\mathbf{f}\right)} \tag{9}$$

(Appendix B; eqn 3 in [27]). Particularly for haploids and diploids, we get $z_\emptyset^\mathrm{LMC} = (n-1)/(2n)$ regardless of the female dispersal rate [4, 6, 18–20, 27, 54]. This dispersal-invariance is due partly to the concomitant effects of producing more daughters on weaker LMC but stronger LRC with these effects exactly canceling one another out (Taylor's [21] cancelling principle; [21, 61]). For haplodiploids, Eqn (8) does depend on dispersal rate but in a negligibly minor manner (almost-invariance in female dispersal; Fig 3B, left panel).

In the case for $d_\mathrm{m} > 0$, male biased sex ratios may occur when d_f is small, in contrast to the almost-invariance result for $d_\mathrm{m} = 0$ (Fig 3B). Increasing $d_\mathrm{m} > 0$ (say 0.5) leads to strongly male-biased sex ratios yet with a possibility of female-bias when d_f is relatively large (Fig 3B). When $d_\mathrm{m} = 1$ ($\ell_\mathrm{MC} = \ell_\mathrm{MB} = 0$), only is male-bias the candidate evolutionary outcome (Fig 3B; see also SI figure in Appendix C). Overall, we find that sex ratio tends to bias towards the more dispersing sex [23, 56, 62].

Effects of LRE: general patterns

We now consider the consequences of LRE ($\alpha > 0$). We found three general patterns. First, both types of LRE drive the evolution of more female-biased sex ratio and less male-biased sex ratios (Fig 4A; see also SI Fig1). Second, the effect of intra-generational LRE is stronger than is trans-generational LRE (Fig 4B); more precisely, the effect of intra-generational LRE is independent of sex dispersal propensities of both sexes, while that of trans-generational LRE decreases with the dispersal rates of both sexes. Finally, $d_\mathrm{m} = 0$ (no male dispersal) as in classic LMC theory predicts that this special case leads to 'almost-invariance results', in which sex ratio is insensitive to female dispersal rate [4, 6, 18–20, 27, 54].

Intra-generational LRE

We deal with general values of dispersal rates (d_f and d_m, each ranging between 0 and 1), but will make an exception for $d_\mathrm{m} = 0$ (no male-dispersal), because the results for $d_\mathrm{m} = 0$ are qualitatively different from the results for general values $0 < d_\mathrm{m} \leq 1$. The other advantage of presenting the special case for $d_\mathrm{m} = 0$ is that it gives a simple formula, that is comparable with the previous theoretical work, and applies to many species like *Melittobia* [60]. As such, we present the results for $d_\mathrm{m} = 0$ and $0 < d_\mathrm{m} \leq 1$ separately; note that $d_\mathrm{m} = d_\mathrm{f} = 0$ means that patches are completely isolated from each other and entails stochastic analyses ([63]), and so we omit this possibility.

We find that Hamilton's rule, which assesses the direction of selection, is equal to:

$$\widehat{Z_{\emptyset}} - z - \underbrace{\kappa}_{\text{scaled relatedness}} \cdot \underbrace{\frac{\alpha(1-z)}{1-\alpha(1-z)} \cdot z}_{=\text{[intra-LRE effect]}>0} > 0 \tag{10}$$

where κ, referred to as 'scaled relatedness', measures the extent to which the extra juveniles produced via LRE are likely to share the common ancestor (see Appendix B for more precise interpretation), as a function of $n, d_{\mathrm{f}}, d_{\mathrm{m}}$. The last term represents the effect of intra-generational LRE on the inclusive fitness of the focal individual. Clearly, with LRE, cESS is smaller than $\widehat{Z_{\emptyset}}$, that is, LRE leads to more female-biased sex ratios (Fig 4A).

We numerically evaluated the cESS to find that larger group sizes favour less female biased sex ratio and the cESS eventually approaches 1/2 (or Fisherian sex ratio) as $n \to +\infty$ (Fig 5, left panels). Increasing α leads to more female-biased sex ratios (Figs 4 and 5). As in the results for no LRE, sex ratios may be biased towards the more dispersing sex, but LRE makes the evolution of female-biased sex ratios more likely.

Example: no male-dispersal, $d_{\mathrm{m}} = 0$

Suppose for now $d_{\mathrm{m}} = 0$, and in this case, we can show that $\kappa = 1/n$ and therefore ploidy has no influence on the effect of LRE nor κ [21, 45]. This is partly because males are fully philopatric, mating takes place in prior to female dispersal, and female dispersal allows males' and females' gametes both to disperse by the same degree, which leads to $\ell_{\mathrm{RC}} = \ell_{\mathrm{MC}} - \ell_{\mathrm{MB}} = (1-d_{\mathrm{f}})^2$ (i.e., males and females are subject to the same degree of local competition). This scenario is similar to plants undergoing gametic (pollen) and zygotic (seed) dispersal when pollen dispersal is fully restricted within a patch (see [48, 64] for more details). That is, decomposing the scale of competition gives otherwise missed fact: when $d_{\mathrm{m}} = 0$, the scale of competition for both sexes is equivalent.

Varying male-dispersal, $d_{\mathrm{m}} > 0$

Now we tune d_{m} from 0 to 1 and assess its impacts upon cESS. We find that increasing d_{m} or d_{f} is likely to favour less or more female-biased sex ratios (Fig 5; respectively), and taking both to 1 leads to Fisherian sex ratio. For an intermediate male dispersal ($d_{\mathrm{m}} = 0.5$), male-bias is still likely but with a possibility of switching from male- to female-bias as α or d_{f} increases. Therefore, under intra-generational LRE, the sex ratios, which could be otherwise male biased, may be biased towards female by natural selection.

Trans-generational LRE

We find that trans-generational LRE also facilitates the evolution of female-biased sex ratio (Fig 4B). Numerical estimation revealed that larger group sizes favour less female biased sex ratio and the cESS eventually approaches 1/2 (or Fisherian sex ratio) as $n \to +\infty$ (Fig 6, left panels), and increasing α leads to more female-biased sex ratio (Fig 6), as in the trans-generational LRE model. The inclusive fitness effect of trans-generational LRE decreases with d_{f}; when $d_{\mathrm{f}} = 1$ (full female dispersal), for instance, the effect of trans-generational LRE vanishes for any $\alpha > 0$ (Fig 6A, midel panel). The trans-generational LRE, which ensues after female dispersal, is sensitive to d_{f} because the probability that females can help their relatives (by remaining in the natal patch, $1 - d_{\mathrm{f}}$) decreases with d_{f}.

Example: No male-dispersal

When $d_{\mathrm{m}} = 0$, we find that Hamilton's rule reads:

$$\widehat{Z_{\emptyset}}\Big|_{d_{\mathrm{m}}=0} - z - \frac{1}{n} \cdot \underbrace{\frac{\alpha \ell_{\mathrm{RC}}(1-z)}{1-\alpha \ell_{\mathrm{RC}}(1-z)} z}_{=[\text{trans-LRE effect}]>0} > 0, \tag{11}$$

where the scaled relatedness is now given by $\kappa = 1/n$ as in the intra-generational model, but the last term on Eqn (11) is clearly smaller than that on Eqn (10); i.e., trans-generational LRE is weaker than is intra-generational LRE in terms of their effects on selection.

Varying male-dispersal

Varying $d_{\mathrm{m}} > 0$ turns out to give complicated form of Hamilton's rule (see Appendix B), except for the extreme case $d_{\mathrm{m}} = 1$:

$$\widehat{Z_{\emptyset}}\Big|_{d_{\mathrm{m}}=1} - z - \underbrace{\frac{c_{\mathrm{m}} R_0^{\mathbf{m}} + c_{\mathrm{f}} R_0^{\mathbf{f}}(1-\ell_{\mathrm{RC}})}{c_{\mathrm{m}} R_{\bullet}^{\mathbf{m}} + c_{\mathrm{f}}\left(R_{\bullet}^{\mathbf{f}} - \ell_{\mathrm{RC}} R_0^{\mathbf{f}}\right)}}_{=\kappa \text{ with } d_{\mathrm{m}}=1} \cdot \frac{\frac{\alpha}{2}\ell_{\mathrm{RC}}(1-z)}{1-\frac{\alpha}{2}\ell_{\mathrm{RC}}(1-z)} z > 0, \tag{12}$$

which tells us that $\alpha \ell_{\mathrm{RC}}$ on Eqn (11) is now replaced with $\alpha \ell_{\mathrm{MC}}/2$, with $1/2$ meaning that half of females' genes are transmitted to females (who, as opposed to males all dispersing, are likely philopatric and thus potentially contribute to the build up of trans-generational relatedness).

Discussion

We found that cooperative interactions between females (LRE) can lead to more female-biased sex ratios than those predicted by local mate competition (LMC) theory. Specifically, we have considered two types of LRE, and found that cooperation from offspring to their parents generation (intra-generational LRE) can lead to more female biased sex ratios than cooperation between members of the same generation (inter-generational LRE). This difference is because intra-generational LRE occurs prior to female dispersal and therefore each juvenile female has direct access to helping genetically related juveniles, thereby increasing the inclusive fitness of producing daughters over sons; in contrast, trans-generational LRE occurs after female dispersal, and dispersed females are unable to provide help to relatives, thereby reducing the inclusive fitness benefit of LRE as d_{f} increases. Our key result is therefore that LRE, alongside LMC, has the potential to generate extremely female-biased sex ratios, of the form that have been observed in nature, in species such as *Melittobia* and *Sclerodemus* wasps [29–31].

As found by previous theory, we found that, in the absence of LRE, selection in general favours the biased sex ratio towards the more dispersing sex [23, 56, 62], which is because kin competition between members of one sex reduces the relative value of producing that sex. In contrast, when females interact cooperatively (LRE), this increases the relative value of producing females, and natural selection thus favours less male-biased or more female-biased sex ratios (Figs 4 and 5; [17, 42, 43, 56, 65, 66]; but see [67]).

Despite the formal similarity between intra- and trans-generational LRE models, there is the quantitative difference in the consequences of dispersal rates for sex ratios. For intra-generational LRE, increasing the intensity of LRE (α) leads to more female-biased sex ratio by increasing the benefit of producing juvenile females who assist their mother (Figs 5 and 6). This selective force acts even when female dispersal rate is high, because intra-generational LRE allows juvenile females to assist their own mother before dispersal. In contrast, the trans-generational LRE predicts that increasing the intensity of LRE (α) has a weaker effect on the selection for the female-bias (Figs 4 and 6) compared to the intra-generaional LRE. The inclusive fitness effect of trans-generational LRE vanishes if females undergo complete dispersal; in other words, $d_{\mathrm{f}} = 1$ implies that cESS is independent of α for the trans-generational LRE. This result is because following complete female-dispersal, dispersed juvenile females (the proportion d_{f}) do not have the access to their relatives and there are unable to engage in helping. Hence, the two models suggest that distinguishing the timing of LRE is of crucial importance for sex ratio evolution in empirical and experimental systems.

