

Sex ratio dependent dispersal when sex ratios vary between patches

Ronald M. Nelson^{a,1}, Jaco M. Greeff^{a,*}

^a Department of Genetics, University of Pretoria, Pretoria, 0002, South Africa

*Corresponding author: JMG

University of Pretoria, Pretoria, 0002, South Africa

Tel: +27 83 257 8761

Fax: +27 (0)12 362 5327

E-mail address: jaco.greeff@up.ac.za

¹ Present address: Swedish University of Agricultural Sciences, Box 7023, 750 07 Uppsala, Sweden. Email address: ronnie.nelson@slu.se

Author Contributions:

RMN planned the study, wrote simulations, did analyses and wrote first draft.

JMG supervised RMN, planned the study, helped with analyses and interpretation and finalizing manuscript.

Abstract

Female biased sex ratios reduce competition between brothers when mating takes place within local patches. Male dispersal prior to mating is another strategy that reduces competition between brothers. One may thus expect these two traits to co-evolve and this is partially met in that sex ratios becomes less female biased as dispersal increases. However, the evolutionary stable degree of dispersal is unaffected by the sex ratio. The analytical models developed to reach these conclusions ignored variance in sex ratios since this increases the structural complexity of models. For similar reasons finite clutch sizes are also routinely ignored. To overcome these shortfalls, we developed individual based simulations that allowed us to

incorporate realistic clutch sizes and binomial variance in sex ratios between patches. We show that under variable sex ratios, males evolve to more readily disperse away from patches with higher sex ratios than lower sex ratios. We show that, while the dispersal rate is insensitive to the sex ratio when sex ratios are precise, it is affected by the number of males with dispersal decreasing as the number of males decreases.

Keywords: Sex allocation, local mate competition, parent offspring conflict, individual based simulation modelling.

1. Introduction

Many arthropods exploit ephemeral resources for oviposition. Females are thus forced to disperse to new patches to oviposit. In contrast, the males of many such species will often remain within their natal patch and mate with any eclosing females (parasitoid wasps: Hamilton, 1967; King, 1987; Godfray, 1994; Hardy, 1994; Hardy and Cook, 1995; Godfray and Cook, 1997; Hardy et al., 1999; parasitoid flies: Godfray, 1994; pollinating fig wasps: Hamilton, 1979; Herre et al., 1997; Ahmed et al., 2009; bark and ambrosia beetles and some species of aphids and mites: Wrensch and Ebbert, 1993). When females lay many eggs per patch, there is potential for competition between brothers for mating opportunities called Local Mate Competition (Hamilton, 1967). Hamilton (1967) argued that mothers can reduce LMC between sons by biasing the sex ratios (defined here as the proportion of sons) towards daughters. In fact, when a single female oviposits in a patch, she should produce just enough sons to fertilize all her daughters and a number of organisms frequently produce female biased sex ratios with surprising accuracy (West and Sheldon, 2002; Greeff and Newman, 2011; but see Orzack, 2002).

However, sex ratios frequently vary between clutches (Hardy, 1992; Hardy and Cook, 1995; Hardy et al., 1998; Nagelkerke, 1996; Krackow et al., 2002; Greeff and Newman, 2011) and this will result in clutches containing either too many or too few sons. Furthermore, mothers frequently produce small clutches and then need to overproduce males to guard against the fitness costs of unmated females (Nagelkerke and Hardy, 1994; Nagelkerke, 1996; Hardy et al., 1998; Kjellberg et al., 2005). One possible resolution to this excess of males could be that the surplus males disperse to other patches to avoid competition with their brothers (Van Valen, 1971; Hamilton and May, 1977; for reviews see Clobert et al., 2001; Ronce, 2007). Male dispersal has indeed been observed in species with local mate competition (Wrensch and Ebbert, 1993; Greeff et al., 2003; Peer and Taborsky, 2005; Nelson and Greeff, 2009). Here we ask if males will evolve to be more likely to disperse away from patches with higher sex ratios?

Many analytical models have been developed to understand the factors that affect the evolution of dispersal, but in most of these the life history differs in crucial aspects from that explained above. Specifically, females disperse before mating and also have an opportunity not to disperse at all. The latter point is not crucial as the current scenario is just a special case where female dispersal is constrained to be 100%. The former point is more serious and the only model that we are aware of that explicitly addressed this life history difference found that it results in higher male dispersal when inbreeding depression occurs (Wild and Taylor, 2004). A relevant finding of Wild and Taylor (2004) is that while sex ratios evolve in response to dispersal, dispersal is not affected by the sex ratio. This may lead one to conclude that males will not evolve to disperse more from patches with higher sex ratios. However, Wild and Taylor's (2004) finding is, in part, an artefact of a simplifying assumption that most analytical sex ratio models make, namely, that sex ratios are precise (Motro, 1982; Frank, 1986; Taylor, 1988; Taylor, 1994; Gandon and Michalakis, 2001; Leturque and Rousset, 2003; Ronce, 2007; but see Green et al., 1982; Griffiths and Godfray, 1988; Nagelkerke, 1996). Hence, a male finding himself in a patch with a high sex ratio will encounter the exact same sex ratio in all

other patches because sex ratios are invariable. Another shortfall of analytical models is that in order to use calculus to obtain evolutionary stable strategies, sex ratio needs to be a continuous trait. This limitation forces the implicit assumption that clutches are very (infinitely) large, which is at odds with the biology of many relevant species. It is also implicitly assumed in most analytical models that all females are mated. But, when clutch sizes are small and males disperse with a high probability, many females will remain unmated – a fitness cost of dispersal that cannot simply be ignored. Finally, most of the developed models aim to understand sex biased dispersal. Here we have a more focused question as we already know that females must disperse and that they do so after mating. We want to know if sex ratio variance will lead to sex ratio dependant dispersal in males.

Genes for dispersal can be expressed in the mother, for instance when she determines whether her son has a dispersing or fighting morphology (Pienaar and Greeff, 2003), or in the sons themselves (Schuster and Wade, 1991). When genes for dispersal are expressed in the mother, dispersal rates are higher than when the genes are expressed in the offspring themselves, indicating parent-offspring conflict (Hamilton and May, 1977; Motro, 1983; Taylor, 1988; Ronce et al., 1998; Gandon, 1999). This difference makes intuitive sense as parents gain more if just enough sons remain in the native patch to mate the daughters, while the remainder disperse (thereby reducing local mate competition and maximising the chance of finding additional mating opportunities). On the other hand, sons that disperse may find no mating opportunities elsewhere, but would have been assured some at home. Mother's knowledge will be restrained by a lack of information of other females' exact strategies, of future developmental mortality etc.. Therefore we believe that expression in mothers is rare and here we will only consider expression in sons themselves.

