Supporting information 1 & 3

A solution to a sex ratio puzzle in *Melittobia* wasps

Jun Abe, Ryosuke Iritani, Koji Tsuchida, Yoshitaka Kamimura,

and Stuart A. West

Contents

Supporting information 1

A solution to a sex ratio puzzle in *Melittobia* wasps

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Field data

We obtained 46 broods of *Melittobia australica* with bamboo traps placed in the wild, and 11 broods by reexposing unparasitized hosts in the field (Table S2-1, S2-2). All of the emerging offspring were obtained with sufficient confidence from 29 of the collected broods, so we analyzed these broods (Table S2-3). Our parentage analysis with the microsatellite genotypic data indicated that all but two of the 29 broods were founded by either only dispersers or only non-dispersers (Table S2-3, S2-4). In the two other broods, non-dispersers produced male and female offspring, while a single disperser added an all-male clutch. In both broods, 5 non-dispersers were collected with developing offspring on the host, while the disperser was not collected (Table S2-4), suggesting that she had left the host before collection. The single dispersers produced 75.0% (50.3/67) and 87.5% (66.5/76) male individuals, respectively, in the broods. We were not certain whether the females producing all-male clutches were virgins, although their behavior is different from that of virgin females in the laboratory, in which they produced only a few (maximally 9) male offspring before they mate with their own sons (Abe *et al*. 2010).

Genetic structure. To examine genetic differentiation depending on the behavior of females laying eggs (dispersers vs. non-dispersers, and all-male producers vs. both-sex producers), we analyzed hierarchical population structure in the microsatellite data of the females using the R package *hierfstat* (Goudet 2005). We considered a structure, in which the entire population of egg-layers ("population") is divided into two types depending on the behavior (type), and each type is subdivided by the genetic lineages of the females (lineage) consisting of the bunches of individual females (individual). We included the hierarchy of lineage, because our analysis for relatedness indicated that non-dispersing females laying eggs on the same host patches are close relatives (see below). When we categorized females into dispersers and non-dispersers, the effect of "type" was not significant ($F_{\text{type/population}} = 0.011$, $P = 0.43$), suggesting that there is no genetic differentiation between these types of females. When we instead divided the entire population into all-male producers and the other females, the effect of "type" was not significant ($F_{\text{type/population}} = –0.020$, $P = 0.30$), suggesting that there is no genetic differentiation between the females that produced all-male clutches and those that produced clutches containing both sexes.

Inbreeding level of females. It was hard to reconstruct pedigrees among the offspring of non-dispersing females using microsatellite data, because non-dispersing females were close relatives. Therefore, we could not estimate genetic relatedness between non-dispersing females and their mating partners in this study. Instead, to examine the inbreeding level of females, we calculated the frequency of homozygosity of female offspring. The average frequencies of homozygosity between the female offspring of dispersers (75.7%) and non-dispersers (82.9%) were not significantly different ($P = 0.47$, nonparametric bootstrap method, in which the dispersal status of each lineage was randomly resampled), suggesting that the level of inbreeding or relatedness to the mates was not different between dispersing and non-dispersing females. In addition, the difference of the average frequencies of homozygosity between dispersing mothers (79.2%) and non-dispersing mothers (79.1%) was also not significant ($P = 0.97$).

The number of females laying eggs. Over 10-fold more non-dispersers laid eggs on a single host (mean ± SD = 16.6 ± 11.9) compared with dispersers (mean ± SD = 1.4 ± 1.1; Table S2-3; $\chi^2_1 = 16.54$, $P < 0.001$). The effect of host species on the number of females laying eggs per brood was marginally non-significant ($\chi^2_5 = 10.81$, $P = 0.055$).

Brood size. Non-dispersers produced more offspring than dispersers in a single brood, although there were no significant effects of females laying eggs or host species (Table S1-1 *A*, S2-3). However, the number of females laying eggs was highly related to the dispersal status of the females, as shown above. When we analyzed the model after removing the dispersal status term, offspring number significantly increased with the number of females, but host species was still non-significant (Table S1-1 *B*).

Table S1-1 A. Analysis of total brood size (with dispersal status).

	Removing two all-male clutches		Removing two mixed broods	
Minimal adequate model				
Dispersal status	$\chi^2_1 = 14.01$	$P < 0.001$	$\chi^2_1 = 13.83$	$P < 0.001$
Non-significant terms deleted				
Female number	$\chi^2_1 = 2.57$	$P = 0.11$	$\chi^2_1 = 2.86$	$P = 0.091$
Host species	$\chi^2_5 = 1.67$	$P = 0.89$	$\chi^2_4 = 1.42$	$P = 0.84$

Table S1-1 B. Analysis of total brood size (without dispersal status).

	Removing two all-male clutches		Removing two mixed broods	
Minimal adequate model				
Female number	$\chi^2_1 = 9.61$	$P = 0.002$	$\chi^2_1 = 13.52$	$P < 0.001$
Non-significant terms deleted				
Host species	$\chi^2_5 = 3.06$	$P = 0.69$	$\chi^2_4 = 2.13$	$P = 0.71$

Relatedness. We adopted relatedness between female offspring in a brood to assess the kinship between individuals on a patch, because we could obtain a sufficient number of female offspring in all the broods analyzed (Table S2-3). Relatedness between female offspring showed a significant interaction between the number of females laying eggs and the dispersal status of the females (Fig. 3 *A*), although brood size and host species were non-significant (Table S1-2 *A*). When we analyzed the model for each dispersal status separately, relatedness significantly decreased with an increasing female number in the broods of dispersers (Table S1-2 *B*), but relatedness was independent of female number in the broods of non-dispersers (Table S1-2 *C*).

Table S1-2 A. Analysis of relatedness between female offspring in a brood (including both types of females).

	Removing two all-male clutches		Removing two mixed broods	
Minimal adequate model				
Female number	NA		NA	
Dispersal status	NA		NA	
Female number : Dispersal status	$\chi^2_1 = 12.34$	$P < 0.001$	$\chi^2_1 = 11.97$	$P < 0.001$
Non-significant terms deleted				
Brood size	$\chi^2_1 = 2.67$	$P = 0.10$	$\chi^2_1 = 2.31$	$P = 0.13$
Host species	$\chi^2_5 = 5.47$	$P = 0.36$	$\chi^2_4 = 5.09$	$P = 0.28$

Table S1-2 B. Analysis of relatedness between female offspring in a brood (only dispersers).

	Removing two all-male clutches		Removing two mixed broods	
Minimal adequate model				
Female number	$\chi^2_1 = 10.15$	$P = 0.001$	$\chi^2_1 = 10.15$	$P = 0.001$

Table S1-2 C. Analysis of relatedness between female offspring in a brood (only non-dispersers).

	Removing two all-male clutches		Removing two mixed broods	
Non-significant terms deleted				
Female number	$\chi^2_1 = 0.93$	$P = 0.33$	$\chi^2_1 = 0.88$	$P = 0.35$

Sex ratio. Sex ratios were clearly categorized into two groups depending on the dispersal status of females (Fig. 3b): the interaction term between the number of females laying eggs and their dispersal status was significant ($\chi^2_1 = 18.95$, $P < 0.001$), although host species and brood size were not significant (Table S3-1 *A*). Separate model analysis for each dispersal status showed that dispersers increased the sex ratio by increasing the number of females laying eggs (Table S3-1 *B*), whereas non-dispersers did not (Table S3-1 *C*). When we analyzed sex ratios against relatedness between female offspring incorporating the broods of both dispersers and non-dispersers, a significant negative relationship between the sex ratio and relatedness was found (Table S1-4).

Table S1-3 A. Analysis of sex ratio (both types of females).

	Removing two all-male clutches		Removing two mixed broods	
Minimal adequate model				
Female number	NA		NA	
Dispersal status	NA		NA	
Female number : Dispersal status	$\chi^2_1 = 18.69$	$P < 0.001$	$\chi^2_1 = 18.70$	$P < 0.001$
Non-significant terms deleted				
Host species	$\chi^2_5 = 8.40$	$P = 0.16$	$\chi^2_4 = 7.40$	$P = 0.12$
Brood size	$\chi^2_1 = 0.095$	$P = 0.76$	$\chi^2_1 = 1.60$	$P = 0.21$

Table S1-3 B. Analysis of sex ratio (only dispersers).

	Removing two all-male clutches		Removing two mixed broods	
Minimal adequate model				
Female number	$\chi^2_1 = 14.62$	$P < 0.001$	$\chi^2_1 = 14.62$	$P < 0.001$

Table S1-3 C. Analysis of sex ratio (only non-dispersers).

	Removing two all-male clutches		Removing two mixed broods	
Non-significant terms deleted				
Female number	$\chi^2_1 = 0.56$	$P = 0.46$	$\chi^2_1 = 0.015$	$P = 0.90$

Table S1-4. Analysis of sex ratio against relatedness between female offspring in a brood.