Our models provide a formal theoretical explanation for the extreme sex ratio biases that have been observed in *Sclerodermus harmand*, and several *Melittobia* wasp species. In both these cases, local mate competition

is likely, but the offspring sex ratios are much more female biased than would be expected from local mate competition theory (LMC; Fig 1). We have shown in our trans-generational model that a combination of cooperative interactions between sisters (LRE) and LMC can lead to more female biased sex ratios, consistent with the empirical data. In *Sclerodermus harmandi*, females cooperate to suppress hosts and care for their brood cares ([31, 32, 41]). In *Melittobia*, females tend to aggregate on the same hosts and cooperatively parasitise them (J. Abe, unpublished;[68]), females fight against the symbiont mites of host species [69], and their female offspring collaborate to tunnel into the materials of host nests to disperse [70]. However, the quantitative discrepancy remains large (Figs 1 and 6), Possible factors may include multiplicativity of LRE $\beta(z) = K/\left(1-\alpha(1-z)^{\theta}\right)$ (as in Appendix B) which lead to even more female-biased sex ratios and LRE from juvenile females that specifically increases the production of daughters (not sons), or alternatively, we may need to consider cohesive dispersal or kin recognition among females that promotes LRE but reduces LRC. Despite this, our models offer a useful framework to study the evolution of sex ratios under LRE and allow further development of theoretical work.

Our models are also applicable to a wide range of other organisms, in which there can be both cooperative (positive) and competitive (negative) interactions with relatives. For example: (i) mammals, birds and insects where offspring help their parents, but can also compete for breeding sites (territories; [35, 36, 40]); (ii) allodapine bees where sisters cooperate to form nests, but offspring can compete for resources [34, 37, 38]; (iii) *Diadasina distincta* bees where individuals must compete for nest sites, but nesting at higher densities can reduce parasitism [39]. In all cases, our general prediction is that a female-biased sex ratio bias is favoured to increase cooperative interactions and reduce competitive interactions.

To conclude, our analysis suggest that LRE from females does promote female-biased sex ratio, but its impacts upon the evolutionary outcomes differ, especially in terms of the consequences of dispersal. One of the possible extensions of the present model is to study joint evolution of sex ratio and other traits under LRE [71, 72]. For instance, how does joint evolution shape the association between sex-biased dispersal and sex allocation strategy, e.g., in birds and vertebrates [36, 73–76]? Future studies could be directed towards more realistic modeling of LRE, by e.g., incorporating the effects of the number of adult females (n) on LRE, or working on intra-sexual LRE ('who helps whom'; [77, 78]). Working with specific organisms of interest based upon multiple approaches may yield a better understanding of the evolution of sex ratios in viscous populations.

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Author contribution

JA conceived the idea; RI carried out the mathematical analyses; JA and RI drafted the first version of the manuscript; all authors contributed to the revision.

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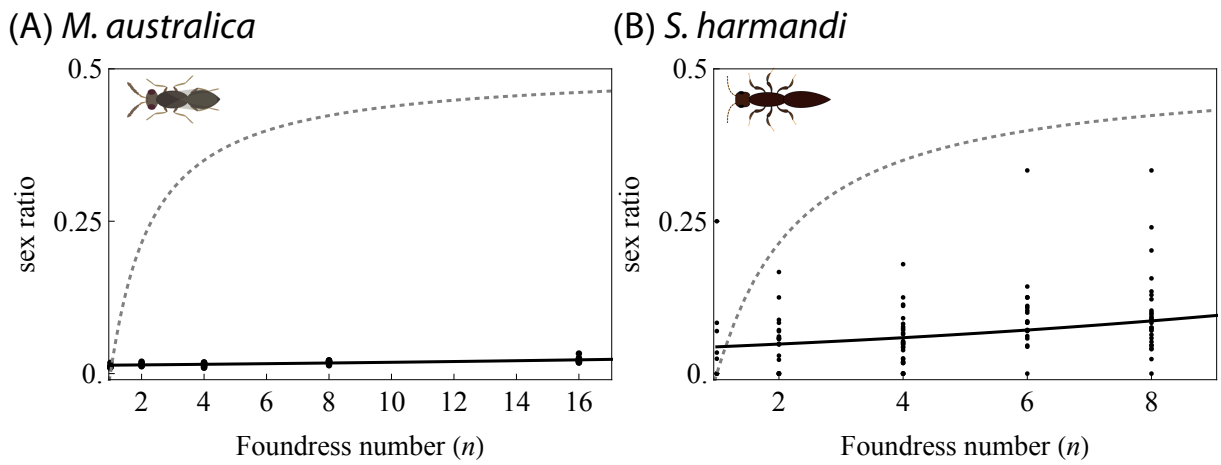


Figure 1: Extremely female-biased sex ratio in (A) *Melittobia australica* from [29], and (B) *Sclerodermus harmandi* from [31, 41]. Outliers removed for (B), as in the original artciles [31, 41]. Note that the horizontal axes are scaled differently. Dotted: $\big((n-1)(4n-2)\big)/\big(2n(4n-1)\big)$ (LMC sex ratio for haplodiploids, for reference). Solid lines in (A): predicted values by generalized linear models; (B): shown in [31].

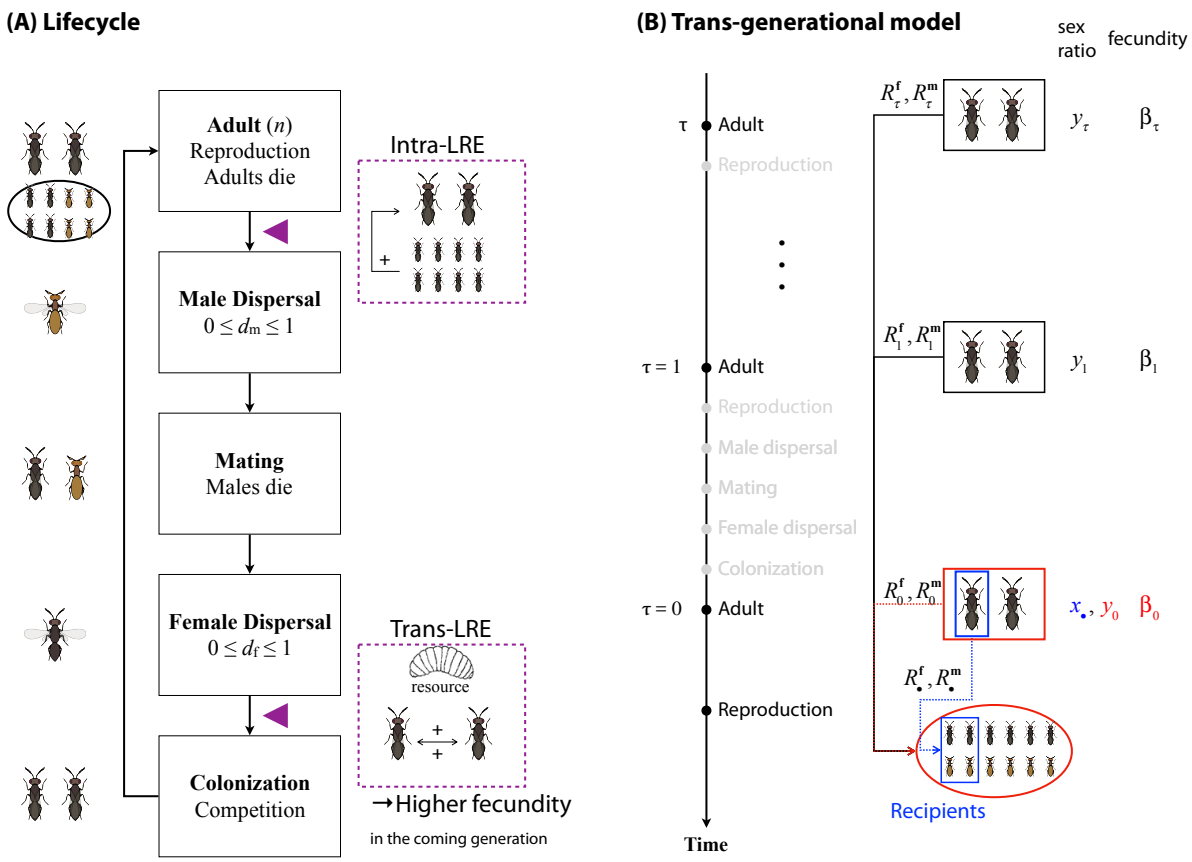


Figure 2: Schematic illustration of (A) lifecycle and (B) trans-generational relatedness. (A) Gray individuals: females. Brown individuals: males. Purple triangle: possible timing of LRE. Model species: *Melittobia australica* (but note that males of this species really are of flightless; [60]). (B) Adult within blue box: the focal individual; juveniles within blue box: the focal individual's offspring; red: average in the patch. We count the generations backwards in time ($\tau = 0$ the present, $\tau = 1$ parental, etc). R are relatedness coefficients, each from the corresponding actor's perspective (arrows).

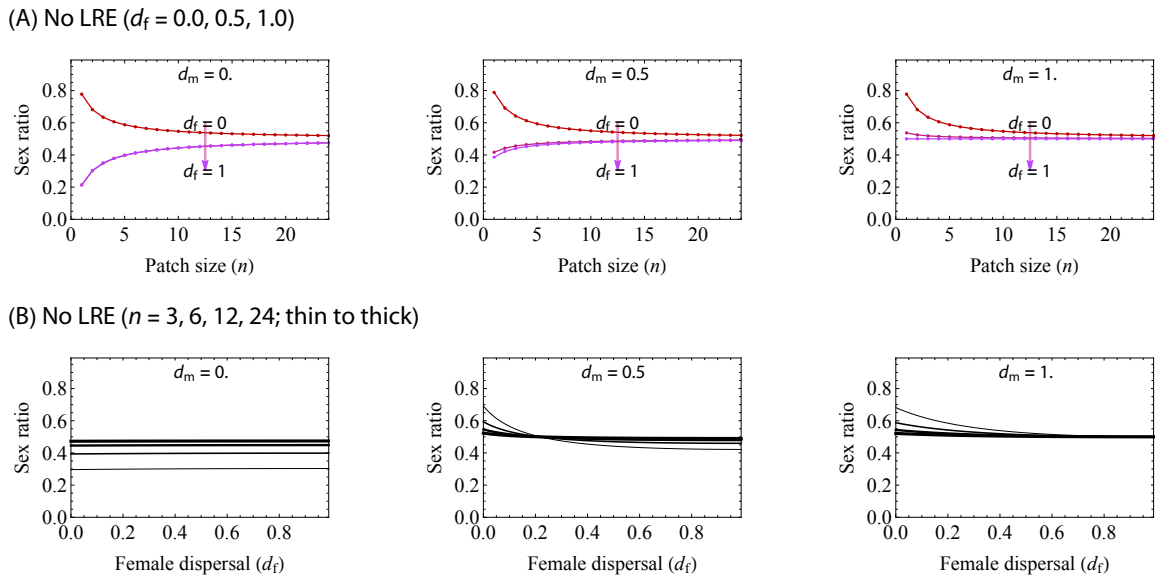


Figure 3: Evolutionary outcomes of sex ratio without LRE under haplodiploidy. (A) Sensitivity to n. Larger n monotonically tends to favour Fisherian sex ratio. Increasing d_f is likely to favour less male-bias. (B) Sensitivity to d_f (with $d_m = 0, 0.5, 1$ from left to right panels, and $n = 2, 4, 8, 16$ from thin to thick curves). Generally, high group sizes (n) favour Fisherian sex ratio. When male dispersal is completely limited (left panel), sex ratio is almost invariant with d_f. Increasing d_m results in a shift to male-bias when female dispersal is small, and as d_f increases, female-bias is likely to be favoured by selection (middle). When male dispersal is complete ($d_m = 1$), the resulting sex ratio is male-biased and approaches Fisherian (1/2) as d_f increases.