Inbreeding depression is an important factor that leads to increased rates of dispersal (Bengtsson, 1978; May, 1979; Motro, 1991; Perrin and Mazalov, 2000; Clobert et al., 2001; Perrin and Goudet, 2001). However, the types of organisms we are interested in routinely

sibmate and are fairly resistant to inbreeding depression (but see Antolin, 1999; Henter, 2003 Greeff et al., 2009), and we do not consider inbreeding depression here.

When there is no cost to dispersal, models normally find that all males should disperse (Frank, 1986; Gandon, 1999). A zero cost to dispersal is unrealistic and will not allow any sex ratio differences to evolve, if all males disperse regardless. We therefore worked with a nominal cost of 0.2 to illustrate that sex ratio dependant dispersal can evolve. A cost of 0.2 means that a male reaches another patch without dying with a probability of 0.2. We also explore how dispersal varies with the cost of dispersal.

To address the shortcomings of analytical models we developed individual based simulations where sex ratios vary, clutches are of finite size and dispersal was allowed to evolve contingent on the sex ratio of the patch. Many mathematically inclined researchers are suspicious of simulation modelling as they may seem like a black box, and in the words of one reviewer give “theoretical raw data rather than theoretical insight”. However, by systematically varying parameters and performing *in silico* experiments it is possible to obtain theoretical insight and to understand how factors interact to give the observed variation. Reciprocally, one must guard against thinking that an analytical solution equals theoretical insight; it reveals preciously little of the interactions of parameters that gave the solution.

Another common misconception with regards simulation models is that kin selection needs to be explicitly introduced. This is a fallacy; Grafen (1984) has already pointed out that the inclusive fitness approach is simply an alternative way of accounting fitness. Kin-advantage must emerge spontaneously in any individual based simulation (Poethke et al., 2007; Gros et al., 2008). Kin selection indeed plays a role in male dispersal with higher dispersal when the relatedness between competing males is high (Frank, 1986). As the number of mothers that contribute to a patch decreases, relatedness increases and male dispersal increases. So much so, that when there is only one mother ovipositing eggs in a patch, then typically more than 50% of males will disperse, even under severe costs to dispersal (Wild and Taylor, 2004).

2. Model description

2.1. State variables and scales

The model comprised three structural levels: individual, patch and population. Each individual is haploid and characterised by the following state variables: identity number, sex, mating status (mated or unmated), patch number (identity of the patch where the individual reside), dispersal genes (an array of genes each responding to a different range of sex ratios) and male sperm (genes obtained by the females after mating). It is important to note that each dispersal gene has a value from 0 to 1 indicating the probability of dispersal. However, each dispersal gene responds to a different range of sex ratios, and therefore only one gene at a time determines if an individual disperses from a patch. For example: if the first gene of a male individual has a value of 0.1 and responds to a sex ratio from 0 to 0.33 the male will have a 10% chance of dispersing. If the sex ratio is not within this range another gene, with its own probability of dispersal, will affect the individual's dispersal. This enables us to obtain evolutionary stable dispersal rates for a number of different sex ratios. In addition, the dispersal genes determine only male dispersal (all the females disperse after mating, irrespective of their dispersal genes). We assume that one male is able to properly fertilize all the females hatching in a patch, while females can mate only once, and the mating status variable is therefore only utilised by female individuals.

Each patch has the following variables: patch identity number, number of foundresses, foundress identity numbers, patch size (number of individuals within patch), number of males, offspring identity numbers, expected sex ratio, observed sex ratio and patch viability. Sex ratio is defined as: $(\text{males})/(\text{males} + \text{females})$. Only offspring (i.e. the current generation) are considered as members of the patch, and used in the determination of the observed sex ratio or patch viability. The expected sex ratio is set before the start of each simulation. The observed

sex ratio is determined after the offspring are formed but before male dispersal takes place (Figure 1). Two modes of sex ratio production were simulated: In experiment 1, the sex of each offspring was assigned with a certain probability (i.e. the expected sex ratio). The sex ratios produced at each patch were binomially distributed around the expected sex ratio. Consequently, the observed sex ratio for each patch was calculated as the proportion of males in that patch. In experiment 2, all the foundress females produced the expected sex ratio and the observed and expected sex ratio were therefore the same. A patch is considered as viable when at least one male and one female are present and is evaluated after offspring formation, male migration and each mating event.

The population is composed of an array of individuals and an array of patches. The population is furthermore characterised by the following variables: population size (i.e. the size of the individual array), number of patches (i.e. the size of the patch array), clutch size, number of generations, number of genes, number of alleles, mutation rate and cost of dispersal. From these variables the fraction of reproducing females are calculated as: population size/clutch size. Patch viability is determined at every generation and the simulation continues only if viable patches remain.

2.2 Simulation process and scheduling (population life history)

The model process sequence is depicted in Fig. 1. The simulation proceeds in discrete generational time steps (i.e. no overlapping generations). In each generation step the events are processed as follows: Females are selected at random in the population to mate. Each female mates once with a male from her local patch (chosen at random from within that patch). After mating, the females disperse to colonize new patches where offspring are produced. All females produce exactly the same clutch size. The offspring sex ratio of each patch is determined. Male offspring have a single opportunity to disperse from their natal patch in response to their natal

patch's sex ratio. Males that disperse are assigned a new patch at random. Finally, the offspring in the new patches replace the old population and their patches and the whole process starts anew. The process is repeated a number of generations (see Table 1). Mutation is a sub-step that precedes mating (see below).

2.3. Design Concepts

Evolutionary stable male dispersal strategies emerge from the population dynamics and their stochastic nature since there is no direct fitness assessment of an individual (i.e. there is no fitness value assigned to the individuals, rather, their fitness becomes apparent through the amount of offspring they have). At each gene, an allele defines the probability that a male disperses. There are 101 possible alleles, each of which is a value from 0 to 1 at regular intervals. As mentioned, each dispersal gene only responds to a specific sex ratio range (see response intervals below). All genes are unlinked and new alleles arise in the population through mutation only. Therefore, each simulation needs to run for a number of generations to ensure that the mutational space is adequately searched and equilibrium reached. Ultimately, males should have a dispersal strategy that takes their local sex ratio and kin structure into account. The probability of dispersal, mutation and the offspring sex ratio are all drawn from binomial distributions. Data gathered for analysis included the probability of dispersal for each gene (averaged for all the individuals in the last generation). The complete genotype for each of the individuals in the last generation is also recorded to ensure each gene reached a single optimum (i.e. at each gene only one allele was found throughout the population). In addition, a graph displaying the average value for each gene at every generation is also saved from which stability of the strategies can be evaluated. All gene values stabilised long before data was recorded from the simulation.