	Removing two all-male clutches		Removing two mixed broods	
Minimal adequate model				
relatedness	$\chi^2_1 = 25.86$	$P < 0.001$	$\chi^2_1 = 24.27$	$P < 0.001$

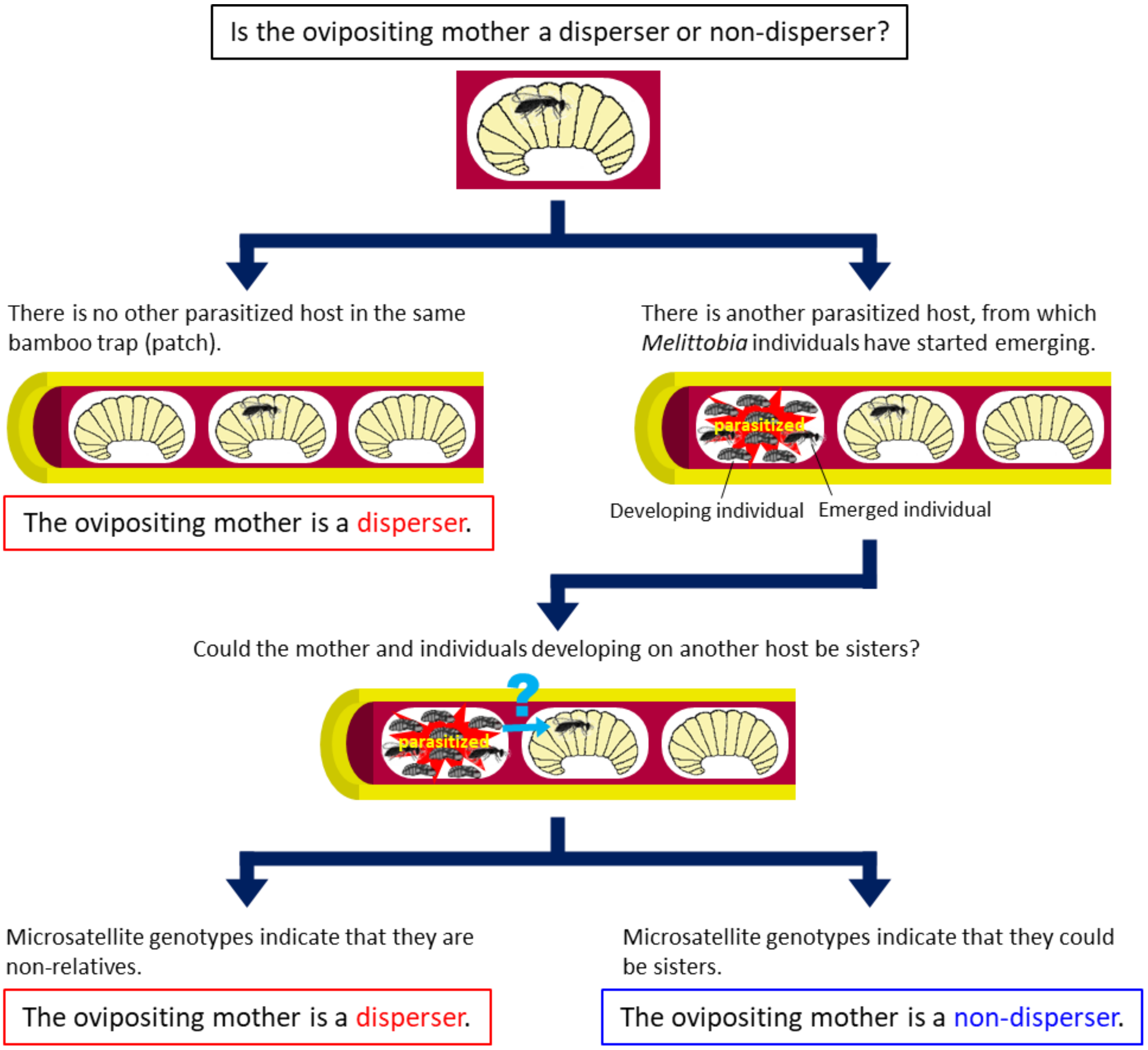

Figure S1-1. Flowchart indicating how females are assigned as "disperser" from a different patch, or "non-disperser" from a different host on the same patch.

Laboratory data

Brood size. The number of offspring produced by a female was not influenced by the treatment (Fig. S1-2 *A*; $\chi^2_2 = 0.70$, $P = 0.70$) or strain ($\chi^2_2 = 3.84$, $P = 0.15$).

Sex ratio. Although the offspring sex ratio was significantly different depending on the treatment ($\chi^2_2 = 21.27$, $P < 0.001$), this relied on the difference in foundress numbers ($\chi^2_1 = 20.5$, $P < 0.001$), but the sex ratios produced by two related and unrelated females were not significantly different (Fig. 5; $\chi^2_1 = 0.66$, $P = 0.42$). The strain did not have a significant effect on the sex ratio (Fig. S1-2 *B*; $\chi^2_2 = 1.50$, $P = 0.47$).

Injury level. Fortuitously, we observed fighting between females in the experiment, which has rarely been documented in *Melittobia* (Matthews & Deyrup 2007). Parts of the antennae and legs of females were likely to be cut off by the opponent female during the 8 days after the introduction of the females (Table S2-8). However, the frequency of the injured females was not influenced by relatedness (Fig. S1-2 *C*; $\chi^2_1 = 0.05$, $P = 0.82$), although female pugnacity significantly varied among the strains of females ($\chi^2_1 = 18.32$, $P < 0.001$). Ultimately, we found no evidence that females adjust their behavior depending on relatedness. Moreover, females could potentially assessed relatedness indirectly on the basis of environmental cues, such as recognizing whether the opponent females emerged from the same or different host. However, the present experiment, in which all females of the same strain that were used were developed on the same host, suggested that this possibility is not the case in the studied species.

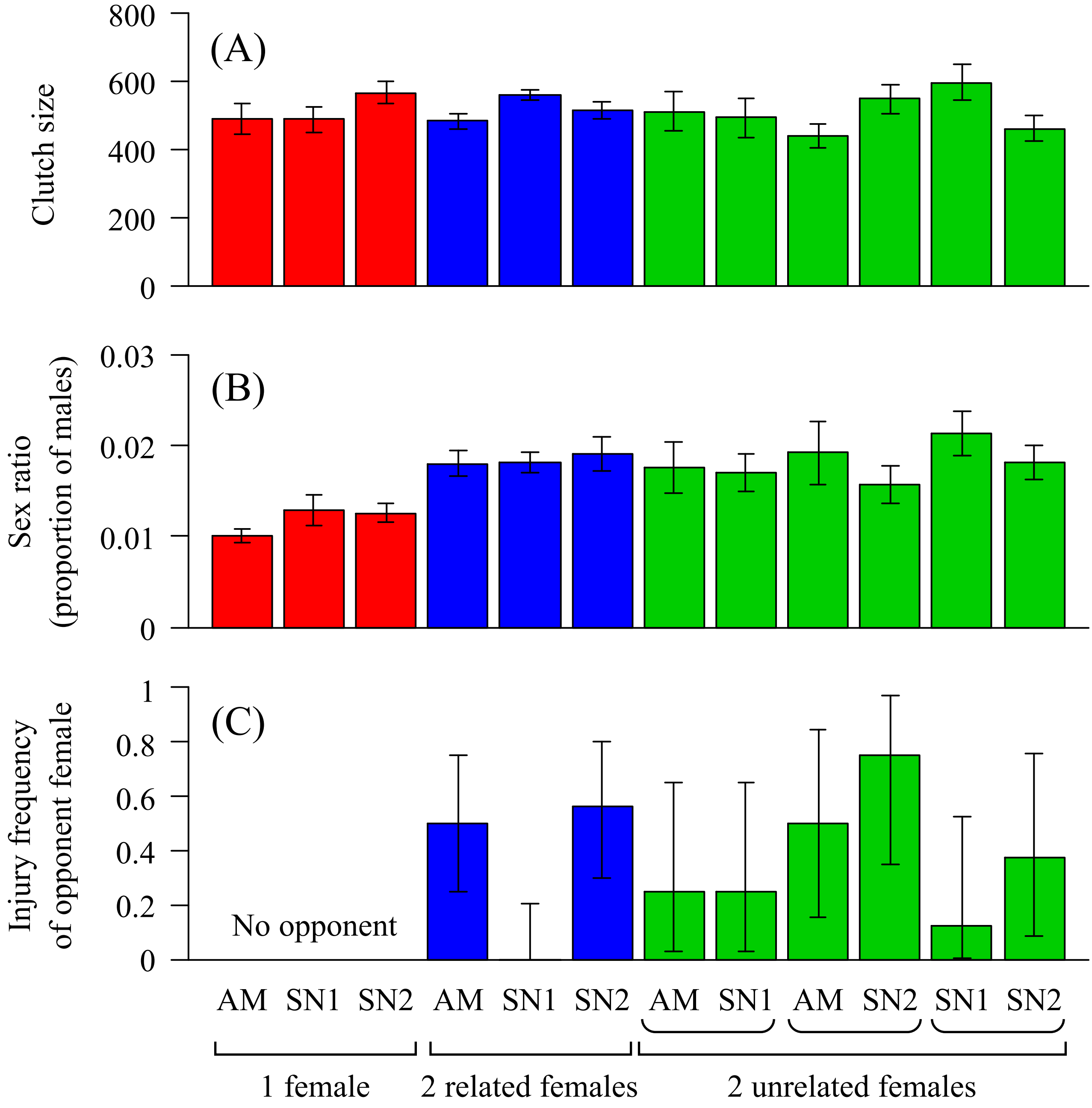

Figure S1-2. Clutch size (A), sex ratio (B), and injury frequency of opponent female (C) depending on treatment regulating female number and their relatedness, and the strains of the females. Error bars represent standard errors (A, B) and 95% binomial confidence intervals (C). The number of replicates was 8 for each strain in all the treatments.