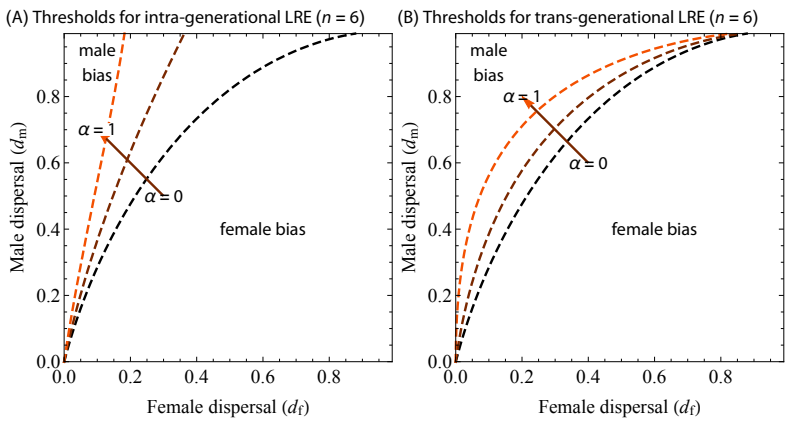


Figure 4: Threshold condition for the biased sex ratio at cESS. Each contour represents the condition for Fisherian sex ratio (1/2) to be cESS and separates the region for female- and male-biased sex ratios. Female biased sex ratio (bottom and right zone) becomes more likely as α increases (where threshold curves plotted for $\alpha = 0, 0.5$ and 1).

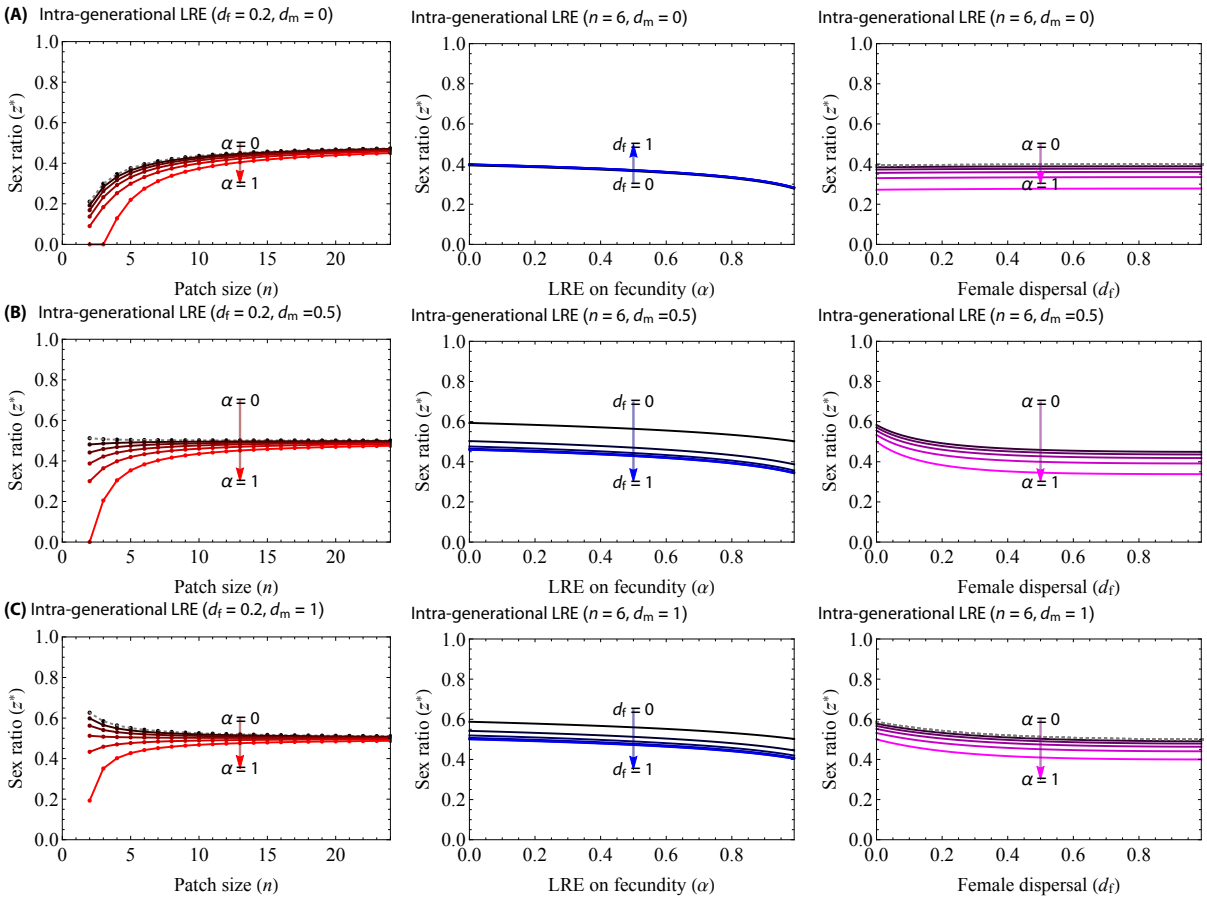


Figure 5: cESS under $d_m = 0$, for intra- generational LRE (top panels, A) and trans-generational LRE (bottom panels, B), under haplodiploidy. Gray dots: results under no LRE.

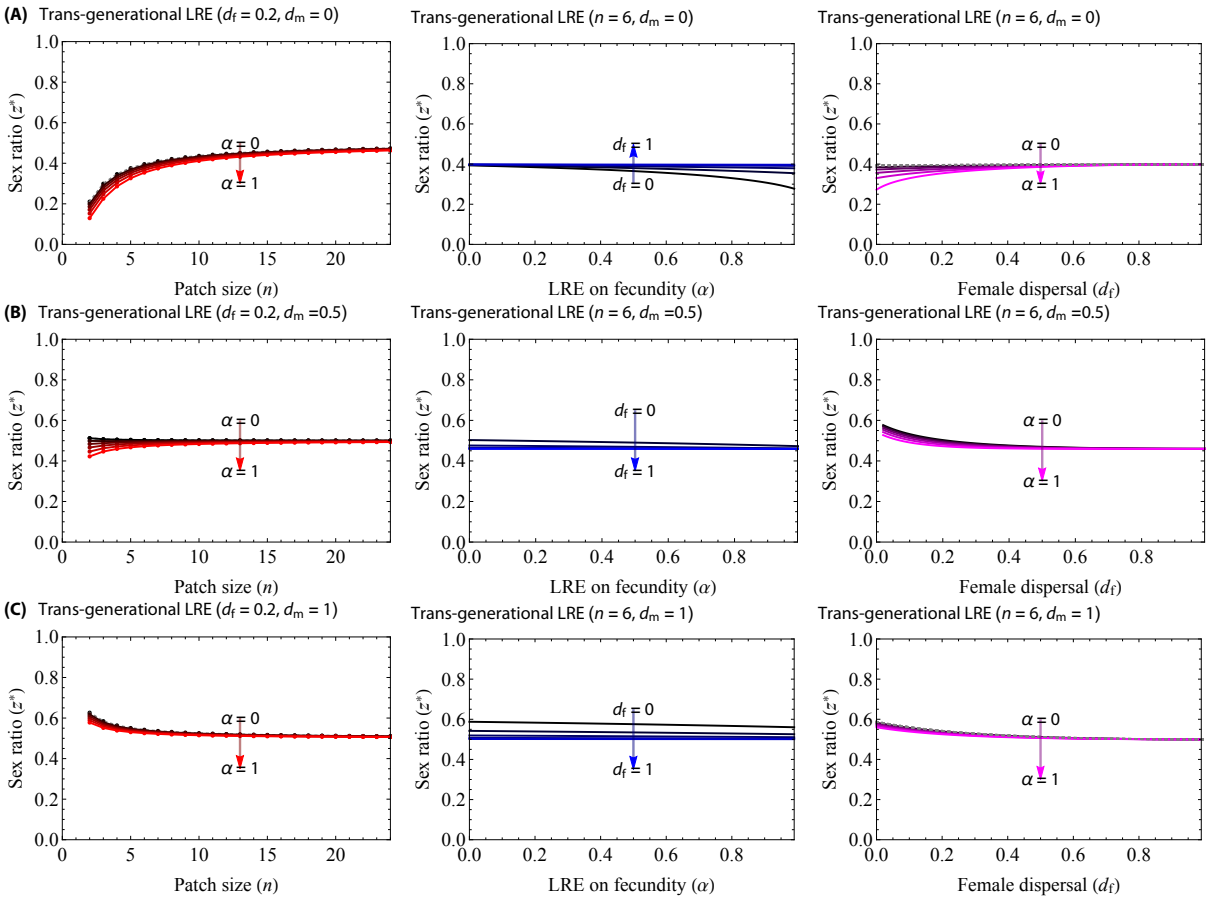


Figure 6: cESS under $d_m = 0$, for intra- generational LRE (top panels, A) and trans-generational LRE (bottom panels, B), under haplodiploidy. Gray dots: results under no LRE.

Appendix

A Fecundity mediated by LRE

Let us for now focus on the intra-generational model. Pick a focal patch and denote the average phenotype on that patch by y_0; on that patch, the fecundity per capita may be the sum of (i) baseline fecundity (denoted by K), and (ii) effects of LRE; the latter occurs from helping behaviors of daughters, and the total number of females per patch is given by $n \cdot (1 - y_0) \cdot \beta(y_0)$, in which such an effect is equally shared by n females and thus should be divided by n (therefore n being canceled), which hence yields:

$$\beta_0 := \beta(y_0) = K + \alpha(1 - y_0)\beta(y_0), \tag{S-1}$$

as in the main text. The same logic gives the corresponding recursion for the trans-generational model, by modifying the equation above to:

$$\beta_0 := K + \alpha\Big((1 - d_\mathrm{f})(1 - y_1)n\beta_1 + d_\mathrm{f}(1 - z)\beta^\circ n\Big)/n, \tag{S-2}$$

which may be reasoned as follows: the first term is a baseline fecundity; the second term overall represents the effect of LRE; the fraction $1 - d_\mathrm{f}$ of females derives from the natal patch, in a density $(1 - y_1)\beta_1 n$; d_f from other patches, in a density $(1 - z)\beta^\circ n$. Assuming that such LRE effect is shared among n individuals, we divide this term by n, obtaining the above expression. We can see that β_0 is a function of (β_1, y_1), and β_1 is a function of (β_2, y_2) (by the same reasoning), and so forth; this means that we need to deal with the nested function of β_0, based upon Lehmann [45, 51].