2.4. Initialization Input

The simulation input values are given in Table 1. The following variables were kept constant for all the simulations: The initial probability of dispersal (0), number of possible alleles per simulation (101), mutation rate (0.0005). During all the simulations the number of reproducing females (1000) was kept constant, irrespective of the population size or number of foundresses per patch. Each set of variables in Table 1 was simulated 10 times.

2.5. Sub models

Mutation rate: The mutational model was a combination of stepwise and jumping mutations. Once an allele was selected to undergo a mutation there was an 80% chance of the allele to step to either of the adjacent alleles and a 20% chance for it to step to any of the other 101 possible alleles.

Dispersal cost: Each male that dispersed had a probability of being excluded from the mating population given by the dispersal cost. All the settling costs and transit costs are subsumed in the single dispersal cost parameter.

Mating: During mating only one of the parents, chosen at random, transferred an allele to the new offspring. This donating parent was selected separately for each of the genes enabling normal Mendelian inheritance for unlinked genes. This haploid sexual model is similar to that seen in fungi for instance, and normally gives the same answer as in diploid models, without any complications of dominance. For haplodiploid organisms the relatedness between brothers, given a fixed amount of sibmating, is slightly lower than for diploids and haploids. This difference is small with a maximum of 0.1 (JMG unpublished calculations), and we can expect slightly less dispersal in haplodiploid organisms than we observe here.

Response intervals: For simulations where individuals had more than one gene (experiment 1) a response interval for each gene was calculated. These intervals were chosen so that the area under the binomial expectation roughly divided into equal parts (as many parts as there were genes). As a result each gene will be expressed with equal frequency and will be under equal selection strength. A specific gene will thus be “switched on” if the observed sex ratio is within the interval. The gene specifies the probability of dispersal for the individual. (Note that the intervals were not assigned from the median of the distribution but started from 0. This skewed the intervals but ensured that the area of each interval were exactly the same size). By dividing the potential sex ratio environment up into sectors under the control of separate genes we allowed genes to develop independently.

3. *In Silico* experiments

3.1. Experiment 1 (binomial sex ratios)

Variation in the sex ratio between the patches was caused by enabling the foundress females to produce binomial sex ratios with an average of 0.25 males. Male dispersal could therefore evolve to respond to a range of sex ratios. Five genes, each responding to a different sex ratio range, were optimised per simulation (see above for response interval). To change the number of foundress females per patch the number of reproducing females was kept constant while the number of available patches was reduced. To test the effect of kin selection, simulations were carried out for 1, 2 and 3 foundress females (see Table 1 for full parameter set).

3.2. Experiment 2 (exact sex ratios)

To show that dispersal is not affected by the sex ratio when all the females in the population produce the same sex ratio, exact sex ratios were simulated. In each simulation all the foundress females produced the same sex ratio (the expected sex ratio) and no variation between patches was produced. We therefore had only one dispersal gene that was optimised per simulation. Sex ratios were however different between simulations (Table 1). Three sets of simulations were performed where the sex ratio was different but the number of males per patch were kept constant (5, 10 and 15 males respectively, Table 1). The sex ratio within each set was therefore changed by keeping the number of sons constant and increasing the clutch size with extra daughters (see Table 1 for full parameter set).

3.3 Experiment 3 (variable cost to dispersal)

To reconfirm the effects of the cost of dispersal as obtained in analytical models we did a third experiment where the cost of dispersal was varied for one and two foundress patches under constant sex ratios (Table 1). Note that we expected dispersal to be lower than model predictions as genes are here expressed in sons rather than mothers.

3.4. Statistics

All statistics on the generated data were performed in R version 2.11.0 (R Development Core Team, 2010). For each simulation we recorded the average allele value (i.e. the probability of dispersal) from all the individuals at the final generation for each of the sex ratio ranges. Most genes had only one, or a few similar alleles (e.g. 0.53 and 0.54), fixed throughout the population. The average would therefore reflect the common dispersal strategy. The differences

between the simulations with the same parameters are due to the interaction of the genes on each other. This is expected, as there may be a range of evolutionary stable strategies when multiple genes respond to a given variable. To test if there was a significant response and to summarise our data for posterity, we used linear modelling as follows:

In experiment 1, dispersal was modelled with the following linear model: $\text{dispersal} \sim \text{foundress} + \text{sexratio} + \text{sexratio}^2 + \text{foundress} \times \text{sexratio} + \text{foundress} \times \text{sexratio}^2$; where foundress was a factor depicting the number of foundresses in a patch. All the higher order terms were tested for significance (see Table 2). For each of the 5 genes we used the weighted midpoint of the gene range, with weighting equal to the frequency of each class, (from the binomial distribution) as the explanatory variable.

The following linear model was used to model the data from experiment 2: $\text{dispersal} \sim \text{sexratio} + \text{males} + \text{sexratio}^2 + \text{males}^2$; where males indicated the number of males in the patch (Table 1). The model was reduced to the minimum adequate model by removing non-significant terms, starting with the higher order terms (Table 2).

Two separate linear models were fitted to single and two foundress patches of experiment 3; the former was $\text{dispersal} \sim \text{cost} + \text{cost}^2$ and in the latter: $\text{dispersal} \sim \text{cost} + \text{cost}^2 + \text{cost}^3$.

Note that although the dependent variable is a ratio the data is not number of successes out of a certain number of trials. The proportion from different runs is thus not binomially distributed but a number of theoretical optimums with no specified number of trials. Therefore, it does not make sense to use a generalised linear model with binomial errors. Second, the curvature in the final models is sufficient to prevent negative proportions or proportions larger than one over the studied predictor variable range. Errors were always confirmed to be normally distributed.

4. Results

When we included variation in our simulation, we found that males disperse more frequently away from patches with higher sex ratios (Figure 2, Table 2). The interaction between sex ratio² and sex ratio and the number of foundresses was significant (Figure 2, Table 2), giving the following model (rows represent the estimates for 1, 2 and 3 foundress simulations respectively):

$$\text{dispersal} = \begin{bmatrix} -0.406 \\ -0.043 \\ 2.045 \end{bmatrix} + (\text{sex ratio}) \times \begin{bmatrix} 7.049 \\ -0.802 \\ -18.239 \end{bmatrix} + (\text{sex ratio})^2 \times \begin{bmatrix} -10.014 \\ 8.583 \\ 41.107 \end{bmatrix}$$

It was also apparent that dispersal increased when the relatedness of the males in a patch was higher, as males from single foundress patches dispersed more readily than males from two foundress patches, followed by males from three foundress patches (Figure 2).

When the sex ratio variation between the patches was removed (experiment 2), we found that sex ratio had no effect on the tendency to disperse (Table 2; Figure 3). Rather, dispersal increased asymptotically with the number of males: $\text{dispersal} = 0.3729 + 0.0454(\text{males}) - 0.00171(\text{males})^2$.