References

Abe, J., Innocent, T. M., Reece, S. E., & West, S. A. (2010) Virginity and the clutch size behaviour of a parasitoid wasp where mothers mate their sons. *Behavioral Ecology,* **21**.4, pp.730–738. doi:10.1093/beheco/arq046

Goudet, J. (2005) A package for R to compute and test hierarchical *F*-statistics. *Molecular Ecology Notes* **5**.1, pp184–186. doi: 10.1111/j.1471-8286.2004.00828.x

Matthews, R. W. & Deyrup, L. D. (2007) Female fighting and host competition among four sympatric species of *Melittobia* (Hymenoptera: Eulophidae). *The Great Lakes Entomologist,* **40**. 1, pp.52-68. Available at: https://scholar.valpo.edu/tgle/vol40/iss1/6

Supporting Information 3 for:

A solution to a sex ratio puzzle in *Melittobia* wasps

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Contents

1 Model assumptions

We use a spatially implicit model of dispersal (Wright's islands model; Wright 1931), in which each patch may go extinct with a probability e. If patches go extinct, the same number of empty patches are recolonized in the next generation. Therefore, each patch is characterized by the age τ, where τ is the number of generations that have passed since a patch was recolonized.

2 Patch dynamics

Let π_τ be the frequency of the patches aged τ. Under completely random extinction, the frequency of patch ages is updated by:

$$\pi_{\tau+1} = (1-e)\pi_\tau, \tag{S-1}$$

with

$$\pi_0 = \underbrace{e \times \sum_{\tau=0}^{+\infty} \pi_\tau}_{\text{extinction}} = e. \tag{S-2}$$

Hence, the stationary distribution of the patches aged τ is given by:

$$\pi_\tau = e(1-e)^\tau; \tag{S-3}$$

that is, τ follows a geometric distribution, with the waiting time until the occurrence of patch extinction given by $1/e$.

3 Consanguinity

Under the assumptions that females and males mate within their natal patches and n non-dispersing females reproduce in persistent patches, while n dispersing females from other patches reproduce in recolonized patches, consanguinity coefficients (the probability that randomly taken homologous genes of interest are identical by descent) may be derived for diploid and haplodiploid populations as below.

3.1. Diploidy

The consanguinity coefficient f_τ between a random mating pair on a patch aged τ is given by a well known recursion (Taylor 1988a,b; Frank 1998; Rousset 2004; Lehmann 2007; Gardner *et al.* 2009):

$$f_{\tau+1} = \frac{1}{n} \cdot \left(\frac{1}{2} \underbrace{\left(\frac{1+f_{\tau-1}}{2} \right)}_{=p^{\mathrm{I}}_\tau} + \frac{1}{2} f_\tau \right) + \frac{n-1}{n} f_\tau, \tag{S-4}$$

in which identical by decent (IBD) between mating partners occurs when (i) they share share the same mother $1/n$, in which case the consanguinity is given by (i-a) the probability that both genes are from the same-sex parent $1/2$ (i.e., both from the mother, or both from their father) times the consanguinity to self $p^{\mathrm{I}}_\tau = (1+f_{\tau-1})/2$ in the previous generation plus (i-b) the probability that their genes derive from opposite-sex parents $1/2$ (i.e., one from mother and the other from father) times the consanguinity between the parents in the previous generation (f_τ), or when (ii) they have different mothers $(1-1/n)$, in which case the consanguinity is given by the probability that two distinct adults share the common ancestor in the previous generation f_τ.

The "initial" consanguinity reads:

$$f_0 = \frac{1}{n} \sum_{\tau=0}^{+\infty} \left(\frac{1}{2} p^{\mathrm{I}}_\tau + \frac{1}{2} f_\tau \right) \pi_\tau + \frac{n-1}{n} \cdot 0, \tag{S-5}$$

which is reasoned as follows: with a probability $1/n$, two female offspring share the dispersed mother, in which case their consanguinity is the metapopulation-wide average of $(1+3f_{\tau-1})/4$. With a probability of $1-1/n$, two female offspring have different, dispersed mothers, in which case consanguinity is null.

Also we need to construct a recursion for p^{I}_τ, which for $\tau \geq 1$ reads:

$$p^{\mathrm{I}}_\tau = \frac{1+f_{\tau-1}}{2}, \tag{S-6}$$

because with probability 1/2, the same homologous allele is sampled, in which case IBD is 1, and with probability 1/2, the other is sampled, in which case IBD is given by the consanguinity with her mating partner $f_{\tau-1}$. The initial condition for p_0^{I} is given by:

$$p_0^{\mathrm{I}} = \sum_{\tau=0}^{+\infty} \frac{1+f_\tau}{2}\pi_\tau \tag{S-7}$$

From these, we get the consanguinity coefficient between a random adult female and her own sons or daughters (p_τ^{S} or p_τ^{D}, respectively) and that between a random adult female and a random offspring born in the same patch (p_τ^{M} or p_τ^{F}, respectively) for $\tau \geq 0$:

$$\begin{aligned} p_{\tau+1}^{\mathrm{S}} &= p_{\tau+1}^{\mathrm{D}} = \frac{1}{2}p_{\tau+1}^{\mathrm{I}} + \frac{1}{2}f_\tau, \\ p_{\tau+1}^{\mathrm{M}} &= p_{\tau+1}^{\mathrm{F}} = \frac{1}{n}p_{\tau+1}^{\mathrm{S}} + \frac{n-1}{n}f_\tau, \end{aligned} \tag{S-8}$$

the first line of which reads as the probability that offspring's allele derives from mother (1/2) times the probability that this allele is IBD with the mother ($p_{\tau+1}^{\mathrm{I}} = (1+f_\tau)/2$), plus the probability that the allele derives from father (1/2) times the probability that this allele is IBD with the mother (f_τ). The second line is because, for a given allele sampled from a random adult female, an allele sampled from one of the offspring born in the same patch derives from the adult female ($1/n$; in which case the consanguinity is $p_{\tau+1}^{\mathrm{S}} = p_{\tau+1}^{\mathrm{D}}$) or another adult female ($1 - {}^{1}\!/_{n}$; in which case the consanguinity is f_τ).

The initial conditions for $\tau = 0$ (with Eqn (S-5)) are given by:

$$\begin{aligned} f_0 &= \sum_{\tau=0}^{+\infty} \frac{p_\tau^{\mathrm{I}} + f_\tau}{2n}\pi_\tau \\ p_0^{\mathrm{S}} &= p_0^{\mathrm{D}} = \sum_{\tau=0}^{+\infty} \frac{p_\tau^{\mathrm{I}} + f_\tau}{2}\pi_\tau, \\ p_0^{\mathrm{M}} &= p_0^{\mathrm{F}} = \frac{1}{n}p_0^{\mathrm{S}} = \frac{1}{n}p_0^{\mathrm{D}} \end{aligned} \tag{S-9}$$

where the first line follows because the consanguinity of a mother to one of her own offspring is the arithmetic mean (1/2) for herself (the former) and her mate (latter).

3.2. Haplodiploidy

We denote the consanguinity of mating partners on the patch aged τ by f_τ; the average consanguinity of two female offspring sharing the same patch aged τ by ϕ_τ; the average consanguinity between two male offspring sharing the same patch aged τ by μ_τ.

The consanguinity between a pair of offspring male and offspring female on the same patch aged $\tau+1$ is given by the probability that they share the same mother (${}^{1}\!/_{n}$) times the consanguinity of full sibs (with probability $1/2$, the offspring female derives her gene from her mother as does the offspring male, in which case the consanguinity is p^{I}_{τ}; with probability $1/2$, the offspring female derives her gene from the father while the offspring male derives his gene from his mother, in which case the consanguinity is f_{τ}) plus the probability that they do not share the same mother $(1-1/n)$ times the probability that their mothers are both non-disperser (which is 1 since $\tau+1 \geq 1$) times the consanguinity of the parents by which their genes are transmitted (which is $\frac{\phi_{\tau}}{2}+\frac{f_{\tau}}{2}$). That is:

$$f_{\tau+1} = \frac{1}{n} \cdot \left(\frac{1}{2} p^{\mathrm{I}}_{\tau} + \frac{1}{2} f_{\tau} \right) + \frac{n-1}{n} \cdot \left(\frac{\phi_{\tau} + f_{\tau}}{2} \right) \tag{S-10}$$

(Taylor 1988a,b; Frank 1998; Rousset 2004; Lehmann 2007; Gardner *et al.* 2009).

The average consanguinity of two female offspring sharing the same patch aged $\tau > 0$, ϕ_{τ}, is given by the probability that they share the same mother $(1/n)$ times the consanguinity of full sisters $(p^{\mathrm{I}}_{\tau}/4 + f_{\tau}/2 + 1/4)$ plus the probability that they do not share the same mother $(1 - 1/n)$ times the probability that their mothers are both non-dispersers (which is 1 since $\tau+1 \geq 1$) (with probability $1/4$ they both derived their genes from their mothers, in which case the consanguinity is ϕ_{τ}; with probability $1/2$ they derived their genes from opposite-sex parents, in which the consanguinity is f_{τ}; with probability $1/4$ they both derived their genes from their fathers, in which case the consanguinity is μ_{τ}). That is,

$$\phi_{\tau+1} = \frac{1}{n} \cdot \left(\frac{1}{4} p^{\mathrm{I}}_{\tau} + \frac{1}{2} f_{\tau} + \frac{1}{4} \right) + \frac{n-1}{n} \cdot \left(\frac{\phi_{\tau} + 2 f_{\tau} + \mu_{\tau}}{4} \right). \tag{S-11}$$

The average consanguinity of two male offspring sharing the same patch (aged $\tau+1 \geq 1$), μ_{τ}, is the probability that they share the same mother $(1/n)$ times the probability of full brothers p^{I}_{τ} plus the probability that they do not share the common mother $1-1/n$ times the probability that both of their mothers are non-disperser (which is 1 since $\tau+1 \geq 1$) times the average consanguinity of two female offspring on the same patch ϕ_{τ}. That is:

$$\mu_{\tau+1} = \frac{1}{n} p^{\mathrm{I}}_{\tau} + \frac{n-1}{n} \phi_{\tau}. \tag{S-12}$$

Finally, $p^{\mathrm{I}}_{\tau+1}$ (the consanguinity for herself) follows a recursion given by:

$$p^{\mathrm{I}}_{\tau+1} = \frac{1+f_{\tau}}{2}, \tag{S-13}$$

as with probability 1/2, the same allele is sampled twice (in which case IBD is 1) and with probability 1/2, two different homologous alleles are sampled (in which case IBD is given by the inbreeding coefficient in the previous generation, f_τ).