B Invasion fitness and the selection gradient: general

The reproductive success of a focal individual occurs through her daughters (winning the breeding opportunity) and her sons (winning the mating opportunity), and therefore we separate these two terms explicitly by using the class reproductive values [50, 55]. We use the subscripts `in` and `tr` to distinguish the two models.

B-1 Success via daughters

First of all, the focal female can produce the total number β_0 of eggs. A proportion $1 - x_\bullet$ of those egges develops into female. Therefore we have $(1 - x_\bullet)\beta_0$ of daughters born to the focal. Pick one of the daughters;

- With a probability of $1 - d_\mathrm{f}$, she stays in her natal patch, ending up with competing with, on average, $(1 - d_\mathrm{f})(1 - y_0)\beta_0$ of juvenile females born in the same patch, plus $d_\mathrm{f}(1 - z)\beta^\circ$ of juvenile females each born in a different patch.
- With a probability of d_f, she disperses to an alternative patch to compete with $(1 - z)\beta^\circ$ of juvenile females.

Therefore, we have:

$$\begin{aligned} W_{\bullet}^{\mathbf{f}}\big(x_{\bullet}, y_0, \beta_0\big) &:= (1-d_{\mathrm{f}})\frac{(1-x_{\bullet})\beta_0}{(1-d_{\mathrm{f}})\big(1-y_0\big)\beta_0 + d_{\mathrm{f}}(1-z)\beta^{\circ}} + d_{\mathrm{f}}\frac{(1-x_{\bullet})\beta_0}{(1-z)\beta^{\circ}} \\ &=: W_{\bullet}^{\mathbf{f}} \end{aligned} \tag{S-3}$$

as displayed in the main text. At phenotypic neutrality (i.e., $x_{\bullet} = y_0 = z$ and $\beta_0 = \beta^{\circ}$), we have $W_{\bullet}^{\mathbf{f}}\big(z, z, \beta^{\circ}\big) \equiv 1$.

B-2 Success via sons

The same logic gives the success via sons. The focal female produces $x_{\bullet}\beta_0$ of sons who may compete against on average $(1-d_{\mathrm{m}})y_0\beta_0 + d_{\mathrm{m}}z\beta^{\circ}$ of juvenile males by staying philopatric (which occurs with a probability of $1-d_{\mathrm{m}}$); in which case, whether the male gamete survives to the next generation or not now relies on whether the mated female wins a breeding opportunity or not. Because mating is fully random within the patch, $W_0^{\mathbf{f}}\big(y_0, y_0, \beta_0\big)$ gives the proportional success of the sons' mating partners. If the sons instead disperse, which occurs with a probability of d_{m}, then they compete with on average $z\beta^{\circ}$ of males, and their mating partners' success is $W_{\bullet}^{\mathbf{f}}\big(z, z, \beta^{\circ}\big) = 1$. Therefore,

$$\begin{aligned} W_{\bullet}^{\mathbf{m}}\big(x_{\bullet}, y_0, \beta_0\big) &:= \frac{(1-d_{\mathrm{m}})x_{\bullet}\beta_0}{(1-d_{\mathrm{m}})y_0\beta_0 + d_{\mathrm{m}}z\beta^{\circ}} \underbrace{\left(\frac{(1-d_{\mathrm{f}})\big(1-y_0\big)\beta_0}{(1-d_{\mathrm{f}})\big(1-y_0\big)\beta_0 + d_{\mathrm{f}}(1-z)\beta^{\circ}} + \frac{d_{\mathrm{f}}\big(1-y_0\big)\beta_0}{(1-z)\beta^{\circ}}\right)}_{=W^{\mathbf{f}}(y_0,y_0,\beta_0)=:W_0^{\mathbf{f}}} \\ &\quad + \frac{d_{\mathrm{m}}x_{\bullet}\beta_0}{z\beta^{\circ}} \\ &=: W_{\bullet}^{\mathbf{m}} \end{aligned} \tag{S-4}$$

as displayed in the main text.

B-3 Total fitness

The total number of genes of the focal individual transmitted to the next generation is therefore given by $W_{\bullet} = c_{\mathrm{f}}W_{\bullet}^{\mathbf{f}} + c_{\mathrm{m}}W_{\bullet}^{\mathbf{m}}$ [27, 49, 50].

B-4 Selection gradient (Hamilton's rule): preliminary

Pick the locus Ξ that encodes the sex ratio and write ξ for the genic value of an allele of the locus from a juvenile in the focal patch, with $\xi^{\mathbf{f}}$ for female and $\xi^{\mathbf{m}}$ for male, respectively. In addition, we denote the breeding value of (i) the juvenile's mother by $\widetilde{\xi}$, (ii) the average breeding value of the adult females in the same patch in the same generation by η_0, (iii) the average breeding value of all adult females in the metapopulation by ζ, and (iv) the average breeding value of the adult females in the same patch τ-generations prior to the present by η_{τ} for $\tau \geq 1$.

Under vanishingly small genetic variation in the metapopulation, the direction of selection can be assessed by

the sign of:

$$\frac{\mathrm{d}W_\bullet}{\mathrm{d}\xi} = c_\mathrm{f}\,\frac{\mathrm{d}W_\bullet^\mathbf{f}}{\mathrm{d}\xi^\mathbf{f}} + c_\mathrm{m}\,\frac{\mathrm{d}W_\bullet^\mathbf{m}}{\mathrm{d}\xi^\mathbf{f}}\,, \tag{S-5}$$

evaluated at $\xi = \xi^\mathbf{f} = \xi^\mathbf{m} = \zeta$, in which c_f (or c_m) is interpreted as the probability that the focal gene lineage is found in a female (or male, respectively). If the above derivative is positive, then selection favours a slightly larger allocation to males.

Further decomposition of the partial derivatives are as follows [27]:

$$\begin{aligned}\frac{\mathrm{d}W_\bullet^\mathbf{f}}{\mathrm{d}\xi^\mathbf{f}} &= \frac{\partial W_\bullet^\mathbf{f}}{\partial x_\bullet}\cdot\frac{\mathrm{d}x_\bullet}{\mathrm{d}\widetilde{\xi}}\cdot\frac{\mathrm{d}\widetilde{\xi}}{\mathrm{d}\xi^\mathbf{f}} + \frac{\partial W_\bullet^\mathbf{f}}{\partial y_0}\cdot\frac{\mathrm{d}y_0}{\mathrm{d}\eta_0}\cdot\frac{\mathrm{d}\eta_0}{\mathrm{d}\xi^\mathbf{f}} + \sum_{\tau=0}^{\infty}\frac{\partial W_\bullet^\mathbf{f}}{\partial \beta_0}\cdot\frac{\partial \beta_0}{\partial y_\tau}\cdot\frac{\mathrm{d}y_\tau}{\mathrm{d}\eta_\tau}\cdot\frac{\mathrm{d}\eta_\tau}{\mathrm{d}\xi^\mathbf{f}} \\ &= \left(\frac{\partial W_\bullet^\mathbf{f}}{\partial x_\bullet}\,Q_\bullet^\mathbf{f} + \frac{\partial W_\bullet^\mathbf{f}}{\partial y_0}\,Q_0^\mathbf{f} + \sum_{\tau=0}^{\infty}\frac{\partial W_\bullet^\mathbf{f}}{\partial \beta_0}\cdot\frac{\partial \beta_0}{\partial y_\tau}\,Q_\tau^\mathbf{f}\right)\sigma,\end{aligned} \tag{S-6}$$

where we have written (i) $Q_\bullet^\mathbf{f}$ for the consanguinity of the focal female to her own daughters, (ii) $Q_0^\mathbf{f}$ for the consanguinity of the focal female to the juvenile females born to the focal patch in the present generation, (iii) $Q_\tau^\mathbf{f}$ for the consanguinity of a random juvenile female and an adult female breeding in the focal patch τ-generations prior to the present (for $\tau \geq 1$), and (iv) σ is an arbitrary constant representing the slope of phenotype on genotype, given by $\mathrm{d}x_\bullet/\mathrm{d}\widetilde{\xi} = \mathrm{d}y_0/\mathrm{d}\eta_0 = \mathrm{d}y_\tau/\mathrm{d}\eta_\tau = \sigma$, which we hereafter rescale $\sigma = 1$.

The similar expansion yields:

$$\begin{aligned}\frac{\mathrm{d}W_\bullet^\mathbf{m}}{\mathrm{d}\xi^\mathbf{m}} &= \frac{\partial W_\bullet^\mathbf{m}}{\partial x_\bullet}\cdot\frac{\mathrm{d}x_\bullet}{\mathrm{d}\widetilde{\xi}}\cdot\frac{\mathrm{d}\widetilde{\xi}}{\mathrm{d}\xi^\mathbf{m}} + \frac{\partial W_\bullet^\mathbf{m}}{\partial y_0}\cdot\frac{\mathrm{d}y_0}{\mathrm{d}\eta_0}\cdot\frac{\mathrm{d}\eta_0}{\mathrm{d}\xi^\mathbf{m}} + \sum_{\tau=0}^{\infty}\frac{\partial W_\bullet^\mathbf{m}}{\partial W_0^\mathbf{f}}\cdot\frac{\partial W_0^\mathbf{f}}{\partial \beta_0}\cdot\frac{\partial \beta_0}{\partial y_\tau}\cdot\frac{\mathrm{d}y_\tau}{\mathrm{d}\eta_\tau}\cdot\frac{\mathrm{d}\eta_\tau}{\mathrm{d}\xi^\mathbf{m}} + \sum_{\tau=0}^{\infty}\frac{\partial W_\bullet^\mathbf{m}}{\partial \beta_0}\cdot\frac{\partial \beta_0}{\partial y_\tau}\cdot\frac{\mathrm{d}y_\tau}{\mathrm{d}\eta_\tau}\cdot\frac{\mathrm{d}\eta_\tau}{\mathrm{d}\xi^\mathbf{m}} \\ &= \frac{\partial W_\bullet^\mathbf{m}}{\partial x_\bullet}\,Q_\bullet^\mathbf{m} + \frac{\partial W_\bullet^\mathbf{m}}{\partial y_0}\,Q_0^\mathbf{m} + \sum_{\tau=0}^{\infty}\frac{\partial W_\bullet^\mathbf{m}}{\partial W_0^\mathbf{f}}\cdot\frac{\partial W_0^\mathbf{f}}{\partial \beta_0}\cdot\frac{\partial \beta_0}{\partial y_\tau}\,Q_\tau^\mathbf{m} + \sum_{\tau=0}^{\infty}\frac{\partial W_\bullet^\mathbf{m}}{\partial \beta_0}\cdot\frac{\partial \beta_0}{\partial y_\tau}\,Q_\tau^\mathbf{m},\end{aligned} \tag{S-7}$$

with basically the same notation as above ($^\mathbf{f}$ being replaced with $^\mathbf{m}$).