As expected dispersal decreased as the cost of dispersal increased and did so faster for two foundress patches (Figure 3, Table 2). Dispersal determined by genes in sons led to lower levels of dispersal than genes expressed in mothers (Figure 3).

5. Discussion

Our simulations in experiment 1 clearly show that dispersal can evolve to be dependent on the sex ratio. This result is supported by field observations. Moore et al. (2006) showed that pollinator males had higher dispersal rates when fewer females were available in a patch.

Similarly, Lawrence (1987) observed a significant increase in dispersal flights of male milkweed beetles as the sex ratio became less female biased. Since the sex ratio of a patch affects the quality of that patch from the view of a given male, this finding is in effect similar to those models showing migration away from weaker patches (Hamilton and May, 1977; Motro, 1982; Frank, 1986; Taylor, 1988; Clobert et al., 2001).

The finding that dispersal increases as foundress number decreases (experiment 1 and 3) can be explained by the fact that competing males are more related and their inclusive fitness would benefit more from male dispersal (Frank, 1986; Gandon, 1999).

Our second set of simulations show that when sex ratios are precise, the level of dispersal that evolve in different simulations, is independent of the sex ratio. This observation stems from the fact that under invariable sex ratios male dispersal cannot improve the sex ratio environment as in our variable sex ratio experiment. These simulations confirm that sex ratio variance is crucial to obtain sex ratio dependant dispersal.

For binomial sex ratio variance our model shows that the difference in the rate of dispersal between the two extreme sex ratio patches can be almost 0.3. This difference is large enough to be biologically significant and should be experimentally detectable.

When females produce more precise sex ratios the variation in patch quality will decrease and the variation in dispersal will become, in the extreme, independent of the sex ratio. On the other hand, in species where there is male dispersal, the fitness penalty of sex ratio variation will be reduced and sex ratios may become less precise (Greeff, 2002). This suggestion is supported by observations that pollinating fig wasps with dispersal have higher variance in their sex ratios (Greeff, 2002; Nelson and Greeff, 2009).

It is tempting to think that with these elements in place, it may be possible that sex ratio variance can fuel a cycle of coevolutionary events where dispersal leads to higher and more variable sex ratios, which leads to more dispersal and which ultimately results in the demise of the local mating pattern. However, this is unlikely for several reasons. 1) Variable sex ratios do

not lead to higher dispersal rates, just more variable dispersal rates. 2) The male optimal dispersal rate is lower than that of the mother's. For instance, Wild and Taylor's (2004) model which looks at the optimal dispersal rate for genes expressed in the mother can be simplified to our conditions giving an optimal dispersal rate of 0.833 for patches with a single mother (where male dispersal = $(C-1/N)/(C^2-1/N)$, with the cost ($C = 0.2$) and the number of mothers ($N = 1$)). Comparing this value to the observed dispersal of 0.583 for 15 males in experiment 2 (Figure 3), it is easy to see that males do not disperse as frequently as that which would optimize their mothers' fitness. Therefore, dispersal by sons will not be sufficient to reduce LMC to a level that is optimal for the mother and she will still keep the number of sons produced low (Nelson and Greeff, 2009).

Hamilton (1967) pointed out that for single mother patches his model predicts a sex ratio of zero, but in reality the mother should produce just enough sons to fertilize all her daughters. We show that the dispersal rate decreases sharply as the number of males goes below 10 and part of the reason is that females will remain unmated if all males disperse. For instance, with a dispersal rate of 0.83 and 3 males in total, almost 60% of patches will lose all their males, and almost 10% of these will not receive any immigrant males leading to unmated females.

This result depends on our model assumption that males act independently of each other. It is conceivable that males will only leave if there are a given number of other males, and then the load of unmated females will not be as high. However, since staying is invariably better than dispersing, it is unclear how such a rule of thumb would select the males that are "doomed" to disperse.

Analytical models are normally preferred over simulation models as they can be more transparent. However, when trait variation is taken into account analytical models can easily become unwieldy. This contention is supported by the near absence of analytical models considering trait variation in the fields of sex allocation and dispersal where the literature is replete with models (but see Green et al., 1982; Griffirths and Godfray 1988; Nagelkerke, 1996

for excellent examples). Simulation models can be simpler to implement when variation is considered and through the use of *in silico* experiments the causative factors can be identified and expected effect sizes can be determined to guide empirical work.

Acknowledgements

The research and RMN were financially supported by the National Research Foundation of South Africa under grants 2053809 and 2072974 to JMG. We thank them and note that any opinion, finding, conclusion or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Research Foundation. We thank Marié Warren and two anonymous reviewers for their helpful comments.

References

- Ahmed, S., Compton, S.G., Butlin, R.K., Gilmartin, P.M., 2009. Wind-borne insects mediate directional pollen transfer between desert fig trees 160 kilometers apart. *Proc. Natl. Acad. Sci. USA* 106, 20342-20347.
- Antolin, M.F., 1999. A genetic perspective on mating systems and sex ratios of parasitoid wasps. *Res. Popul. Ecol.* 41, 29-37.
- Bengtsson, O.B., 1978. Avoiding inbreeding: at what cost? *J. Theor. Biol.* 73, 439-444.
- Clobert, J., Danchin, E., Dhondt, A.A., Nichols, J.D., 2001. *Dispersal*. Oxford: Oxford University Press.
- Frank, S.A., 1986. Dispersal polymorphism in subdivided populations. *J. Theor. Biol.* 122, 303-309.
- Gandon, S., 1999. Kin competition, the cost of inbreeding and the evolution of dispersal. *J. Theor. Biol.* 200, 345-364.

- Gandon, S., Michalakis, Y., 2001. Multiple causes of the evolution of dispersal. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. Dispersal. Oxford: Oxford University Press. pp. 155-179.
- Godfray, H.C.J., 1994. Parasitoids. Princeton: Princeton University Press.
- Godfray, H.C.J., Cook, J.M., 1997. Mating system of parasitoid wasps. In: Choe JC, Crespi BJ, editors. The Evolution of Mating Systems in Insects and Arachnids. Cambridge: Cambridge University Press. pp. 211-225.
- Grafen, A., 1984. Natural selection, kin selection and group selection. In: Krebs JR, Davies NB, editors. Behavioural ecology: An evolutionary approach. Oxford: Blackwell Scientific Publications.
- Greeff, J.M., 2002. Mating system and sex ratios of a pollinating fig wasp with dispersing males. Proc. R. Soc. Lond. B. 269, 2317-2323.
- Greeff, J.M., Newman, D.V.K., 2011. Testing models of facultative sex ratio adjustment in the pollinating fig wasp *Platyscapa awekei*. Evolution 65, 203–219.
- Greeff, J.M., Jansen van Vuuren, G.J., Kryger, P., Moore, J.C., 2009. Outbreeding and possibly inbreeding depression in a pollinating fig wasp with a mixed mating system. Heredity 102, 349–356.
- Greeff, J.M., van Noort, S., Rasplus, J.Y., Kjellberg, F., 2003. Dispersal and fighting in male pollinating fig wasps. C. R. Biol. 326, 121-130.
- Green, R.F., Gordh, G., Hawkins, B.A., 1982. Precise sex ratios in highly inbred parasitic wasps. Am. Nat. 120, 653-665.
- Griffiths, N.T., Godfray, H.C.J., 1988. Local mate competition, sex ratio and clutch size in bethylid wasps. Behav. Ecol. Sociobiol. 22, 211-217.
- Gros, A., Hovestadt, T., Poethke, H.J., 2008. Evolution of sex-biased dispersal: The role of sex-specific dispersal costs, demographic stochasticity, and inbreeding. Ecol. Model. 219, 226-233.