For a patch that is newly recolonized (i.e., aged $\tau = 0$), kinship is possible for sibs (i.e., only by sharing the mother). The consanguinity between a pair of mating partners on the patch is given by the probability that they share the mother ($1/n$) times the spatial average of the consanguinity of full sibs:

$$f_0 = \frac{1}{n} \bullet \sum_{\tau=0}^{+\infty} \frac{1+3f_\tau}{4} \pi_\tau. \tag{S-14}$$

Similarly,

$$\begin{aligned}
\phi_0 &= \frac{1}{n} \bullet \sum_{\tau=0}^{+\infty} \frac{3+5f_\tau}{8} \pi_\tau, \\
\mu_0 &= \frac{1}{n} \bullet \sum_{\tau=0}^{+\infty} \frac{1+f_\tau}{2} \pi_\tau, \\
p_0^{\mathrm{I}} &= \sum_{\tau=0}^{+\infty} \frac{1+f_\tau}{2} \pi_\tau.
\end{aligned} \tag{S-15}$$

$(f_0, \phi_0, \mu_0, p_0^{\mathrm{I}})$ gives the initial condition of the recursion. Solved recursively, $(f_\tau, \phi_\tau, \mu_\tau, p_\tau^{\mathrm{I}})$ specifies the consanguinity between a mating pair, female offspring, and male offspring, respectively. From these, we get:

$$\begin{aligned}
p_\tau^{\mathrm{S}} &= p_\tau^{\mathrm{I}}, \\
p_\tau^{\mathrm{M}} &= \frac{1}{n} p_\tau^{\mathrm{S}} + \frac{n-1}{n} \phi_{\tau-1} \equiv \mu_\tau, \\
p_\tau^{\mathrm{D}} &= \frac{p_\tau^{\mathrm{I}} + f_{\tau-1}}{2} = \frac{1+3f_{\tau-1}}{4}, \\
p_\tau^{\mathrm{F}} &= \frac{1}{n} p_\tau^{\mathrm{D}} + \frac{n-1}{n} \bullet \frac{\phi_{\tau-1} + f_{\tau-1}}{2} \equiv f_\tau.
\end{aligned} \tag{S-16}$$

The initial condition for $\tau = 0$ is given by:

$$
\begin{aligned}
p_0^{\mathtt{S}} &= \sum_{\tau=0}^{+\infty} \frac{1+f_\tau}{2}\pi_\tau,\\
p_0^{\mathtt{M}} &= \frac{p_0^{\mathtt{S}}}{n},\\
p_0^{\mathtt{D}} &= \sum_{\tau=0}^{+\infty} \frac{1+3f_\tau}{4}\pi_\tau,\\
p_0^{\mathtt{F}} &= \frac{p_0^{\mathtt{D}}}{n}.
\end{aligned}
\tag{S-17}
$$

4 Average and initial consanguinity coefficients

4.1. Diploidy

We consider the average values of f_τ and p_τ^{I} over the distribution π_τ:

$$
\begin{aligned}
\overline{f} &:= \sum_{\tau=0}^{+\infty} f_\tau \pi_\tau\\
\overline{p^{\mathrm{I}}} &:= \sum_{\tau=0}^{+\infty} p_\tau^{\mathrm{I}} \pi_\tau.
\end{aligned}
\tag{S-18}
$$

By multiplying $\pi_{\tau+1} = (1-e)\pi_\tau$ with Eqns (S-4) and (S-6) and then summing up both sides over $\tau = 0$ to ∞, we get:

$$
\begin{aligned}
\overline{f} - \pi_0 f_0 &= (1-e)\left(\frac{\overline{p^{\mathrm{I}}} + \overline{f}}{2n} + \frac{n-1}{n}\cdot\overline{f}\right),\\
\overline{p^{\mathrm{I}}} - \pi_0 p_0^{\mathrm{I}} &= (1-e)\frac{1+\overline{f}}{2}.
\end{aligned}
\tag{S-19}
$$

With Eqn (S-7), we get:

$$\begin{aligned} f_0 &= \frac{1+e(n-1)}{n(1+4e(n-1))}, \\ p_0^{\mathrm{I}} &= \frac{1+2e(n-1)}{1+4e(n-1)}, \\ \overline{f} &= \frac{1}{1+4e(n-1)}, \\ \overline{p^{\mathrm{I}}} &= \frac{1+2e(n-1)}{1+4e(n-1)}\left(=p_0^{\mathrm{I}}\right), \end{aligned} \tag{S-20}$$

which recovers Gardner *et al.*'s (2009) results by replacing e with $1-\left(1-d\right)^2$ (where d is female-dispersal rate after mating). From this calculation, one may see that the well-known recursions for the consanguinity coefficients (Taylor 1988a,b; Frank 1998; Rousset 2004; Lehmann 2007; Gardner *et al.* 2009) are evaluated at metapopulation-wide avarage over the patch-age distribution.

4.2. Haplodiploidy

Similarly, let us denote the spatially averaged $f_\tau, \phi_\tau, \mu_\tau$ over the distribution π_τ by $\overline{f}, \overline{\phi}, \overline{\mu}$, repsectively:

$$\begin{aligned} \overline{f} &= \sum_{\tau=0}^{+\infty} \pi_\tau f_\tau, \\ \overline{\phi} &= \sum_{\tau=0}^{+\infty} \pi_\tau \phi_\tau, \\ \overline{\mu} &= \sum_{\tau=0}^{+\infty} \pi_\tau \mu_\tau, \\ \overline{p^{\mathrm{I}}} &= \sum_{\tau=0}^{+\infty} \pi_\tau p_\tau^{\mathrm{I}}. \end{aligned} \tag{S-21}$$

Then the initial values $(f_0, \phi_0, \mu_0, p^{\mathrm{I}}_0)$ are written as

$$\begin{aligned} f_0 &= \frac{1+3\overline{f}}{4n}, \\ \phi_0 &= \frac{3+5\overline{f}}{8n}, \\ \mu_0 &= \frac{1+\overline{f}}{2n}, \\ p^{\mathrm{I}}_0 &= \frac{1+\overline{f}}{2} \end{aligned} \tag{S-22}$$

(because coalescence between offspring born in a patch aged $\tau = 0$ may occur only if they share the same mother $1/n$). Also, multiplying $\pi_\tau = \pi_{\tau-1} \bullet (1-e)$ with the recursions for $(f_\tau, \phi_\tau, \mu_\tau, p^{\mathrm{I}}_\tau)$ (Eqns (S-10) to (S-13)) and then summing up both sides over $\tau = 1, 2, \ldots$, we get:

$$\begin{aligned} \sum_{\tau=1}^{+\infty} \pi_\tau f_\tau &= \sum_{\tau=1}^{+\infty} (1-e)\pi_{\tau-1} \left(\frac{1+3f_{\tau-1}}{4n} + \frac{n-1}{2n}\left(f_{\tau-1} + \phi_{\tau-1}\right)\right) \\ &= (1-e)\left(\frac{\overline{p^{\mathrm{I}}} + \overline{f}}{2n} + \frac{n-1}{2n}(\overline{f} + \overline{\phi})\right) \end{aligned} \tag{S-23}$$

whereas the LHS is $\overline{f} - \pi_0 f_0 = \overline{f} - e\dfrac{\overline{p^{\mathrm{I}}} + \overline{f}}{2n}$. Using the similar algebra for $(\phi_\tau, \mu_\tau, p^{\mathrm{I}}_\tau)$, we get a closed relation for $(\overline{f}, \overline{\phi}, \overline{\mu}, \overline{p^{\mathrm{I}}})$:

$$\begin{aligned} \overline{f} - e\frac{\overline{p^{\mathrm{I}}} + \overline{f}}{2n} &= (1-e)\frac{\overline{p^{\mathrm{I}}} + \overline{f}}{2n} + (1-e)\frac{n-1}{2n}\left(\overline{f} + \overline{\phi}\right), \\ \overline{\phi} - e\frac{3+5\overline{f}}{8n} &= (1-e)\frac{\overline{p^{\mathrm{I}}} + 2\overline{f} + 1}{4n} + (1-e)\frac{n-1}{4n}\left(\overline{\phi} + 2\overline{f} + \overline{\mu}\right), \\ \overline{\mu} - e\frac{\overline{p^{\mathrm{I}}}}{n} &= (1-e)\frac{\overline{p^{\mathrm{I}}}}{n} + (1-e)\frac{n-1}{n}\overline{\phi}, \\ \overline{p^{\mathrm{I}}} - e\frac{1+\overline{f}}{2} &= (1-e)\frac{1+\overline{f}}{2}, \end{aligned} \tag{S-24}$$

the last line of which implies $\overline{p^{\mathrm{I}}} = (1+\bar{f})/2$, which further implies $\bar{\phi} = \left(\bar{f}+\bar{\mu}\right)/2$. With some arrangement, we have:

$$\begin{aligned} \bar{f} &= \frac{1+3\bar{f}}{4n} + (1-e)\cdot\frac{n-1}{n}\cdot\frac{3\bar{f}+\bar{\mu}}{4}, \\ \bar{\mu} &= \frac{1+\bar{f}}{2n} + (1-e)\cdot\frac{n-1}{n}\cdot\frac{\bar{f}+\bar{\mu}}{2}. \end{aligned} \tag{S-25}$$