From these, the selection gradient reads:

$$
\begin{aligned}
g(z) := c_{\mathrm{f}} \frac{\mathrm{d}W_{\bullet}^{\mathbf{f}}}{\mathrm{d}\xi^{\mathbf{f}}} + c_{\mathrm{m}} \frac{\mathrm{d}W_{\bullet}^{\mathbf{m}}}{\mathrm{d}\xi^{\mathbf{m}}} = & \underbrace{c_{\mathrm{f}}\left(\frac{\partial W_{\bullet}^{\mathbf{f}}}{\partial x_{\bullet}} Q_{\bullet}^{\mathbf{f}} + \frac{\partial W_{\bullet}^{\mathbf{f}}}{\partial y_0} Q_0^{\mathbf{f}}\right) + c_{\mathrm{m}}\left(\frac{\partial W_{\bullet}^{\mathbf{m}}}{\partial x_{\bullet}} Q_{\bullet}^{\mathbf{m}} + \frac{\partial W_{\bullet}^{\mathbf{m}}}{\partial y_0} Q_0^{\mathbf{m}} + \frac{\partial W_{\bullet}^{\mathbf{m}}}{\partial W_0^{\mathbf{f}}} \frac{\partial W_0^{\mathbf{f}}}{\partial y_0} Q_0^{\mathbf{m}}\right)}_{=:g_{\emptyset}(z)} \\
& + \underbrace{\left(c_{\mathrm{f}} \frac{\partial W_{\bullet}^{\mathbf{f}}}{\partial \beta_0} \frac{\partial \beta_0}{\partial y_0} Q_0^{\mathbf{f}} + c_{\mathrm{m}} \frac{\partial W_{\bullet}^{\mathbf{m}}}{\partial \beta_0} \frac{\partial \beta_0}{\partial y_0} Q_0^{\mathbf{m}} + c_{\mathrm{m}} \frac{\partial W_{\bullet}^{\mathbf{m}}}{\partial W_0^{\mathbf{f}}} \frac{\partial W_0^{\mathbf{f}}}{\partial \beta_0} \frac{\partial \beta_0}{\partial y_0} Q_0^{\mathbf{m}}\right)}_{=:g_{\mathtt{in}}(z)} \\
& + \underbrace{\sum_{\tau=1}^{\infty}\left(c_{\mathrm{f}} \frac{\partial W_{\bullet}^{\mathbf{f}}}{\partial \beta_0} \frac{\partial \beta_0}{\partial y_\tau} Q_\tau^{\mathbf{f}} + c_{\mathrm{m}} \frac{\partial W_{\bullet}^{\mathbf{m}}}{\partial \beta_0} \frac{\partial \beta_0}{\partial y_\tau} Q_\tau^{\mathbf{m}} + c_{\mathrm{m}} \frac{\partial W_{\bullet}^{\mathbf{m}}}{\partial W_0^{\mathbf{f}}} \frac{\partial W_0^{\mathbf{f}}}{\partial \beta_0} \frac{\partial \beta_0}{\partial y_\tau} Q_\tau^{\mathbf{m}}\right)}_{=:g_{\mathtt{tr}}(z)}.
\end{aligned}
\tag{S-8}
$$

From this we define Hamilton's rule by:

$$
\frac{g(z)}{z(1-z)\cdot\left(c_{\mathrm{f}}\left(Q_{\bullet}^{\mathbf{f}} - \ell_{\mathrm{RC}} Q_0^{\mathbf{f}}\right) + c_{\mathrm{m}}\left(Q_{\bullet}^{\mathbf{m}} - (\ell_{\mathrm{MC}} - \ell_{\mathrm{MB}}) Q_0^{\mathbf{f}}\right)\right)} > 0. \tag{S-9}
$$

B-5 Partial derivatives

We use the following partial derivatives (each evaluated at neutrality):

$$
\begin{aligned}
\frac{\partial W_{\bullet}^{\mathbf{f}}}{\partial x_{\bullet}} &= -\frac{1}{1-z}; \\
\frac{\partial W_{\bullet}^{\mathbf{f}}}{\partial y_0} &= \frac{\ell_{\mathrm{RC}}}{1-z}; \\
\frac{\partial W_{\bullet}^{\mathbf{m}}}{\partial x_{\bullet}} &= \frac{1}{z}; \\
\frac{\partial W_{\bullet}^{\mathbf{m}}}{\partial y_0} &= \frac{-(1-d_{\mathrm{m}})^2}{z} = -\frac{\ell_{\mathrm{MC}}}{z}; \\
\frac{\partial W_{\bullet}^{\mathbf{f}}}{\partial \beta_0} &= \frac{1-\ell_{\mathrm{RC}}}{\beta^{\circ}}; \\
\frac{\partial W_{\bullet}^{\mathbf{m}}}{\partial W_0^{\mathbf{f}}} \cdot \frac{\partial W_0^{\mathbf{f}}}{\partial \beta_0} &= \frac{\ell_{\mathrm{MB}}}{\beta^{\circ}} \\
\frac{\partial W_{\bullet}^{\mathbf{m}}}{\partial \beta_0} &= \frac{1-\ell_{\mathrm{MC}}}{\beta^{\circ}}.
\end{aligned}
\tag{S-10}
$$

B-6 Intra-generational consanguinities

We denote the consanguinity between (i) a juvenile female and male sharing the same patch by $Q_0^{\mathbf{fm}}$, (ii) two juvenile males sharing the same patch by $Q_0^{\mathbf{mm}}$, and (iii) two juvenile females sharing the same patch by $Q_0^{\mathbf{ff}}$, each in the same generation $\tau = 0$.

Using the standard method, for haplodioloids

$$\begin{aligned} Q_0^{\mathbf{ff}} &= \frac{1}{n}\left(\frac{Q_\bullet + 2(1-d_\mathrm{m})Q_0^{\mathbf{fm}} + 1}{4}\right) + \frac{n-1}{n}\ell_\mathrm{RC}\left(\frac{Q_0^{\mathbf{ff}} + 2(1-d_\mathrm{m})Q_0^{\mathbf{fm}} + (1-d_\mathrm{m})^2 Q_0^{\mathbf{mm}}}{4}\right), \\ Q_0^{\mathbf{fm}} &= \frac{1}{n}\left(\frac{Q_\bullet + (1-d_\mathrm{m})Q_0^{\mathbf{fm}}}{2}\right)\frac{n-1}{n}\ell_\mathrm{RC}\left(\frac{Q_0^{\mathbf{ff}} + (1-d_\mathrm{m})Q_0^{\mathbf{fm}}}{2}\right), \\ Q_0^{\mathbf{mm}} &= \frac{1}{n}Q_\bullet + \frac{n-1}{n}\ell_\mathrm{RC}Q_0^{\mathbf{ff}} \end{aligned} \tag{S-11}$$

[20, 79]. Solving these to find the unique solution, we can determine each consanguinity coefficient.

The consanguinity of an adult female to

(i) herself is $Q_\bullet = \big(1 + (1-d_\mathrm{m})Q_0^{\mathbf{fm}}\big)/2$,
(ii) her daughter is $Q_\bullet^{\mathbf{f}} := \big(Q_\bullet + (1-d_\mathrm{m})Q_0^{\mathbf{fm}}\big)/2$,
(iii) her son is $Q_\bullet^{\mathbf{m}} := \big(1 + (1-d_\mathrm{m})Q_0^{\mathbf{fm}}\big)/2$,
(iv) a random juvenile female born in the same patch in the present generation is $Q_0^{\mathbf{f}} := \big(Q_\bullet^{\mathbf{f}} + (1-d_\mathrm{m})Q_0^{\mathbf{fm}}\big)/n + (1-d_\mathrm{f})^2\big(1-1/n\big)\big(Q_0^{\mathbf{ff}} + (1-d_\mathrm{m})Q_0^{\mathbf{fm}}\big)/2$, which turns out to equal $Q_0^{\mathbf{fm}}$, and
(v) a random juvenile male in the same patch born in the present generation is $Q_0^{\mathbf{m}} := Q_\bullet^{\mathbf{m}}/n + (1-d_\mathrm{f})^2\big(1-1/n\big)Q_0^{\mathbf{ff}} = Q_0^{\mathbf{mm}}$.

Also, the relatedness coefficient, from the adult female's perspective [20, 54], to

(i) her daughter is $R_\bullet^{\mathbf{f}} := Q_\bullet^{\mathbf{f}}/Q_\bullet$,
(ii) a random juvenile female on the same patch born in the present generation is $R_0^{\mathbf{f}} := Q_0^{\mathbf{f}}/Q_\bullet$,
(iii) her son is $R_\bullet^{\mathbf{m}} := Q_\bullet^{\mathbf{m}}/Q_\bullet$, and
(iv) a random juvenile male on the same patch born in the present generation is $R_0^{\mathbf{m}} := Q_0^{\mathbf{m}}/Q_\bullet$.

B-7 No LRE

Substituting $\alpha = 0$, no LRE, which leads to $g_{\mathtt{in}} \equiv g_{\mathtt{tr}} \equiv 0$, obtains the expression for cESS (candidate ESS), of

$$\widehat{z_\emptyset} = \frac{c_\mathrm{m}\big(Q_\bullet^{\mathbf{m}} - \ell_\mathrm{MC}Q_0^{\mathbf{m}}\big)}{c_\mathrm{m}\big(Q_\bullet^{\mathbf{m}} - (\ell_\mathrm{MC} - \ell_\mathrm{MB})Q_0^{\mathbf{m}}\big) + c_\mathrm{f}\big(Q_\bullet^{\mathbf{f}} - \ell_\mathrm{RC}Q_0^{\mathbf{f}}\big)}, \tag{S-12}$$

which recovers the cESS displayed in the main text.

Taylor's cancelling principle

We shall here show that when we have made the expressions for the consanguinities with $d_{\mathrm{m}} = 0$, it follows that:

$$\frac{\overline{R_0} - \ell_{\mathrm{RC}}\overline{R_0}}{\overline{R_\bullet} - \ell_{\mathrm{RC}}\overline{R_0}} = \frac{1}{n} \tag{S-13}$$

[21], where:

$$\begin{aligned} \overline{R_\bullet} &:= c_{\mathrm{f}} R_\bullet^{\mathbf{f}} + c_{\mathrm{m}} R_\bullet^{\mathbf{m}}, \\ \overline{R_0} &:= c_{\mathrm{f}} R_0^{\mathbf{f}} + c_{\mathrm{m}} R_0^{\mathbf{m}}, \\ \ell_{\mathrm{RC}} &:= (1 - d_{\mathrm{f}})^2. \end{aligned} \tag{S-14}$$

Eqn (S-13) is equivalent to:

$$\overline{R_0} = \frac{\overline{R_\bullet}}{n} + \frac{n-1}{n}\ell_{\mathrm{RC}}\overline{R_0} \iff c_{\mathrm{f}} Q_0^{\mathbf{f}} + c_{\mathrm{m}} Q_0^{\mathbf{m}} = \frac{c_{\mathrm{f}} Q_\bullet^{\mathbf{f}} + c_{\mathrm{m}} Q_\bullet^{\mathbf{m}}}{n} + \frac{n-1}{n}\ell_{\mathrm{RC}}\left(c_{\mathrm{f}} Q_0^{\mathbf{f}} + c_{\mathrm{m}} Q_0^{\mathbf{m}}\right); \tag{S-15}$$

thus we shall show this equality instead.