- Hamilton, W.D., 1967. Extraordinary sex ratios. *Science* 156, 477-488.
- Hamilton, W.D., 1979. Wingless and fighting males in fig wasps and other insects. In: Blum MS, Blum NA, editors. *Reproductive Competition, Mate Choice and Sexual Selection in Insects*. New York and London: Academic Press. pp 167-220.
- Hamilton, W.D., May, R.M., 1977. Dispersal in stable habitats. *Nature* 269, 578-581.
- Hardy, I.C.W., 1992. Non-binomial sex allocation and brood sex ratio variances in the parasitoid Hymenoptera. *Oikos* 65, 143-158.
- Hardy, I.C.W., 1994. Sex ratio and mating structure in the parasitoid Hymenoptera. *Oikos*. 69, 3-20.
- Hardy, I.C.W., Cook, J.M., 1995. Brood sex ratio variance, developmental mortality and virginity in a gregarious parasitoid wasp. *Oecologia* 103, 162-169.
- Hardy, I.C.W., Dijkstra, L.J., Gillis, J.E.M., Luft, P., 1998. Patterns of sex ratio, virginity and developmental mortality in gregarious parasitoids. *Biol. J. Linn. Soc.* 64, 239-270.
- Hardy, I.C.W., Pedersen, J.B., Sejr, M.K., Linderøth, U.H., 1999. Local mating, dispersal and sex ratio in a gregarious parasitoid wasp. *Ethology* 105, 57-72.
- Henter, H.J., 2003. Inbreeding depression and haplodiploidy: Experimental measures in a parasitoid and comparisons across diploid and haplodiploid taxa. *Evolution* 57, 1793-1803.
- Herre, E.A., West, S.A., Cook, J.M., Compton, S.G., Kjellberg, F., 1997. Fig-associated wasps: pollinators and parasites, sex ratio adjustment and male polymorphism, population structure and its consequences. In: Choe JC, Crespi BJ, editors. *The Evolution of Mating Systems in Insects and Arachnids*. Cambridge: Cambridge University Press. pp 226-239.
- King, B.H., 1987. Offspring sex ratios in parasitoid wasps. *Q. Rev. Biol.* 62, 367-396.
- Kjellberg, F., Bronstein, J.L., van Ginkel, G., Greeff, J.M., Moore, J.C., Bossu-Dupriez, N., Chevolut, M., Michaloud, G., 2005. Clutch size: a major sex ratio determinant in fig pollinating wasps? *C. R. Biol.* 328, 471-476.

- Krackow, S., Meelis, E., Hardy, I.C.W., 2002. Analysis of sex ratio variances and sequences of sex allocation. In: Hardy ICW, ed Sex Ratios Concepts and Research Methods. Cambridge: Cambridge University Press. pp. 112-131.
- Lawrence, W.S., 1987. Effects of sex ratio on milkweed beetle emigration from host plant patches. *Ecology* 68, 539-546.
- Leturque, H., Rousett, F., 2003. Joint evolution of sex ratio and dispersal: conditions for higher dispersal rates from good habitats. *Evol. Ecol.* 17, 67-84.
- May, R.M., 1979. When to be incestuous. *Nature* 297, 192-194.
- Moore, J.C., Loggenberg, A., Greeff, J.M., 2006. Kin competition promotes dispersal in male pollinating fig wasps. *Biol. Lett.* 2, 17-19.
- Motro, U., 1982. Optimal rates of dispersal I. Haploid populations. *Theor. Popul. Biol.* 21, 394-411.
- Motro, U., 1983. Optimal rates of dispersal. III. Parent-offspring conflict. *Theor. Popul. Biol.* 23, 159-168.
- Motro, U., 1991. Avoiding inbreeding and sibling competition: The evolution of sexual dimorphism for dispersal. *Am. Nat.* 137, 108-115.
- Nagelkerke, C.J., 1996. Discrete clutch sizes, local mate competition, and the evolution of precise sex allocation. *Theor. Popul. Biol.* 49, 314-343.
- Nagelkerke, C.J., Hardy, I.C.W., 1994. The influence of developmental mortality on optimal sex allocation under local mate competition. *Behav. Ecol.* 5, 401-411.
- Nelson, R.M., Greeff, J.M., 2009. Evolution of the scale and manner of brother competition in pollinating fig wasps. *Anim. Behav.* 77, 639-700.
- Orzack, S.H., 2002. Using sex ratios: the past and the future. In: Hardy ICW, ed Sex Ratios Concepts and Research Methods. Cambridge Cambridge University Press. pp. 383-398.
- Peer, K., Taborsky, M., 2005. Outbreeding depression, but not inbreeding depression in haplodiploid *Ambrosia* beetles with regular sib mating. *Evolution.* 59, 317-323.

- Perrin, N., Goudet, J., 2001. Inbreeding, kinship and the evolution of natal dispersal. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. *Dispersal*. Oxford: Oxford University Press. pp. 123-142.
- Perrin, N., Mazalov, V., 2000. Local competition, inbreeding and the evolution of sex-biased dispersal. *Am. Nat.* 155, 116-127.
- Poethke, H.J., Pfenning, B., Hovestadt, T., 2007. The relative contribution of individual- and kin-selection to the evolution of density-dependent dispersal rates. *Evol. Ecol. Res.* 9, 41-50.
- R Development Core Team, 2010. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria
- Ronce, O., 2007. Like a rolling stone? Ten questions about dispersal evolution. *Annu. Rev. Ecol. Syst.* 38, 231-253.
- Ronce, O., Clobert, J., Massot, M., 1998. Natal dispersal and senescence. *Proc. Natl. Acad. Sci. USA.* 95, 600-605.
- Taylor, P.D., 1988. An inclusive fitness model for dispersal of offspring. *J. Theor. Biol.* 130, 363-378.
- Taylor, P.D., 1994. Sex ratio in a stepping stone population with sex specific dispersal. *Theor. Pop. Biol.* 45, 203-218.
- Van Valen, L., 1971. Group selection and the evolution of dispersal. *Evolution* 25, 591-598.
- West, S.A., Sheldon, B.C., 2002. Constraints in the evolution of sex ratio adjustment. *Science* 295, 1685-1688.
- Wild, G., Taylor, P.D., 2004. Kin selection for the co-evolution of the sex ratio and sex-specific dispersal. *Evol. Ecol. Res.* 6, 481-502.
- Wrensch, L.D., Ebbert, M.A., 1993. *Evolution and Diversity of Sex Ratio in Insects and Mites*. Chapman & Hall, New York.

