

## Budding dispersal and the sex ratio

A. GARDNER,\* A. ARCE\* & J. ALPEDRINHA\*†

\**Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, UK*

†*Instituto Gulbenkian de Ciencia, Oeiras, Portugal*

### Keywords:

class structure;  
group selection;  
inclusive fitness;  
kin selection;  
local mate competition;  
relatedness;  
reproductive value;  
scale of competition;  
sex allocation;  
viscous population.

### Abstract

There is much interest in understanding how population demography impacts upon social evolution. Here, we consider the impact of rate and pattern of dispersal upon a classic social evolutionary trait – the sex ratio. We recover existing analytical results for individual dispersal, and we extend these to allow for budding dispersal. In particular, while a cancelling of relatedness and kin competition effects means that the sex ratio is unaffected by the rate of individual dispersal, we find that a decoupling of relatedness and kin competition means that budding dispersal favours increasingly female-biased sex ratios. More generally, our analysis illustrates the relative ease with which biological problems involving class structure can be solved using a kin selection approach to social evolution theory.

### Introduction

In recent years there has been much interest in the impact of population demography on social evolution. Of particular interest has been the problem of social evolution in ‘viscous’ populations (Queller, 1992a; West *et al.*, 2002). Hamilton (1964, 1971) suggested that cooperative behaviours should be especially favoured in those populations where individuals do not disperse far during the course of their lifetime, owing to the high relatedness that is expected to build up between neighbours. However, limited dispersal leads to intensified kin competition, and in the simplest possible scenario – Wright’s (1931) infinite island model – this exactly cancels the effect of increased relatedness, such that cooperation evolves no more readily in a viscous population than in a fully mixing population (Taylor, 1992). This result holds for sexual and asexual populations, under haploid, diploid and haplodiploid modes of inheritance.

This surprising dispersal-independence result appears to have been first reported by Bulmer (1986), in the context of a reanalysis of Hamilton’s (1967) local mate competition (LMC) model that allowed for incomplete dispersal of diploid individuals after mating. Bulmer’s

numerical results suggested that individual dispersal had no or limited impact upon the evolution of the sex ratio – i.e. proportion of offspring that are male. Frank (1986a) recovered the same results from an analytical examination of Bulmer’s model, and explained these on the basis of opposing relatedness and kin competition effects. Later, Taylor (1988) extended the analysis to haplodiploids revealing that, while the cancellation of relatedness and kin competition was no longer exact, the impact of individual dispersal on the sex ratio remained negligible.

A huge amount of literature has been generated in pursuit of simple mechanisms that could allow population viscosity to promote social behaviours. One mechanism that has received recent attention is ‘budding’ dispersal, whereby individuals disperse away from their social groups (relaxing kin competition) but alongside other group mates (ensuring high relatedness; Haldane, 1932; Pollock, 1983; Wilson *et al.*, 1992; Goodnight, 1992; Gardner & West, 2006; Lehmann *et al.*, 2006). The ability for budding dispersal to favour cooperation has been confirmed analytically (Gardner & West, 2006; Lehmann *et al.*, 2006) and experimentally (Kümmerli *et al.*, 2009). Owing to its simplicity, this mechanism has the potential to explain cooperation at all levels of biological organization, from replicating molecules to bacterial cells to social insects.

Although budding dispersal can be important for the evolution of cooperation, its impact upon sex ratio evolution is poorly understood. Avilés (1993) has

*Correspondence:* Andy Gardner, Institute of Evolutionary Biology, University of Edinburgh, King’s Buildings, West Mains Road, Edinburgh EH9 3JT, UK.

Tel.: +44 (0) 131 535 4110; fax: +44 (0) 131 650 6564;  
e-mail: andy.gardner@ed.ac.uk

suggested that budding dispersal may be responsible for the strikingly female-biased sex ratios of certain species of social spider, which are on the order of one male to every ten females. Social spider populations are structured into colonies, between which there is little or no migration of individuals. Unlike those of the eusocial insects, social spider colonies are not characterized by a sterile caste, and essentially all individuals in the colony are reproductive. Colonies reproduce by budding once they have grown to a threshold size, which varies between species from a few dozen to several thousand individuals. Avilés (1993) found that this problem was not amenable to mathematical treatment, although support for the idea that budding dispersal promotes a female-biased sex ratio was obtained by numerical simulation. However, the underlying reasons for extreme female bias remain obscure.