First, from the recursions we have:

$$\begin{aligned} \frac{Q_\bullet^{\mathbf{f}}}{n} + \frac{n-1}{n}\ell_{\mathrm{RC}}\frac{Q_0^{\mathbf{ff}} + Q_0^{\mathbf{fm}}}{2} &\overset{\text{(i)}}{=} Q_0^{\mathbf{f}} \overset{\text{(ii)}}{=} Q_0^{\mathbf{fm}}, \\ \frac{Q_\bullet^{\mathbf{m}}}{n} + \frac{n-1}{n}\ell_{\mathrm{RC}} Q_0^{\mathbf{ff}} &\overset{\text{(i)}}{=} Q_0^{\mathbf{m}} \overset{\text{(ii)}}{=} Q_0^{\mathbf{mm}}, \end{aligned} \tag{S-16}$$

the first equalities (i)s of which, substituted into the LHS in Eqn (S-15), give us:

$$c_{\mathrm{f}} Q_0^{\mathbf{f}} + c_{\mathrm{m}} Q_0^{\mathbf{m}} = \frac{c_{\mathrm{f}} Q_\bullet^{\mathbf{m}} + c_{\mathrm{m}} Q_\bullet^{\mathbf{f}}}{n} + \frac{n-1}{n}\ell_{\mathrm{RC}} \underbrace{\left(c_{\mathrm{f}} \frac{Q_0^{\mathbf{ff}} + Q_0^{\mathbf{fm}}}{2} + c_{\mathrm{m}} Q_0^{\mathbf{ff}}\right)}_{= c_{\mathrm{f}} Q_0^{\mathbf{ff}} + c_{\mathrm{m}} Q_0^{\mathbf{fm}}}. \tag{S-17}$$

Second, the second equalities (ii)s in Eqn (S-16), with $2Q_0^{\mathbf{ff}} = Q_0^{\mathbf{fm}} + Q_0^{\mathbf{mm}}$ and $c_{\mathrm{f}} = 2c_{\mathrm{m}} = 2/3$, imply that:

$$\begin{aligned} c_{\mathrm{f}} Q_0^{\mathbf{f}} + c_{\mathrm{m}} Q_0^{\mathbf{m}} &= c_{\mathrm{f}} Q_0^{\mathbf{fm}} + c_{\mathrm{m}} Q_0^{\mathbf{mm}} \\ &= c_{\mathrm{f}} Q_0^{\mathbf{fm}} + c_{\mathrm{m}}\left(2Q_0^{\mathbf{ff}} - Q_0^{\mathbf{fm}}\right) \\ &= c_{\mathrm{f}} Q_0^{\mathbf{ff}} + c_{\mathrm{m}} Q_0^{\mathbf{fm}}, \end{aligned} \tag{S-18}$$

which, being inserted into the last term of the RHS in Eqn (S-17), supplies:

$$c_{\mathrm{f}} Q_0^{\mathbf{f}} + c_{\mathrm{m}} Q_0^{\mathbf{m}} = \frac{c_{\mathrm{f}} Q_\bullet^{\mathbf{f}} + c_{\mathrm{m}} Q_\bullet^{\mathbf{m}}}{n} + \frac{n-1}{n}\ell_{\mathrm{RC}}\left(c_{\mathrm{f}} Q_0^{\mathbf{f}} + c_{\mathrm{m}} Q_0^{\mathbf{m}}\right), \tag{S-19}$$

which verifies Eqn (S-15) and thus the original equation to be established, Eqn (S-13).

B-8 Trans-generational consanguinities

We desigtante $Q_\tau^{\mathbf{f}}$ (or $Q_\tau^{\mathbf{m}}$) for the probability of consanguinity between (i) a juvenile female (or male) randomly sampled right after its birth in the present generation and (ii) a random adult female in the same patch in the τ-th generation ($\tau \geq 0$). Then the trans-generatioinal consanguinities are given by:

$$\begin{aligned}\begin{pmatrix} Q_{\tau+1}^{\mathbf{f}} \\ Q_{\tau+1}^{\mathbf{m}} \end{pmatrix} &= \underbrace{\begin{pmatrix} 1-d_{\mathrm{f}} & 0 \\ 0 & 1-d_{\mathrm{f}} \end{pmatrix}}_{\text{female dispersal}} \underbrace{\begin{pmatrix} \pi_{\mathrm{ff}} & \pi_{\mathrm{fm}} \\ \pi_{\mathrm{mf}} & \pi_{\mathrm{mm}} \end{pmatrix}}_{\text{inheritance}} \underbrace{\begin{pmatrix} 1 & 0 \\ 0 & 1-d_{\mathrm{m}} \end{pmatrix}}_{\text{male dispersal}} \begin{pmatrix} Q_\tau^{\mathbf{f}} \\ Q_\tau^{\mathbf{m}} \end{pmatrix} \\ &= \underbrace{\begin{pmatrix} \frac{1-d_{\mathrm{f}}}{2} & \frac{(1-d_{\mathrm{f}})(1-d_{\mathrm{m}})}{2} \\ 1-d_{\mathrm{f}} & 0 \end{pmatrix}}_{=\mathbf{P}} \begin{pmatrix} Q_\tau^{\mathbf{f}} \\ Q_\tau^{\mathbf{m}} \end{pmatrix};\end{aligned} \tag{S-20}$$

the initial condition reads $Q_0^{\mathbf{f}} = Q_0^{\mathbf{fm}}$ and $Q_0^{\mathbf{m}} = Q_0^{\mathbf{mm}}$. The first matrix determines the decay of genetic relatedness due to female emigration, in which mated females disperse and therefore males' gametes may emigrate together (the bottom-right element should not be 1); the second describes the genetic inheritance (ploidy; πs are all 1/2 for haploids and diploids), or movement of genes between sexes due to mating; the third represents the male dispersal, in which females do not disperse.

The subcomponent of the selection gradient of trans-generational LRE then reads:

$$\begin{aligned} g_{\mathtt{tr}}(z) &= \sum_{\tau=1}^{+\infty} \left(c_{\mathrm{f}} \left(\frac{\partial W_\bullet^{\mathbf{f}}}{\partial \beta_0} \cdot \frac{\partial \beta_0}{\partial y_\tau} \right) Q_\tau^{\mathbf{f}} + c_{\mathrm{m}} \left(\frac{\partial W_\bullet^{\mathbf{m}}}{\partial \beta_0} \cdot \frac{\partial \beta_0}{\partial y_\tau} + \frac{\partial W_\bullet^{\mathbf{m}}}{\partial W_0^{\mathbf{f}}} \frac{\partial W_0^{\mathbf{f}}}{\partial \beta_0} \cdot \frac{\partial \beta_0}{\partial y_\tau} \right) Q_\tau^{\mathbf{m}} \right) \\ &= -\frac{1}{1-z} \sum_{\tau=1}^{+\infty} \left(\underbrace{c_{\mathrm{f}}(1-\ell_{\mathrm{RC}})}_{=:u_{\mathrm{f}}} Q_\tau^{\mathbf{f}} + \underbrace{c_{\mathrm{m}} \Big(1-(1-d_{\mathrm{m}})^2 + (1-d_{\mathrm{m}})(1-\ell_{\mathrm{RC}}) \Big)}_{=:u_{\mathrm{m}}} Q_\tau^{\mathbf{m}} \right) \big(\alpha(1-d_{\mathrm{f}})(1-z) \big)^\tau \end{aligned} \tag{S-21}$$

[45, 51].

Now let $\mathbf{V} := \alpha(1-d_{\mathrm{f}})(1-z)\mathbf{P}$; then its spectral radius is lower than unity in modulus and therefore $(\mathbf{I}-\mathbf{V})^{-1} = \sum_{\tau=1}^{\infty} \mathbf{V}^\tau$ does exist (with $\mathbf{I}$ the identity). Then

$$\begin{aligned} g_{\mathtt{tr}}(z) &= -\frac{1}{1-z} (u_{\mathrm{f}}, u_{\mathrm{m}}) \sum_{\tau=1}^{+\infty} \mathbf{V}^\tau \begin{pmatrix} Q_0^{\mathbf{f}} \\ Q_0^{\mathbf{m}} \end{pmatrix} \\ &= -\frac{1}{1-z} (u_{\mathrm{f}}, u_{\mathrm{m}}) (\mathbf{I}-\mathbf{V})^{-1} \mathbf{V} \begin{pmatrix} Q_0^{\mathbf{f}} \\ Q_0^{\mathbf{m}} \end{pmatrix}. \end{aligned} \tag{S-22}$$

After algebraic manipulation (one may want to use *Mathematica*® notebook file we submitted), we find that the trans-generational subcomponent, $g_{\mathtt{tr}}(z)$, is given by

$$-\frac{\phi}{2}\cdot\frac{c_{\mathrm{f}}(1-\ell_{\mathrm{RC}})\Big(\big(1+(1-d_{\mathrm{m}})\phi\big)Q_0^{\mathbf{f}}+(1-d_{\mathrm{m}})Q_0^{\mathbf{m}}\Big)+c_{\mathrm{m}}(1-\ell_{\mathrm{m}})\big(2Q_0^{\mathbf{f}}+(1-d_{\mathrm{m}})\phi Q_0^{\mathbf{m}}\big)}{(1-z)\Big(1-\frac{\phi}{2}\big(1+(1-d_{\mathrm{m}})\phi\big)\Big)} \tag{S-23}$$

for haplodiploids, where $\ell_{\mathrm{m}} := (1-d_{\mathrm{m}})^2-(1-d_{\mathrm{m}})(1-\ell_{\mathrm{RC}})$ and $\phi := \ell_{\mathrm{RC}}\alpha(1-z)$.

C Robustness under $d_{\mathrm{m}} = 0$

C-1 Different functional form: additive

Intra-generational model

Suppose the fecundity of individuals in the present generation is given by:

$$\beta_0 = \frac{K}{1+A\big((1-d_{\mathrm{f}})y_0+d_{\mathrm{f}}z\big)} \tag{S-24}$$

where A represents the strength of LRE, and we therefore have:

$$\frac{\partial\beta_0}{\partial y_0} = -\beta^{\circ}\frac{(1-d_{\mathrm{f}})A}{1+Az}. \tag{S-25}$$

Replacing α in the main text with $A = \alpha/(1-\alpha)$ gives the corresponding analyses; therefore, the present extension is analogous to the analysis given in the main text.

Trans-generational model

Suppose that β obeys the following recursion:

$$\beta_{\tau-1} = K - A\Big((1-d_{\mathrm{f}})\beta_\tau y_\tau + d_{\mathrm{f}}\overline{\beta}z\Big), \tag{S-26}$$

with:

$$\begin{aligned}\beta^{\circ} = \overline{\beta} &= \frac{K}{(1+Az)},\\ \frac{\partial\beta_{\tau-1}}{\partial\beta_\tau} &= -A(1-d_{\mathrm{f}})z,\\ \frac{\partial\beta_{\tau-1}}{\partial y_\tau} &= -A(1-d_{\mathrm{f}})\beta^{\circ},\end{aligned} \tag{S-27}$$

which constitutes a negative niche-construction (fecundities of the present and previous generations are negatively correlated), or aggressiveness towards offspring (of any sex) from males. In this case, a straightforward calculation

similar to the analyses performed above yields:

$$g_{\mathtt{tr}}(z) = -(1-\ell_{\mathrm{RC}})\Big(c_{\mathrm{f}}Q_0^{\mathbf{f}} + c_{\mathrm{m}}Q_0^{\mathbf{m}}\Big)\frac{A\ell_{\mathrm{RC}}}{1+A\ell_{\mathrm{RC}}z}. \tag{S-28}$$

Rewriting $A = \alpha/(1-\alpha\ell_{\mathrm{RC}})$, we have:

$$g_{\mathtt{tr}}(z) = -(1-\ell_{\mathrm{RC}})\Big(c_{\mathrm{f}}Q_0^{\mathbf{f}} + c_{\mathrm{m}}Q_0^{\mathbf{m}}\Big)\frac{\alpha\ell_{\mathrm{RC}}}{1-\alpha\ell_{\mathrm{RC}}+\alpha\ell_{\mathrm{RC}}z}, \tag{S-29}$$

which is equivalent to the one obtained in the original, trans-generational model, with a difference in feasibility conditions: the original α varies from 0 to 1 while A may vary from 0 to $1/(1-\ell_{\mathrm{RC}}) > 1$, suggesting that the upper bound for the strength of LRE depends on the dispersal rate. Therefore, our results are robust against this simple recursion for β_τ, and the original approach presented in the main text may be suitable for experimental confirmation.