Table 1. Population and patch parameters for each simulation

Experiments	<i>Population parameters</i>						<i>Patch parameters</i>			
	Population		Clutch				Males	Offspring	Sex	
	size	Patches	size	Generations	Genes	Cost	Foundresses	/patch	/patch	ratio
Experiment 1	100000	1000	100	100000	5	0.2	1	25*	100	0.250
	100000	500	100	100000	5	0.2	2	50*	200	0.250
	100000	333	100	100000	5	0.2	3	75*	300	0.250
Experiment 2	30000	1000	30	30000	1	0.2	1	5	30	0.167
	15000	1000	15	30000	1	0.2	1	5	15	0.333
	10000	1000	10	30000	1	0.2	1	5	10	0.500
	8000	1000	8	30000	1	0.2	1	5	8	0.625
	7000	1000	7	30000	1	0.2	1	5	7	0.714
	60000	1000	60	30000	1	0.2	1	10	60	0.167
	30000	1000	30	30000	1	0.2	1	10	30	0.333
	20000	1000	20	30000	1	0.2	1	10	20	0.500
	15000	1000	15	30000	1	0.2	1	10	15	0.667
	12000	1000	12	30000	1	0.2	1	10	12	0.833
	90000	1000	90	30000	1	0.2	1	15	90	0.167
	45000	1000	45	30000	1	0.2	1	15	45	0.333
	30000	1000	30	30000	1	0.2	1	15	30	0.500
	23000	1000	23	30000	1	0.2	1	15	23	0.652
	18000	1000	18	30000	1	0.2	1	15	18	0.833
Experiment 3	30000	1000	30	30000	1	0	1	15	30	0.5
	30000	1000	30	30000	1	0.1	1	15	30	0.5
	30000	1000	30	30000	1	0.2	1	15	30	0.5
	30000	1000	30	30000	1	0.3	1	15	30	0.5
	30000	1000	30	30000	1	0.4	1	15	30	0.5
	30000	1000	30	30000	1	0.5	1	15	30	0.5
	30000	1000	30	30000	1	0.6	1	15	30	0.5
	30000	1000	30	30000	1	0.7	1	15	30	0.5

30000	1000	30	30000	1	0.8	1	15	30	0.5
30000	1000	30	30000	1	0.9	1	15	30	0.5
30000	1000	30	30000	1	1.0	1	15		0.5
30000	500	30	30000	1	0	2	15	60	0.5
30000	500	30	30000	1	0.1	2	15	60	0.5
30000	500	30	30000	1	0.2	2	15	60	0.5
30000	500	30	30000	1	0.3	2	15	60	0.5
30000	500	30	30000	1	0.4	2	15	60	0.5
30000	500	30	30000	1	0.5	2	15	60	0.5
30000	500	30	30000	1	0.8	2	15	60	0.5

(* Average number of males per patch when binomial variation was introduced. Each parameter set was simulated 10 times)

Table 2. ANOVA table for experiments

	df	F	P
Experiment 1: Adjusted R ² = 0.946			
Retained terms			
# foundress \times sexratio ²	2	8.056	<0.001
# foundress \times sexratio	2	7.707	<0.001
Experiment 2: Adjusted R ² = 0.579			
Retained terms			
# males ²	1	33.513	<0.001
# males	1	57.930	<0.001
Deleted terms			
sexratio ²	1	1.510	0.2211
sexratio	1	1.550	0.2151
Experiment 3: 1 Foundress: Adjusted R ² = 0.861			
Retained terms			
cost ²	1	120.743	<0.001
cost	1	17.994	<0.001
Experiment 3: 2 Founresses: Adjusted R ² = 0.975			
Retained terms			
cost ³	1	50.278	<0.001
cost ²	1	127.822	<0.001
cost	1	516.601	<0.001