In a vector form,

$$\begin{pmatrix} \bar{f} \\ \bar{\mu} \end{pmatrix} = \begin{pmatrix} \frac{1}{4n} \\ \frac{1}{2n} \end{pmatrix} + \begin{pmatrix} \frac{3}{4}\left(\left(1-\frac{1}{n}\right)(1-e)+\frac{1}{n}\right) & \frac{1-\frac{1}{n}}{4}(1-e) \\ \frac{1}{2}\left(\left(1-\frac{1}{n}\right)(1-e)+\frac{1}{n}\right) & \frac{1-\frac{1}{n}}{2}(1-e) \end{pmatrix} \begin{pmatrix} \bar{f} \\ \bar{\mu} \end{pmatrix}, \tag{S-26}$$

which gives:

$$\begin{pmatrix} \bar{f} \\ \bar{\mu} \end{pmatrix} = \left(\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} - \begin{pmatrix} \frac{3}{4}\left(\left(1-\frac{1}{n}\right)(1-e)+\frac{1}{n}\right) & \frac{1-\frac{1}{n}}{4}(1-e) \\ \frac{1}{2}\left(\left(1-\frac{1}{n}\right)(1-e)+\frac{1}{n}\right) & \frac{1-\frac{1}{n}}{2}(1-e) \end{pmatrix} \right)^{-1} \begin{pmatrix} \frac{1}{4n} \\ \frac{1}{2n} \end{pmatrix}, \tag{S-27}$$

which is solved by:

$$\begin{aligned} \bar{f} &= \frac{n}{e^2n^2-2e^2n+e^2+3en^2-2en-e+n}, \\ \bar{\phi} &= \frac{ne-e+2n}{2\left(e^2n^2-2e^2n+e^2+3en^2-2en-e+n\right)}, \\ \bar{\mu} &= \frac{ne-e+n}{e^2n^2-2e^2n+e^2+3en^2-2en-e+n}. \end{aligned} \tag{S-28}$$

Substituting $\overline{f}$ into the following equations gives the average values of p's which read:

$$\begin{aligned}
\overline{p^{\mathrm{I}}} &= \frac{1+\overline{f}}{2},\\
\overline{p^{\mathrm{S}}} &= \frac{1+\overline{f}}{2},\\
\overline{p^{\mathrm{M}}} &= \overline{\mu}\\
\overline{p^{\mathrm{D}}} &= \frac{1+3\overline{f}}{4},\\
\overline{p^{\mathrm{F}}} &= \overline{f}.
\end{aligned} \tag{S-29}$$

5 Fitness subcomponents

Let us focus on a patch aged τ. We denote the mutant sex allocation on the focal patch by x_τ, the average sex allocation on the same patch by y_τ, and the wild type sex allocation on the patch aged τ by z_τ. In that patch, a focal female produces $J(1-x_\tau)$ of females (where J is the number of eggs per capita), who mate with the males born on the same patch. If that patch is persistent (with a probability of $1-e$), female offspring either disperse to recolonize empty patches with a probability of d, or else remain on their natal patch with a probability of $1-d$; if they do not disperse, they compete for reproduction on the patch against $J\big(1-d\big)(1-y_\tau)$ of non-dispersing females (and therefore the factor $J\big(1-d\big)$ is cancelled out). If a patch is not persistent (with a probability of e), all females disperse for empty patches (e of the whole patches), and such dispersed offspring ($J(1-x_\tau)\big((1-e)d+e\big)$) compete against on average $(1-\overline{z})J\Big(\big((1-e)d+e\big)\Big)$ of female offspring (and therefore $J\big((1-e)d+e\big)$ is cancelled out).

The daughter-fitness of a focal individual inhabiting on the focal patch $W_\tau^{\mathbf{F}}$ is therefore given by:

$$W_\tau^{\mathbf{F}} = (1-e)\frac{\big(1-d\big)(1-x_\tau)}{\big(1-d\big)(1-y_\tau)} + e\frac{\big((1-e)d+e\big)(1-x_\tau)}{\big((1-e)d+e\big)(1-\overline{z})}, \tag{S-30}$$

where we have written the spatial averaged sex allocation for $\overline{z} = \sum_{j=0}^{+\infty}\pi_j z_j$, and the son-fitness of the focal adult female inhabiting in a patch aged τ, $W_\tau^{\mathbf{M}}$, is given by:

$$W_\tau^{\mathbf{M}} = \frac{x_\tau}{y_\tau}\left((1-e)\frac{1-y_\tau}{1-y_\tau} + e\frac{1-y_\tau}{1-\overline{z}}\right), \tag{S-31}$$

where we have eliminated the cancelling factors. Note that these fitness functions are defined so that neutrality ($\mathbf{x} = \mathbf{y} = \mathbf{z}$) leads to $\sum_{\tau=0}^{+\infty} W_\tau^{\mathbf{F}} \equiv \sum_{\tau=0}^{+\infty} W_\tau^{\mathbf{M}} \equiv 1$.

Though we presumed in the main text that catastrophic extinction of patches occur after reproduction, Eqns (S-30) and (S-31) can also hold in other situations; for example: (i) a fraction $1-d$ of females stays on their natal patch, and a fraction d disperses in the both persistent and non-persistent patches, (ii) all females stay on persistent patches, while all females disperse on non-persistent patches, and (iii) a fraction $1-d$ of females stay and a fraction d disperse on persistent patches, while no females survive on non-persistent (extinct) patches. In all cases, the dispersal parameter d is cancelled out, and the fitness functions for daughters and sons are simplified to Eqns (S-30) and (S-31), respectively.

We can write the invasion fitness subcomponents in a general form as:

$$\begin{aligned} W_\tau^{\mathbf{F}} &= w^{\mathbf{F}}(x_\tau, y_\tau, \bar{z}), \\ W_\tau^{\mathbf{M}} &= w^{\mathbf{M}}(x_\tau, y_\tau, \bar{z}), \end{aligned} \tag{S-32}$$

with

$$\begin{aligned} w^{\mathbf{F}}(x,y,z) &:= (1-e)\frac{1-x}{1-y} + e\frac{1-x}{1-z}, \\ w^{\mathbf{M}}(x,y,z) &:= \frac{x}{y}\left((1-e)\frac{1-y}{1-y} + e\frac{1-y}{1-z}\right). \end{aligned} \tag{S-33}$$

It is of use to write down the derivatives:

$$\begin{aligned} \frac{\partial}{\partial x} w^{\mathbf{F}}(x,y,z)\bigg|_{(x,y,z)=(z_\tau,z_\tau,\bar{z})} &= -(1-e)\frac{1}{1-z_\tau} - e\frac{1}{1-\bar{z}} \\ \frac{\partial}{\partial y} w^{\mathbf{F}}(x,y,z)\bigg|_{(x,y,z)=(z_\tau,z_\tau,\bar{z})} &= (1-e)\frac{1}{1-z_\tau}, \\ \frac{\partial}{\partial x} w^{\mathbf{M}}(x,y,z)\bigg|_{(x,y,z)=(z_\tau,z_\tau,\bar{z})} &= (1-e)\frac{1}{z_\tau} + e\frac{1-z_\tau}{z_\tau(1-\bar{z})} \\ \frac{\partial}{\partial y} w^{\mathbf{M}}(x,y,z)\bigg|_{(x,y,z)=(z_\tau,z_\tau,\bar{z})} &= -(1-e)\frac{1}{z_\tau} - e\frac{1}{1-\bar{z}} - e\frac{1-z_\tau}{z_\tau(1-\bar{z})}, \end{aligned} \tag{S-34}$$

where note that the derivatives are evaluated at $(x,y,z) = (z_\tau, z_\tau, \bar{z})$. These quantities will be used below to assess the direction of selection under weak selection (Taylor & Frank 1996; Frank 1998; Rousset & Billiard 2000; Rousset 2004; Taylor *et al.* 2007).

6 Total fitness

Summing up the daughter- and son-mediated fitness functions (per capita) each multiplied by the class reproductive values, averaged over the patch-age distribution, obtains the total invasion fitness:

$$W = \sum_{\tau=0}^{+\infty} \left(c_\tau^{\mathbf{M}} W_\tau^{\mathbf{M}} + c_\tau^{\mathbf{F}} W_\tau^{\mathbf{F}} \right) \pi_\tau \tag{S-35}$$

(Bulmer 1994; Taylor & Frank 1996; Frank 1998; Rousset 2004; Taylor *et al.* 2007; Lehmann & Rousset 2010). In particular, if the stratetegy is $\mathbf{z} = (z_{\mathsf{E}}, z_{\mathsf{N}})$ (with a distribution $e : 1-e$), W simplifies to:

$$\begin{aligned} W = e\Big(& c^{\mathbf{M}} w^{\mathbf{M}} \left(x_{\mathsf{E}}, y_{\mathsf{E}}, e z_{\mathsf{E}} + (1-e) z_{\mathsf{N}} \right) + c^{\mathbf{F}} w^{\mathbf{F}} \left(x_{\mathsf{E}}, y_{\mathsf{E}}, e z_{\mathsf{E}} + (1-e) z_{\mathsf{N}} \right) \Big) \\ & + (1-e) \Big(c^{\mathbf{M}} w^{\mathbf{M}} \left(x_{\mathsf{N}}, y_{\mathsf{N}}, e z_{\mathsf{E}} + (1-e) z_{\mathsf{N}} \right) + c^{\mathbf{F}} w^{\mathbf{F}} \left(x_{\mathsf{N}}, y_{\mathsf{N}}, e z_{\mathsf{E}} + (1-e) z_{\mathsf{N}} \right) \Big) \end{aligned} \tag{S-36}$$

where the subscript $_{\mathsf{E}}$ accounts for disperser (Emigrant) females (hence inhabiting on the patch aged $\tau = 0$), while $_{\mathsf{N}}$ accounts for non-disperser females (hence on the patch aged $\tau > 0$). Also we have here made it explicit that $\bar{z} = e z_{\mathsf{E}} + (1-e) z_{\mathsf{N}}$. Also, class reproductive values (Taylor 1990; Caswell 2001) are denoted $c^{\mathbf{M}}$ for male and $c^{\mathbf{F}}$ for females.