C-2 Different functional form: multiplicative

Intra-generational model

Here we assume that LRE is generated by a multiplicative functional form given by:

$$\beta_0 = \big(1-y_0\big)^{\alpha}K^{\alpha}\beta_0^{\alpha} \tag{S-30}$$

(for $0 \leq \alpha < 1$), which satisfies:

$$\begin{aligned} \beta^{\circ} &= (1-z)^{\frac{\alpha}{1-\alpha}}K^{\frac{\alpha}{1-\alpha}}, \\ \frac{\partial\beta_0}{\partial y_0} &= -\frac{\beta^{\circ}}{1-z}\cdot\frac{\alpha}{1-\alpha} \end{aligned} \tag{S-31}$$

at neutrality. Therefore,

$$g_{\mathtt{in}}(z) = -\Big(c_{\mathrm{f}}Q_0^{\mathbf{f}} + c_{\mathrm{m}}Q_0^{\mathbf{m}}\Big)(1-\ell_{\mathrm{RC}})\frac{1}{1-z}\cdot\frac{\alpha}{1-\alpha}, \tag{S-32}$$

telling us that the effect of LRE is independent of the dispersal rate. Hamilton's rule is thus given by:

$$z_{\emptyset}^{\mathrm{LMC}} - z - \frac{1}{n}\cdot z\cdot\frac{\alpha}{1-\alpha} > 0, \tag{S-33}$$

which determines the cESS as:

$$\widehat{z_{\mathtt{in}}} = \frac{z_{\emptyset}^{\mathrm{LMC}}}{1+\dfrac{\alpha}{(1-\alpha)n}}. \tag{S-34}$$

This expression immediately tells us that $\alpha \to 1$ leads to $\widehat{z_{\mathtt{in}}} \to 0$.

Trans-generational model

Similarly, consider:

$$\begin{aligned}\beta_\tau &= B\big(\beta_{\tau+1}, y_{\tau+1}\big)\\ &= \Big((1-d_{\mathrm{f}})\big(1-y_{\tau+1}\big)\beta_{\tau+1} + d_{\mathrm{f}}(1-z)\overline{\beta}\Big)^{\alpha} K^{\alpha},\end{aligned} \tag{S-35}$$

which, at equilibrium, should satisfy:

$$\beta^{\circ} = (1-z)^{\frac{\alpha}{1-\alpha}} K^{\frac{\alpha}{1-\alpha}}. \tag{S-36}$$

Partial differentiation gives:

$$\begin{aligned}\frac{\partial \beta_0}{\partial y_1} &= -\alpha \frac{1-d_{\mathrm{f}}}{1-z}\beta^{\circ},\\ \frac{\partial \beta_\tau}{\partial \beta_{\tau+1}} &= \alpha(1-d_{\mathrm{f}}).\end{aligned} \tag{S-37}$$

Hence,

$$g_{\mathtt{tr}}(z) = -\sum_{\tau=1}^{\infty}\Big(c_{\mathrm{f}} Q_0^{\mathbf{f}} + c_{\mathrm{m}} Q_0^{\mathbf{m}}\Big)(1-\ell_{\mathrm{RC}}) \cdot \frac{(\alpha \ell_{\mathrm{RC}})^{\tau}}{1-z}, \tag{S-38}$$

which, for $0 \leq \alpha < 1$, converges to:

$$-\Big(c_{\mathrm{f}} Q_0^{\mathbf{f}} + c_{\mathrm{m}} Q_0^{\mathbf{m}}\Big)(1-\ell_{\mathrm{RC}}) \frac{1}{1-z} \cdot \frac{\alpha \ell_{\mathrm{RC}}}{1-\alpha \ell_{\mathrm{RC}}}. \tag{S-39}$$

Therefore, Hamilton's rule is given by:

$$z_{\emptyset}^{\mathrm{LMC}} - z - \frac{1}{n} \cdot \frac{\alpha \ell_{\mathrm{RC}}}{1-\alpha \ell_{\mathrm{RC}}} z > 0, \tag{S-40}$$

supplying the cESS, of:

$$\widehat{z_{\mathtt{tr}}} = \frac{z_{\emptyset}^{\mathrm{LMC}}}{1 + \frac{1}{n} \cdot \frac{\alpha \ell_{\mathrm{RC}}}{1-\alpha \ell_{\mathrm{RC}}}}. \tag{S-41}$$

Overall, we can observe that the effects of LRE on $\widehat{z}$ are much more pronounced compared to the additive one (SI Fig 2), which is because with this multiplicative formula $z = 1$ gives $\beta = 0$: producing females is a prerequisite for producing offspring. Though much simpler in any associated expressions, the model may overestimate the LRE effect. For this reason, we presented the additive formula for LRE in the main text.

C-3 LRE from males: additive

We here demonstrate a minimal analysis for LRE supplied by juvenile males.

Intra-generational model

Suppose that the fecundity of the females in the focal patch (with its average phenotype y_0) is given by:

$$\beta_0 = K + \alpha y_0 \beta_0 = \frac{K}{1-\alpha y_0}, \tag{S-42}$$

which means that:

$$\begin{aligned} \beta^\circ &= \frac{K}{1-\alpha z}, \\ \frac{\partial \beta_0}{\partial y_0} &= \beta^\circ \frac{\alpha}{1-\alpha z} \end{aligned} \tag{S-43}$$

at neutrality. The preceding logic shows that Hamilton's rule is given by:

$$z_\emptyset^{\mathrm{LMC}} - z + \frac{1}{n} \cdot \frac{\alpha z}{1-\alpha z}(1-z) > 0, \tag{S-44}$$

which gives:

$$\widehat{z_{\mathtt{in}}} = \frac{z_\emptyset^{\mathrm{LMC}} + \frac{1}{n} \cdot \frac{\alpha \widehat{z_{\mathtt{in}}}}{1-\alpha \widehat{z_{\mathtt{in}}}}}{1 + \frac{1}{n} \cdot \frac{\alpha \widehat{z_{\mathtt{in}}}}{1-\alpha \widehat{z_{\mathtt{in}}}}}, \tag{S-45}$$

from which, by the intermediate value theorem, we can find a unique $\widehat{z_{\mathtt{in}}}$ lying between 0 and 1.

Trans-generational model

We use the function of the form:

$$\beta_0 = K + \alpha\Big((1-d_{\mathrm{f}})y_1\beta_1 + d_{\mathrm{f}} z \overline{\beta}\Big), \tag{S-46}$$

which has the equilibrium solution given by:

$$\beta^\circ = \overline{\beta} = \frac{K}{1-\alpha z} \tag{S-47}$$

at neutrality, and satisfies:

$$\begin{aligned} \frac{\partial \beta_0}{\partial y_1} &= \alpha \beta^\circ (1-d_{\mathrm{f}}), \\ \frac{\partial \beta_0}{\partial \beta_1} &= \alpha z (1-d_{\mathrm{f}}), \end{aligned} \tag{S-48}$$

once again at neutrality. Therefore we can obtain Hamilton's rule of:

$$z_{\emptyset}^{\mathrm{LMC}} - z + \frac{1}{n} \cdot \frac{\alpha z \ell_{\mathrm{RC}}}{1 - \alpha z \ell_{\mathrm{RC}}}(1 - z) > 0, \tag{S-49}$$

which gives the cESS $\widehat{z_{\mathtt{tr}}}$ as $\widehat{z_{\mathtt{in}}}|_{\alpha \to \alpha \ell_{\mathrm{RC}}}$ in Eqn (S-45).

C-4 LRE from males: multiplicative

Intra-generational model

Suppose the fecundity function of the form:

$$\beta_0 = y_0^{\alpha} K^{\alpha} \beta_0^{\alpha} = \left(y_0 K\right)^{\frac{\alpha}{1-\alpha}}, \tag{S-50}$$

with:

$$\frac{\partial \beta_0}{\partial y_0} = \beta^{\circ} \frac{\alpha}{1 - \alpha} \cdot \frac{1}{z}, \tag{S-51}$$

implying that Hamilton's rule reads:

$$z_{\emptyset}^{\mathrm{LMC}} - z + \frac{1}{n} \cdot \frac{\alpha}{1 - \alpha}(1 - z) > 0, \tag{S-52}$$

which gives:

$$\widehat{z_{\mathtt{in}}} = \frac{z_{\emptyset}^{\mathrm{LMC}} + \frac{1}{n}\frac{\alpha}{1-\alpha}}{1 + \frac{1}{n}\frac{\alpha}{1-\alpha}} \tag{S-53}$$

Trans-generational model

The same logic supplies Hamilton's rule as:

$$z_{\emptyset}^{\mathrm{LMC}} - z + \frac{1}{n} \cdot \frac{\alpha \ell_{\mathrm{RC}}}{1 - \alpha \ell_{\mathrm{RC}}}(1 - z) > 0, \tag{S-54}$$

with the resulting cESS of:

$$\widehat{z_{\mathtt{tr}}} = \frac{z_{\emptyset}^{\mathrm{LMC}} + \frac{1}{n}\frac{\alpha \ell_{\mathrm{RC}}}{1-\alpha \ell_{\mathrm{RC}}}}{1 + \frac{1}{n}\frac{\alpha \ell_{\mathrm{RC}}}{1-\alpha \ell_{\mathrm{RC}}}}. \tag{S-55}$$

We here remark that the trans-generational LRE from juvenile males is unlikely, because males do not disperse and therefore have no access to post-dispersal, founding females. One may want to apply an alternative model to specific organisms with a specific lifecycle.