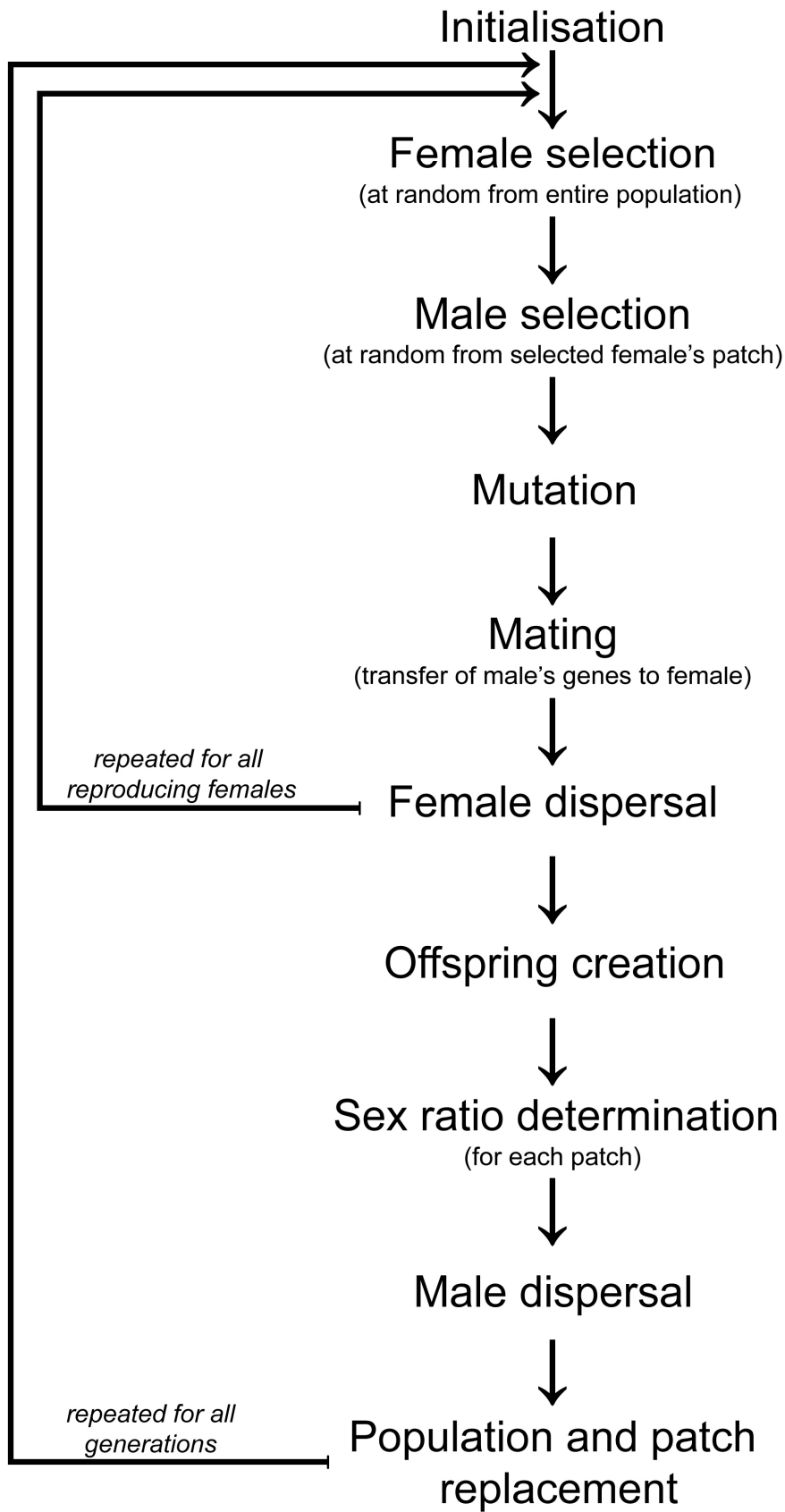


Fig. 1. Life history of individuals (process sequence of model).

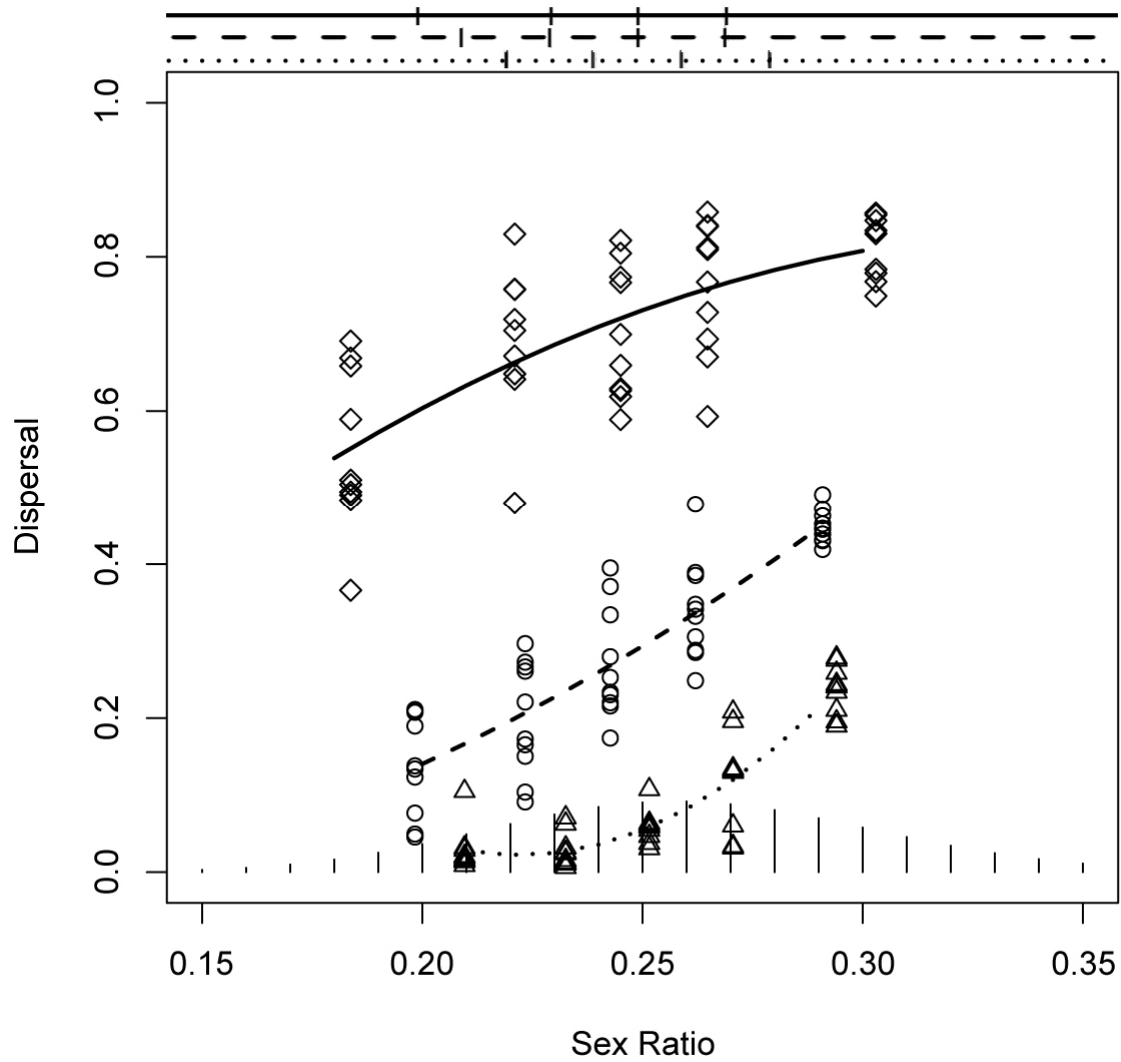


Fig. 2. Modelled relationships between dispersal and sex ratio with binomial sex ratio variance (experiment 1, see Table 2). Diamonds and solid lines presents 1-foundress simulations; circles and dashed lines present 2-foundress simulations; triangles and dotted lines present 3-foundress simulations. Vertical lines at the bottom is a histogram of the binomially distributed sex ratio with an average of 0.25 males. The response intervals for each of the simulations are indicated above the graph.