In this article, we examine the impact of budding dispersal upon the evolution of the sex ratio. Our aim is to provide an illustrative overview of how and why budding dispersal promotes the evolution of female-biased sex ratios. To this end, we derive solutions for haploid, diploid and haplodiploid modes of inheritance, in a generic model that is not tailored to the specific biology of any particular taxon (such as social spiders). For ease of comparison and in order to better conceptualize our results, we also re-derive the results of Bulmer (1986), Frank (1986a) and Taylor (1988) for individual dispersal, using more recent developments in kin selection methodology to simplify and clarify their original analyses.

## Models and analyses

### Individual dispersal

We assume an infinite island model (Wright, 1931), in which each patch is founded by  $n$  mated females. We focus our attention upon a particular adult female, and we denote her proportional allocation of reproductive resources into sons (hereafter, 'sex ratio strategy') by  $x$ , the average sex ratio strategy of her patch by  $y$  and the average sex ratio strategy of all females in the population by  $z$ . In particular, we assume that each female produces a large number  $K$  of juvenile sons and the same large number  $K$  of juvenile daughters, but has only sufficient resources to raise half of these offspring; hence, the focal female successfully raises  $Kx$  sons and  $K(1-x)$  daughters to maturity, at which point she dies. These offspring mate at random within patches, with each female mating only once, but males mating potentially numerous times. Males then die, and each mated female either disperses to a new, randomly chosen patch with probability  $d_1$ , or else remains in her natal patch with probability  $1-d_1$ . After dispersal, random density dependent culling leaves  $n$  mated females in each patch, returning the population to the beginning of the lifecycle. Table 1 provides a summary of model notation.

**Table 1** A summary of model notation.

Symbol	Definition
$d_1$	Individual dispersal rate
$d_B$	Budding dispersal rate
$K$	Female fecundity
$m$	Migration rate (after density-dependent regulation)
$n$	Number of adult females per patch
$p_X$	Consanguinity of adult female and individual X
$D$	Juvenile daughter of focal adult female
$F$	Random juvenile female on same patch as focal adult female
$S$	Juvenile son of focal adult female
$M$	Random juvenile male on same patch as focal adult female
$P$	Juvenile sharing patch with focal adult female
$O$	Offspring of focal adult female
$G$	Locus controlling sex ratio
$g$	Genic value
$\tilde{g}$	Genetic breeding value of mother of focal individual
$\tilde{g}'$	Genetic breeding value of adult female on same patch as focal individual
$\bar{g}$	Population average genetic breeding value
$\gamma$	Genotype-phenotype map
$c_f$	Class reproductive value of females
$c_m$	Class reproductive value of males
$f$	Consanguinity of mating partners (inbreeding coefficient)
$\phi$	Consanguinity of two juvenile females from same patch
$\mu$	Consanguinity of two juvenile males from same patch
$r_X$	Relatedness of individual X to focal adult female
$r$	Relatedness of same-patch juvenile, relative to own offspring, from perspective of focal adult female
$a$	Scale of competition
$w_f$	Expected fitness of a daughter of focal adult female
$\bar{w}_f$	Mean fitness of daughters
$W_f$	Relative fitness of a daughter of focal adult female
$w_m$	Expected fitness of a son of focal adult female
$\bar{w}_m$	Mean fitness of sons
$W_m$	Relative fitness of a son of focal adult female
$x$	Sex ratio strategy of focal adult female
$y$	Average sex ratio strategy of adult females in focal patch
$z$	Average sex ratio strategy of adult females in population
$z^*$	Convergence stable sex ratio

With these assumptions, we may write the fitness of a juvenile daughter of the focal female as the product of her probability of survival to adulthood and her probability of survival through density-dependent regulation:

$$w_f = (1-x) \left\{ (1-d_1) \frac{1}{(1-d_1)K(1-y) + d_1K(1-z)} + d_1 \frac{1}{K(1-z)} \right\}, \quad (1)$$

and the fitness of a juvenile son of the focal female is given by the product of his survival to adulthood, his expected number of mates and the expected survival of his mates through density-dependent regulation:

$$w_m = x \frac{1-y}{y} \left\{ (1-d_1) \frac{1}{(1-d_1)K(1-y) + d_1K(1-z)} + d_1 \frac{1}{K(1-z)} \right\}. \quad (2)$$

Analysing these fitness functions using the neighbour-modulated fitness methodology of Taylor & Frank (1996) (see also Taylor, 1996; Frank, 1997, 1998; Taylor *et al.*, 2007), we find that the convergence stable sex ratio ( $z^*$ ; Eshel & Motro, 1981; Christiansen, 1991; Taylor, 1996) is given by:

$$z^* = \frac{c_m(r_S - r_M)}{c_f(r_D - (1 - d_1)^2 r_F) + c_m(r_S - (1 - d_1)^2 r_M)}, \quad (3)$$

where  $r_D$  and  $r_S$  are the kin selection coefficients of relatedness for a daughter and son, respectively, from the perspective of their mother;  $r_F$  and  $r_M$  are the relatedness of a random juvenile female and random juvenile male, respectively, from the perspective of a random adult female in the same patch; and  $c_f$  and  $c_m$  are the class reproductive values for females and males respectively. A full derivation is given in the Appendix. This general equation applies to any genetic system with two sexes and no further class structure – here we are interested in haploidy, diploidy and haplodiploidy, but eqn 3 equally describes the sex ratio for triploidy, haplotriploidy or any other conceivable system of inheritance.