Combining additivity and multiplicativity: Combinational LRE

We here consider

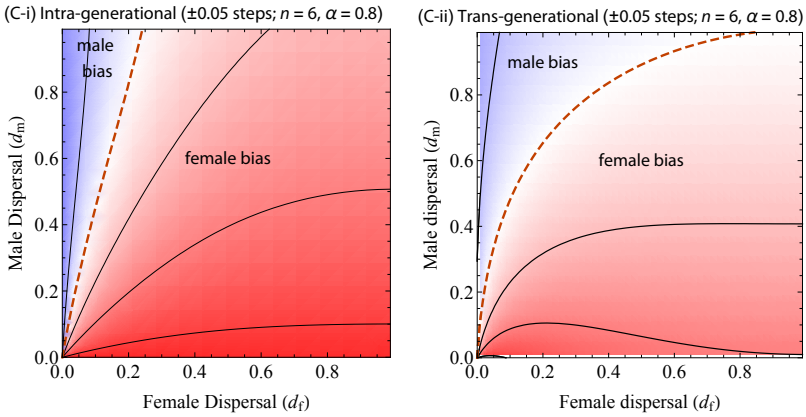
$$\beta_0 = K + \alpha\big(1 - y_0\big)^{\theta}\beta_0, \tag{S-56}$$

or

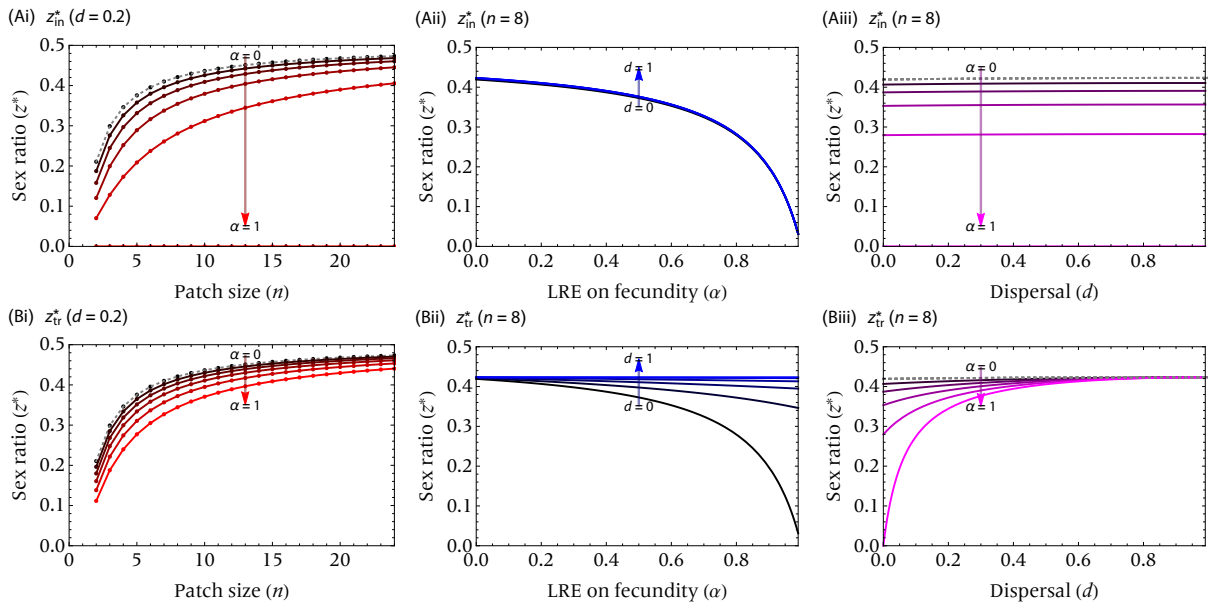
$$\beta_0 = \frac{K}{1 - \alpha\big(1 - y_0\big)^{\theta}}. \tag{S-57}$$

for $0 < \theta < 1$, and the resulting cESS does not have analytical formula. The numerical solutions are given in SI Fig 5.

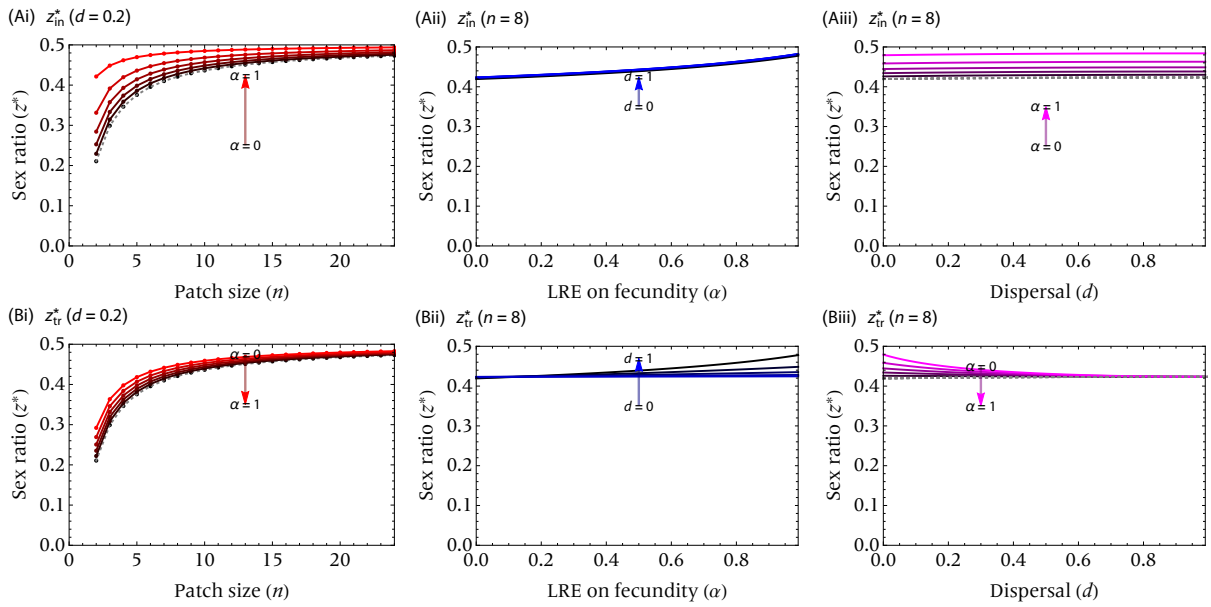
Inserting $d_{\mathrm{m}} = 0$ or $d_{\mathrm{m}} = 1$ into the above equation and then rescaling the whole equation (Eqn (S-9)) leads to the expression given in the main text.



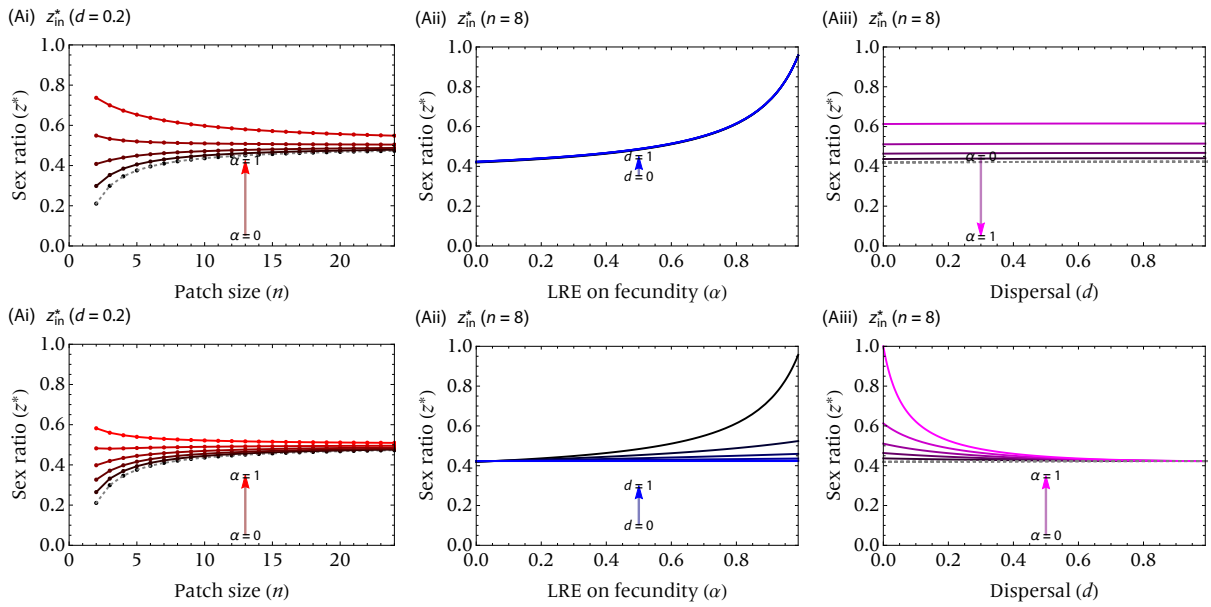
SI Figure 1: Evolutionary outcomes plotted against sex-dependent dispersal rates. Orange dotted contour: Fisherian sex ratio ($z = .5$), and the others are ± 0.05 steps deviation from Fisherian.



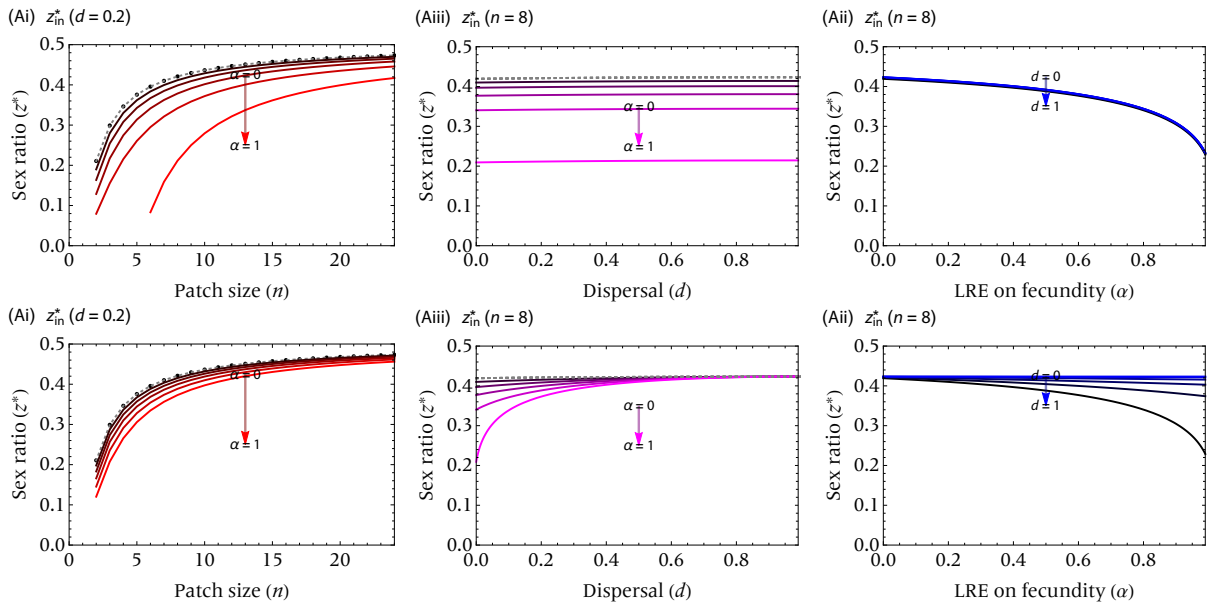
SI Figure 2: Multiplicative female-LRE.



SI Figure 3: Additive male-LRE.



SI Figure 4: Multiplicative male-LRE. Note the difference from the previous graphic figures in the ordinate range (0 to 1).



SI Figure 5: Combinational female-LRE. $\theta = \alpha = 0.5$. Other parameters as shown.

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