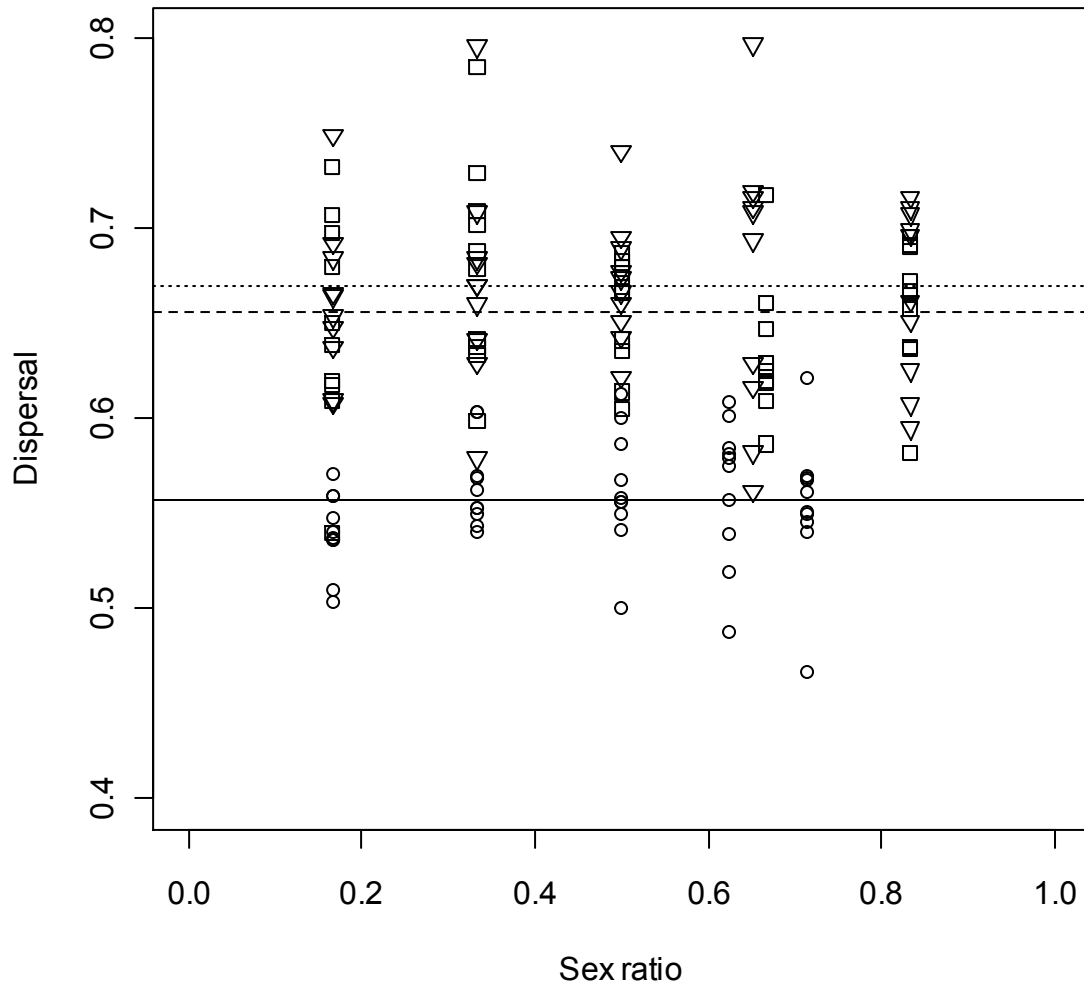


Fig. 3. Modelled relationships between dispersal and sex ratio with no sex ratio variance within a population (experiment 2, see Table 2). Circles and the solid line indicate runs with 5 males per patch; Squares and the dashed line indicate runs with 10 males per patch; Triangles and the dotted line indicate runs with 15 males per patch.

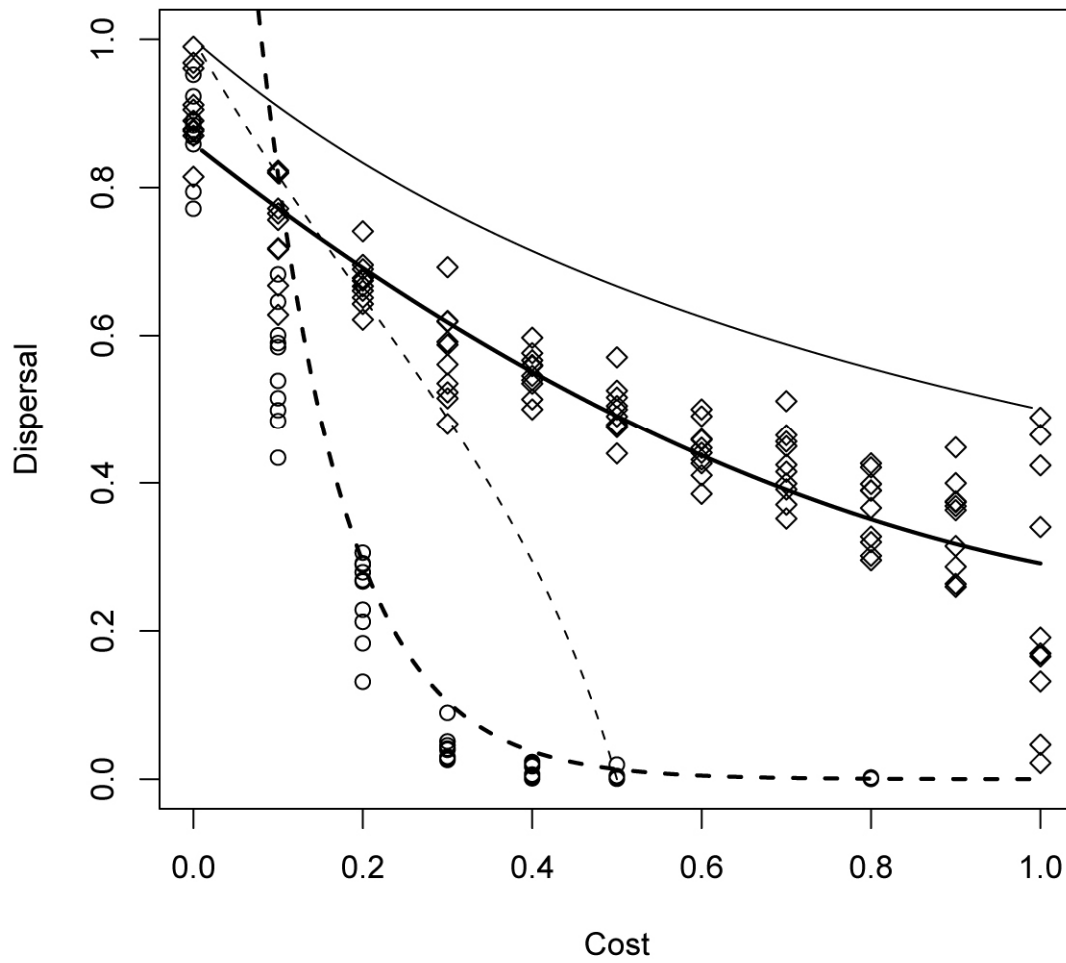


Fig. 4. Modelled relationships between dispersal rate and cost of dispersal from experiment 3. Diamonds and solid lines indicate one foundress; Circles and dashed lines indicate two foundresses. Bold lines indicate our results, thin lines is the predicted dispersal under maternal control.