7 Reproductive value

As the patch-age generates no difference in reproductive capacity, the class reproductive values are independent of patch ages and are fully determined by the ploidy: $c^{\mathbf{M}} = c^{\mathbf{F}} = {}^1/_2$ for diploidy, and $c^{\mathbf{M}} = {}^1/_3, c^{\mathbf{F}} = {}^2/_3$ for haplodiploidy (Taylor 1990; Caswell 2001).

8 Selection gradient

We outline the analyses for the general case in which the trait to evolve is patch age-specific sex ratio sorted as $\mathbf{z} = (z_0, z_1, \ldots, z_\tau, \ldots)$, where z_τ represents the sex ratio strategy of a female breeding on a patch aged τ. The selection gradients for dispersers' and non-dispersers' strategy z_{E} (E for emigrants) and z_{N} (N for non-disperser) are, using the neighbor-modulated fitness approach (Taylor & Frank

1996; Frank 1998; Rousset & Billiard 2000; Rousset 2004; Taylor *et al.* 2007), given by:

$$\begin{aligned}
S_{\mathsf{E}}(z_{\mathsf{E}},z_{\mathsf{N}}) &= \left(\frac{\mathrm{d}W_0}{\mathrm{d}g_0}\right)^{\circ} = c^{\mathbf{M}}\left(\frac{\partial W_0^{\mathbf{M}}}{\partial x_0}p_0^{\mathsf{S}} + \frac{\partial W_0^{\mathbf{M}}}{\partial y_0}p_0^{\mathsf{M}}\right)^{\circ} + c^{\mathbf{F}}\left(\frac{\partial W_0^{\mathbf{F}}}{\partial x_0}p_0^{\mathsf{D}} + \frac{\partial W_0^{\mathbf{F}}}{\partial y_0}p_0^{\mathsf{F}}\right)^{\circ},\\
S_{\tau}(z_{\mathsf{E}},z_{\mathsf{N}}) &= \left(\frac{\mathrm{d}W_\tau}{\mathrm{d}g_\tau}\right)^{\circ} = c^{\mathbf{M}}\left(\frac{\partial W_\tau^{\mathbf{M}}}{\partial x_\tau}p_\tau^{\mathsf{S}} + \frac{\partial W_\tau^{\mathbf{M}}}{\partial y_\tau}p_\tau^{\mathsf{M}}\right)^{\circ} + c^{\mathbf{F}}\left(\frac{\partial W_\tau^{\mathbf{F}}}{\partial x_\tau}p_\tau^{\mathsf{D}} + \frac{\partial W_\tau^{\mathbf{F}}}{\partial y_\tau}p_\tau^{\mathsf{F}}\right)^{\circ},\\
S_{\mathsf{N}}(z_{\mathsf{E}},z_{\mathsf{N}}) &= \frac{1}{1-e}\sum_{\tau=1}^{+\infty}\pi_\tau S_\tau(z_{\mathsf{E}},z_{\mathsf{N}}),
\end{aligned} \tag{S-37}$$

where $^{\circ}$ represents neutrality, (i.e., the derivatives are evaluated at $\mathbf{x}=\mathbf{y}=\mathbf{z}$). g_τ represents the genic value of a gene sampled from a locus (denoted $\mathcal{G}$, that encodes the sex allocation) of a female offspring (Falconer 1975; Grafen 1985; Bulmer 1994; Taylor & Frank 1996; Frank 1998; Gardner *et al.* 2009). Also, p-values are the consanguinities of an adult female with an corresponding offspring sharing the same patch (age τ): S designates her own son, M male offspring, D her own daughter, and F female offspring, respectively.

9 Unconditional strategy

When females exhibit unconditional strategy (i.e., $z_\tau \equiv z_{\mathsf{U}}$ for all $\tau \geq 0$), the selection gradient reads:

$$S_{\mathsf{U}}(z_{\mathsf{U}}) = \sum_{\tau=0}^{+\infty}\pi_\tau S_\tau(z_{\mathsf{U}},z_{\mathsf{U}}). \tag{S-38}$$

ESS allocation (which obtains from $S_{\mathsf{U}}(z_{\mathsf{U}})=0$) simplifies down to:

$$z_{\mathsf{U}}^{*} = \frac{n-1}{2n} \tag{S-39}$$

for diploids, and:

$$\begin{aligned}
z_{\mathsf{U}}^{*} &= \frac{c^{\mathbf{M}}\left(\overline{p^{\mathsf{S}}}-\overline{p^{\mathsf{M}}}\right)}{c^{\mathbf{M}}\left(\overline{p^{\mathsf{S}}}-(1-e)\overline{p^{\mathsf{M}}}\right)+c^{\mathbf{F}}\left(\overline{p^{\mathsf{D}}}-(1-e)\overline{p^{\mathsf{F}}}\right)}\\
&= \frac{(n-1)(-1-e+3n+en)}{2n(-e+3n+en)}
\end{aligned} \tag{S-40}$$

for haplodiploids. We therefore recover Gardner *et al.*'s (2009) results by replacing e with $1-\left(1-d\right)^2$ (where d is female-dispersal rate after mating).

10 Dispersers' strategy

Higher male allocation is favored for a disperser female if:

$$\begin{matrix} c^{\mathbf{F}}\left(-\frac{1-e}{1-z_{\mathsf{E}}}-\frac{e}{1-\bar{z}}\right)p_0^{\mathsf{D}} & +c^{\mathbf{F}}\left(\frac{1-e}{1-z_{\mathsf{E}}}\right)p_0^{\mathsf{F}} \\ +c^{\mathbf{M}}\left(\frac{1-e}{z_{\mathsf{E}}}+\frac{e(1-z_{\mathsf{E}})}{z_{\mathsf{E}}(1-\bar{z})}\right)p_0^{\mathsf{S}} & +c^{\mathbf{M}}\left(-\frac{1-e}{z_{\mathsf{E}}}-\frac{e}{1-\bar{z}}-\frac{e(1-z_{\mathsf{E}})}{z_{\mathsf{E}}(1-\bar{z})}\right)p_0^{\mathsf{M}} \end{matrix} > 0. \tag{S-41}$$

If we divide both sides by $p_0^{\mathsf{I}} = \left(1+\bar{f}\right)/2$ (the consanguinity of a mother to herself), we get the Hamilton's rule of the main text, after clearing the fractions.

11 Non-dispersers' strategy

Higher male allocation is favored for a non-disperser female if:

$$\sum_{\tau=1}^{+\infty}\pi_\tau\left(\begin{matrix} c^{\mathbf{F}}\left(-\frac{1-e}{1-z_{\mathsf{N}}}-\frac{e}{1-\bar{z}}\right)p_\tau^{\mathsf{D}} & +c^{\mathbf{F}}\left(\frac{1-e}{1-z_{\mathsf{N}}}\right)p_\tau^{\mathsf{F}} \\ +c^{\mathbf{M}}\left(\frac{1-e}{z_{\mathsf{N}}}+\frac{e(1-z_{\mathsf{N}})}{z_{\mathsf{N}}(1-\bar{z})}\right)p_\tau^{\mathsf{S}} & +c^{\mathbf{M}}\left(-\frac{1-e}{z_{\mathsf{N}}}-\frac{e}{1-\bar{z}}-\frac{e(1-z_{\mathsf{N}})}{z_{\mathsf{N}}(1-\bar{z})}\right)p_\tau^{\mathsf{M}} \end{matrix}\right) > 0. \tag{S-42}$$

The quantities inside the bracket are dependent on patch age τ only through consanguinity, p-values. Therefore, what matters is the average values of p's (minus ep_0), given that she is in a patch aged $\tau \geq 1$:

$$\left(\begin{matrix} c^{\mathbf{F}}\left(-\frac{1-e}{1-z_{\mathsf{N}}}-\frac{e}{1-\bar{z}}\right)\frac{\overline{p^{\mathsf{D}}}-ep_0^{\mathsf{D}}}{1-e} & +c^{\mathbf{F}}\left(\frac{1-e}{1-z_{\mathsf{N}}}\right)\frac{\overline{p^{\mathsf{F}}}-ep_0^{\mathsf{F}}}{1-e} \\ +c^{\mathbf{M}}\left(\frac{1-e}{z_{\mathsf{N}}}+\frac{e(1-z_{\mathsf{N}})}{z_{\mathsf{N}}(1-\bar{z})}\right)\frac{\overline{p^{\mathsf{S}}}-ep_0^{\mathsf{S}}}{1-e} & +c^{\mathbf{M}}\left(-\frac{1-e}{z_{\mathsf{N}}}-\frac{e}{1-\bar{z}}-\frac{e(1-z_{\mathsf{N}})}{z_{\mathsf{N}}(1-\bar{z})}\right)\frac{\overline{p^{\mathsf{M}}}-ep_0^{\mathsf{M}}}{1-e} \end{matrix}\right) > 0. \tag{S-43}$$

Dividing both sides by $\sum_{\tau\geq 1} p_\tau^{\mathsf{I}}\pi_\tau/(1-e)$ (average consanguinity of a mother to herself in a patch aged τ), we get Hamilton's rule of the main text, after clearing the fractions.