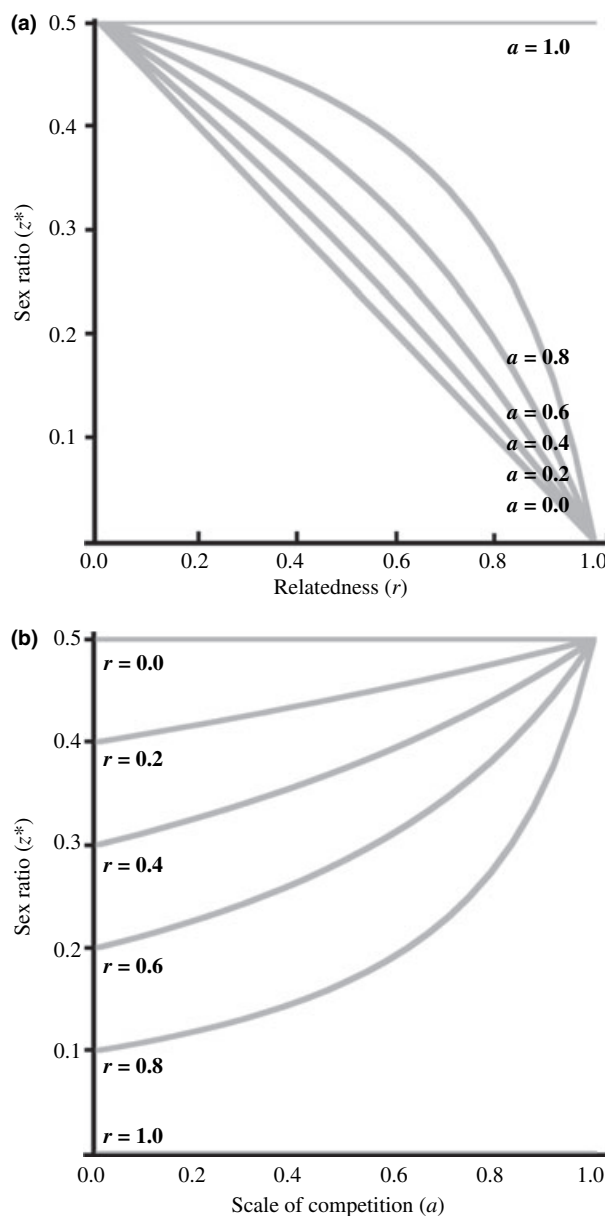
Restricting our attention to haploidy and diploidy for now, we have class reproductive values  $c_f = c_m = 1/2$ , relatedness to offspring  $r_D = r_S = r_O$  and relatedness to random same-patch juveniles  $r_F = r_M = r_P$ , and eqn 3 can be rewritten as:

$$z^* = \frac{1 - r}{2(1 - ar)}, \quad (4)$$

where  $r = r_P/r_O$  is the relatedness of a random same-patch juvenile as a fraction of the relatedness of one's own offspring, from the perspective of an adult female; and  $a = (1 - d_1)^2$  is the degree of local resource competition, being the probability that two randomly chosen adult females experiencing density-dependent regulation in the same patch are both native to that patch (Frank, 1986a; see also Gardner & West, 2006).

A special case of the above model is Hamilton's (1967) diploidy model of LMC. Owing to complete dispersal of females after mating ( $d_1 = 1$ ) in Hamilton's model, here we have  $r = 1/n$  and  $a = 0$ , and eqn 4 gives the usual result  $z^* = (n - 1)/2n$ . More generally, eqn 4 reveals the impact of relatedness and local resource competition on the sex ratio in viscous populations: the RHS of eqn 4 is a decreasing function of  $r$  and an increasing function of  $a$ , hence higher within-patch relatedness favours more female-biased sex ratios (Fig. 1a; Frank, 1985), and higher local resource competition favours less female-biased sex ratios (Fig. 1b; Frank, 1986a).