12 Evolutionary outcomes

We obtained evolutionary outcomes $(z_{\mathrm{E}}^*, z_{\mathrm{N}}^*)$ by nullifying the Hamilton's rules, and we call the pair of the evolutionary outcomes as cESSs (the candidate ESSs; Maynard Smith & Price 1973; Hofbauer & Sigmund 1990; Geritz *et al.* 1998).

Dependence on the number of females ovipositing on a patch, *n*

The cESSs monotonically increase with n, and eventually lead to Fisherian sex ratio 1/2 with $n \to +\infty$ (Figure S3- 1A). When we compare z_{E}^* and z_{N}^*, we found that $z_{\mathrm{E}}^* > z_{\mathrm{N}}^*$ always holds true for diploids. The cESSs generally increase with decreasing patch extinction rate e (Figure S3- 1A; but except large n for haplodiploidy), which is likely to be because local competition between related females increases with smaller e (Bulmer 1986; Taylor 1988b; Frank 1998; Gardner *et al.* 2009).

However, we found the predicted patterns complicated for haplodiploids. For intermediate or high extinction rates (for example, $e = 0.5$ or 0.8), $z_{\mathrm{E}}^* > z_{\mathrm{N}}^*$ is also favoured. In contrast, for small $e (= 0.2)$, small n favours $z_{\mathrm{E}}^* > z_{\mathrm{N}}^*$ while the opposite $z_{\mathrm{E}}^* < z_{\mathrm{N}}^*$ appears to occur when n is larger. This trend can be explained by relatedness asymmetry for haplodiploid sex determination. For dispersers, inbreeding increases relatedness of mothers to their daughters, but does not relatedness to their sons, which favours a more female-biased sex ratio for haplodiploid than diploid species (Figure S3- 1A; Frank 1985; Herre 1985). This trend is remarkable with smaller e (i.e., higher inbreeding rates). For non-dispersers, mothers are related not only with their own offspring but also with offspring produced by other mothers on the same patch. This leads to almost identical cESSs between diploids and haplodiploids (Figure S3- 1A; Hamilton's rules for non-dispersers are exactly identical for diploids and haplodiploids). Consequently, z_{E}^* is predicted to be more female biased than z_{N}^*, when e is small and n is large.

Overall, the cESSs are predicted to increase with n, and decrease with inbreeding rates, in agreement with to the prediction by a theoretical model assuming that females are able to adjust their offspring sex ratio according to the number and kinship of females laying eggs on a patch (Gardner & Hardy 2021).

Dependence on the relatedness between offspring on a patch

In the present model, the influences of the number of mothers and relatedness between mothers on a patch can be summarized to one parameter, relatedness between offspring on a patch. We define relatedness between female offspring on a patch produced by dispersers and non-dispersers as:

$$R_{\mathrm{E}}^{\mathbf{F}} := \frac{f_0}{p_0^{\mathrm{I}}} \tag{S-44}$$

and

$$R_{\mathrm{N}}^{\mathbf{F}} := \frac{\frac{1}{1-e}\sum_{\tau\geq 1} f_\tau \pi_\tau}{\frac{1}{1-e}\sum_{\tau\geq 1} p_\tau^{\mathrm{I}} \pi_\tau} = \frac{\overline{f} - ef_0}{\overline{p^{\mathrm{I}}} - ep_0^{\mathrm{I}}} \tag{S-45}$$

respectively. We first assessed the effects of n (the number of mothers ovipositing on a patch) on the relatedness coefficients, and found that relatedness coefficients decrease with n and that $R_{\mathrm{N}}^{\mathbf{F}} > R_{\mathrm{E}}^{\mathbf{F}}$ (Figure S3- 2), which is because non-disperser females are more likely to be related with neighboring females than are disperser females (El Mouden & Gardner 2008; Wild & Fernandes 2009).

By plotting the cESSs against the relatedness (by tuning n), we found that more female-biased sex ratios are favoured with increasing relatedness between offspring (Figure S3- 1B). This negative relationship is predicted for both dispersers and non-dispersers, although the detailed patterns depend on the difference of ploidy. While z_{N}^* is similar for diploids and haplodiploids, z_{E}^* is more female biased for haplodiploid than diploids especially with smaller $R_{\mathrm{E}}^{\mathbf{F}}$ and smaller e. Consequently, cESSs for dispersers and non-dispersers are predicted to switch at an intermediate value of relatedness for haplodiploid species (Figure S3- 1B).

By plotting the cESSs in terms of relatedness, we can separately investigate the effects of relatedness and local competition between relatives (Cooper *et al.* 2018). Here, the scale of competition equals $1-e$, which is the probability that two randomly chosen females laying eggs on a patch are derived from the same patch (Frank 1998). We found that less female-biased sex ratios are predicted with higher local competition (smaller e) for both dispersers and non-dispersers (Figure S3- 1B; see also Gardner *et al.* 2009, in which the scale of competition is $(1-d)^2$, where d is female dispersal rate). In the natural populations, the effects of relatedness and local competition between relatives are likely to influence the evolution of sex ratio, with its extent dependent upon life history details, such as population structure and whether females can assess if they are with closer relatives (Frank 1985; Frank 1986; Frank 1998; Bulmer 1986; Taylor 1988b; Gardner *et al.* 2009; Lehmann & Rousset 2010; Cooper *et al.* 2018; Gardner & Hardy 2021).

13 Possible extensions in future studies

A bounded patch age

Suppose that the patches aged $\tau = T$ necessarily go extinct. The resulting recursion for π_τ reads:

$$\begin{aligned} \pi_0 &= \pi_T + e(1-\pi_T), \\ \pi_{\tau+1} &= (1-e)\pi_\tau \end{aligned} \tag{S-46}$$

for $\tau = 0, 1, \ldots, T-1$. The first line yields $(1-e)\pi_T = \pi_0 - e$ while the second line, recursively, leads to $\pi_T = (1-e)^T \cdot \pi_0$ (i.e., two equations with two variables under study), which supplies:

$$\pi_\tau = \frac{e}{1-(1-e)^{1+T}}(1-e)^\tau. \tag{S-47}$$

That is, the patch ages follow a conditional geometric distribution. When $T = 0$ (i.e., if all patches are extinct immediately) or equivalently $e = 1$, the model simplifies down to Hamilton's (1967) original LMC model.

With this modification, we can similarly obtain the recursions for consanguinity coefficients, the invasion fitness, and the corresponding selection gradients (formally by replacing "∞" with T).

Analogy to the haystack-model

Our model structure is not identical but similar to the classic haystack model (Bulmer & Taylor 1980; Nagelkerke & Sabelis 1996). We suppose that (i) n mated females reproduce in a haystack in each generation, (ii) each haystack is persisting with a probability of $1-e$ per generation (otherwise catastrophically collapsed), while exporting emigrants to empty haystacks, and (iii) is eventually collapsed at the T-th generation with probability 1. As a result, the generations of the haystacks are not synchronized (but follow the conditional geometric distribution given by Eqn (S-47)). Therefore, the key differences with the haystack model are the asynchrony of haystacks' ages and the possibility of extinction in each generation. Future studies may investigate these extensions to assess and revisit the effects of haystacks and their ages on sex ratio evolution.

References

Bulmer, M. G. (1986). Sex ratio theory in geographically structured populations. *Heredity*, **56**.1, pp. 69–73. DOI: 10.1038/hdy.1986.10.

Bulmer, M. G. (1994). *Evolutionary theoretical ecology*. Sinauer Associates, Sunderland, MA.

Bulmer, M. G. & Taylor, P. D. (1980). Sex ratio under the haystack model. *Journal of Theoretical Biology*, **86**.1, pp. 83–89. DOI: 10.1016/0022-5193(80)90066-1.

Caswell, H. (2001). *Matrix population models*. Wiley Online Library.

Cooper, G. A., Levin, S. R., Wild, G., & West, S. A. (2018). Modeling relatedness and demography in social evolution. *Evolution Letters*, **2**.4, pp. 260–271. DOI: 10.1002/evl3.69.

El Mouden, C & Gardner, A (2008). Nice natives and mean migrants: the evolution of dispersal-dependent social behaviour in viscous populations. *Journal of Evolutionary Biology*, **21**.6, pp. 1480–1491. DOI: 10.1111/j.1420-9101.2008.01614.x.

Falconer, D. S. (1975). *Introduction to quantitative genetics*. Pearson Education India.

Frank, S. A. (1985). Hierarchical selection theory and sex ratios. II. On applying the theory, and a test with fig wasps. *Evolution*, **39**.5, pp. 949–964. DOI: 10.1111/j.1558-5646.1985.tb00440.x.

Frank, S. A. (1986). Dispersal polymorphisms in subdivided populations. *Journal of Theoretical Biology*, **122**.3, pp. 303–309. DOI: 10.1016/s0022-5193(86)80122-9.

Frank, S. A. (1998). *Foundations of social evolution*. Princeton University Press.

Gardner, A., Arce, A., & Alpedrinha, J. (2009). Budding dispersal and the sex ratio. *Journal of Evolutionary Biology*, **22**.5, pp. 1036–1045. DOI: 10.1111/j.1420-9101.2009.01719.x.

Gardner, A. & Hardy, I. C. W. (2021). Adjustment of sex allocation to co-foundress number and kinship under local mate competition: an inclusive-fitness analysis. *Journal of Evolutionary Biology*, DOI: 10.1111/jeb.13719.

Geritz, S. A., Mesze, G, & Metz, J. A. (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology*, **12**.1, pp. 35–57.

Grafen, A. (1985). A geometric view of relatedness. *Oxford surveys in Evolutionary Biology*, **2**.2, pp. 28–89.

Hamilton, W. D. (1967). Extraordinary sex ratios. *Science*, **156**.3774, pp. 477–488. DOI: 10.1126/science.156.3774.477.

Herre, E. A. (1985). Sex ratio adjustment in fig wasps. *Science*, **228**.4701, pp. 896–898. DOI: 10.1126/science.228.4701.896.

Hofbauer, J. & Sigmund, K. (1990). Adaptive dynamics and evolutionary stability. *Applied Mathematics Letters*, **3**.4, pp. 75–79. DOI: 10.1016/0893-9659(90)90051-c.

Lehmann, L. (2007). The evolution of trans-generational altruism: kin selection meets niche construction. *Journal of Evolutionary Biology*, **20**.1, pp. 181–189. DOI: 10.1111/j.1420-9101.2006.01202.x.

Lehmann, L. & Rousset, F. (2010). How life history and demography promote or inhibit the evolution of helping behaviours. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**.1553, pp. 2599–2617. DOI: 10.1098/rstb.2010.0138.

Maynard Smith, J. & Price, G. R. (1973). The Logic of Animal Conflict. *Nature*, **246**, p. 15. DOI: 10.1038/246015a0.

Nagelkerke, C. J. & Sabelis, M. W. (1996). Hierarchical Levels of Spatial Structure and Their Consequences for the Evolution of Sex Allocation in Mites and Other Arthropods. *The American Naturalist*, **148**.1, pp. 16–39. DOI: 10.1086/285909.

Rousset, F. (2004). *Genetic Structure and Selection in Subdivided Populations (MPB-40)*. Princeton University Press.

Rousset, F. & Billiard, S. (2000). A theoretical basis for measures of kin selection in subdivided populations: finite populations and localized dispersal. *Journal of Evolutionary Biology*, **13**.5, pp. 814–825. DOI: `10.1046/j.1420-9101.2000.00219.x`.

Taylor, P. D. (1988a). An inclusive fitness model for dispersal of offspring. *Journal of Theoretical Biology*, **130**.3, pp. 363–378. DOI: `10.1016/s0022-5193(88)80035-3`.

— (1988b). Inclusive fitness models with two sexes. *Theoretical Population Biology*, **34**.2, pp. 145–168. DOI: `10.1016/0040-5809(88)90039-1`.

— (1990). Allele-frequency change in a class-structured population. *The American Naturalist*, **135**, pp. 95–106. DOI: `10.1086/285034`.

Taylor, P. D. & Frank, S. A. (1996). How to make a kin selection model. *Journal of Theoretical Biology*, **180**.1, pp. 27–37. DOI: `10.1006/jtbi.1996.0075`.

Taylor, P. D., Wild, G., & Gardner, A. (2007). Direct fitness or inclusive fitness: how shall we model kin selection? *Journal of Evolutionary Biology*, **20**.1, pp. 301–309. DOI: `10.1111/j.1420-9101.2006.01196.x`.

Wild, G. & Fernandes, A. D. (2009). Investment in the public good through conditional phenotypes ï¿½ of large effect. *Journal of Evolutionary Biology*, **22**.5, pp. 927–941. DOI: `10.1111/j.1420-9101.2009.01711.x`.

Wright, S. (1931). Evolution in Mendelian populations. *Genetics*, **16**.2, p. 97. DOI: `10.1007/bf02459575`.

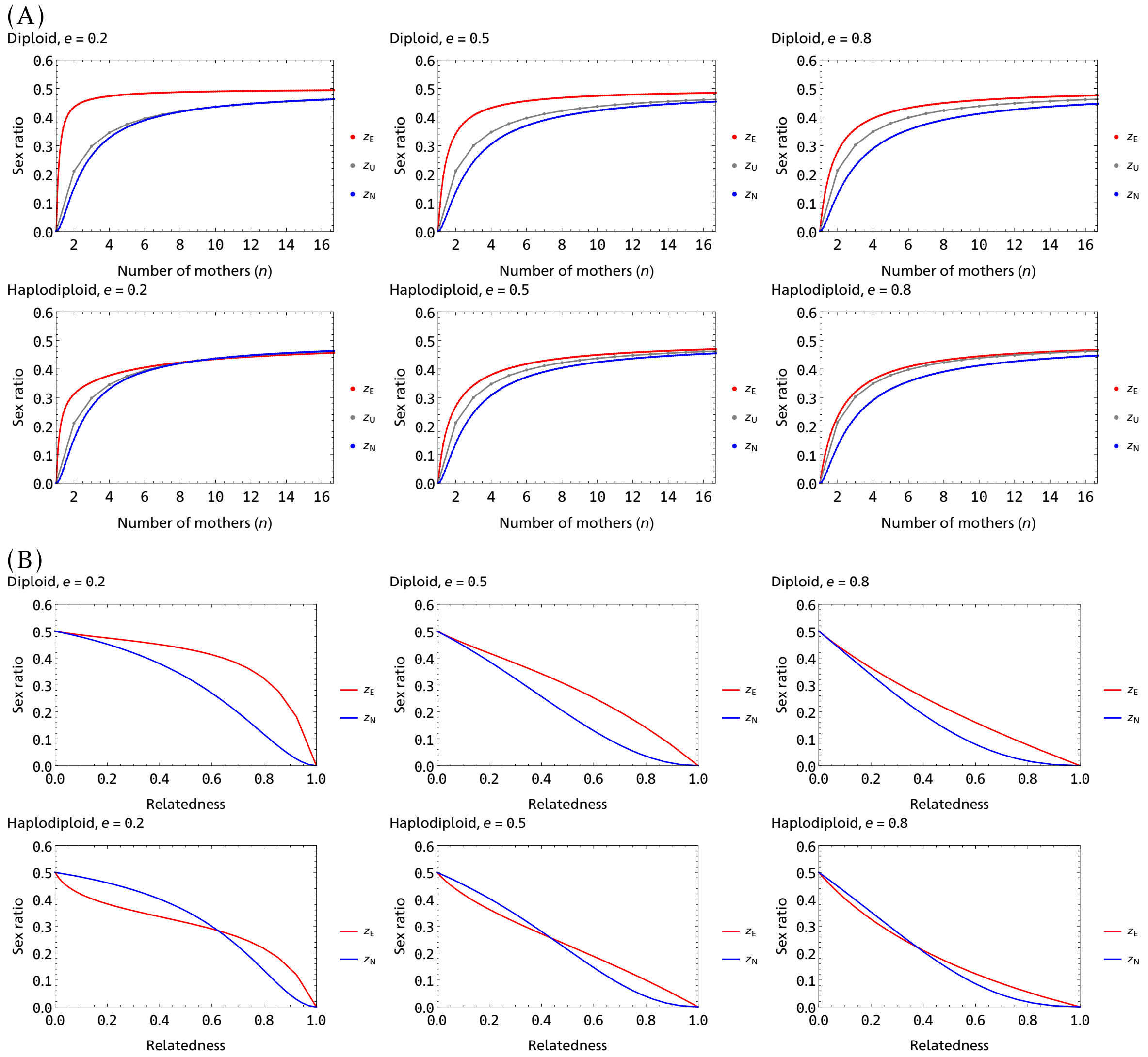

Figure S3- 1: Predicted sex ratio (proportion sons) plotted against the number of females ovipositing on a patch (n; panel A) and against the relatedness coefficient for female offspring on a patch $R_E^{\mathbf{F}}$ for dispersers and $R_N^{\mathbf{F}}$ for non-dispersers (panel B).

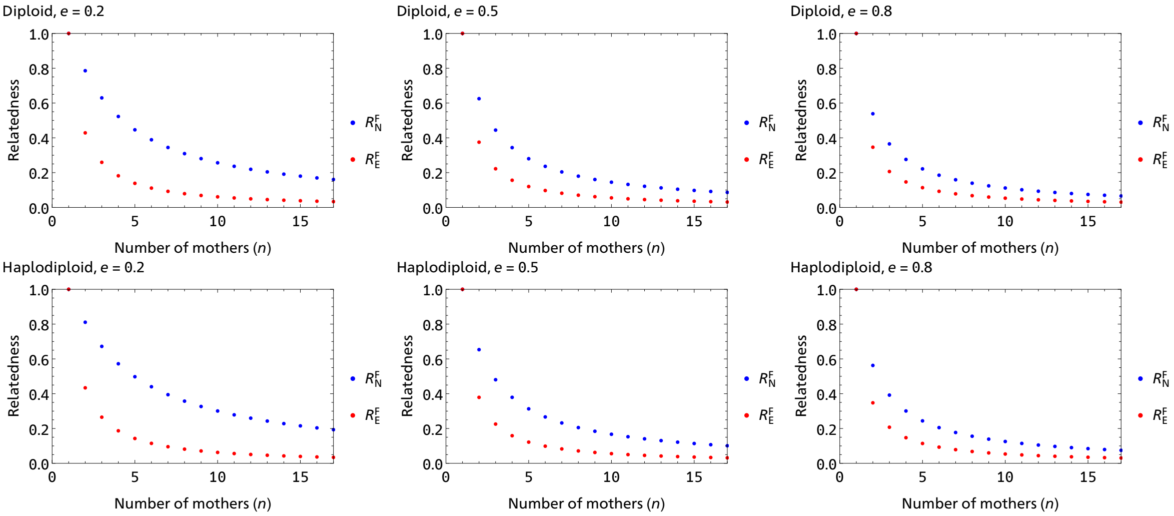

Figure S3- 2: Relatedness coefficients plotted against n.