Because the relatedness and competition effects of population viscosity impact upon the sex ratio in opposing ways, inspection of eqn 4 does not reveal the overall impact of population viscosity upon the sex ratio. In order to make a concrete prediction, we are required to specify the precise relationship between individual dispersal, within-patch relatedness, and local resource

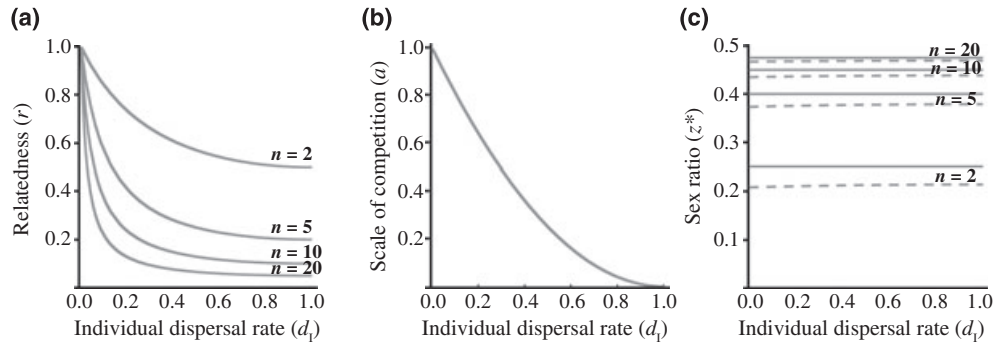


**Fig. 1** Impact of relatedness and scale of competition upon the sex ratio. (a) The convergence stable sex ratio ( $z^*$ ) as a function of within-group relatedness ( $r$ ), for varying degrees of competition ( $a = 0.0, 0.2, 0.4, 0.6, 0.8$  &  $1.0$ ). (b) The convergence stable sex ratio ( $z^*$ ) as a function of scale of competition ( $a$ ), for varying degrees of relatedness ( $r = 0.0, 0.2, 0.4, 0.6, 0.8$  &  $1.0$ ).

competition. For both haploidy and diploidy, we find that the within-patch relatedness is given by:

$$r = \frac{1}{n - (n - 1)(1 - d_1)^2}, \quad (5)$$

(mathematical details are given in the Appendix; see also Frank, 1986a). Hence, we find that relatedness decreases with increasing individual dispersal, and is also mediated



**Fig. 2** Individual dispersal and the sex ratio. (a) Within-group relatedness ( $r$ ) as a function of individual dispersal rate ( $d_i$ ), for varying patch size ( $n = 2, 5, 10$  &  $20$ ). (b) Scale of competition ( $a$ ) as a function of individual dispersal rate ( $d_i$ ). (c) The convergence stable sex ratio ( $z^*$ ) as a function of individual dispersal rate ( $d_i$ ), for varying patch size ( $n = 2, 5, 10$  &  $20$ ). Bold lines represent the convergence stable sex ratio for haploids and diploids, dashed lines represent the convergence stable sex ratio for haplodiploids.

by patch size (Fig. 2a). Above, we showed that the local resource competition is given by  $a = (1 - d_i)^2$ . Hence, competition also decreases with increasing individual dispersal (Fig. 2b). Having made relatedness and competition explicit functions of individual dispersal, we may substitute these expressions into eqn 4, giving us:

$$z^* = \frac{n - 1}{2n}. \tag{6}$$

We have recovered the surprising result – shown numerically by Bulmer (1986) and derived analytically by Frank (1986a) – that individual dispersal does not impact upon the sex ratio, the latter taking the same value that it would in a fully dispersing population (Fig. 2c, solid lines). Although population viscosity impacts upon relatedness and competition, and both of these mediate sex ratio, the two effects exactly cancel so that there is no overall impact of population viscosity upon the sex ratio. This was previously shown for the diploid case, and here we have shown that the result also extends to haploids.

For haplodiploids,  $c_f = 2/3$  and  $c_m = 1/3$ , and  $r_D \neq r_S$  and  $r_F \neq r_M$ , so eqn 3 cannot be reduced to the simple form of eqn 4. In this case, the convergence stable sex ratio is given by:

$$z^* = \frac{n - 1}{2n} \frac{4n - (n - 1)(1 - d_i)^2 - 2}{4n - (n - 1)(1 - d_i)^2 - 1}, \tag{7}$$

(mathematical details are given in the Appendix; see also Taylor, 1988). Here, the sex ratio is no longer independent of the individual dispersal rate. However, numerical analysis reveals that the impact of individual dispersal is negligible (Fig. 2c, dashed lines). In particular, although a more female-biased sex ratio is predicted in a more viscous population, the discrepancy between this and the sex ratio for a fully mixing population is always less than 0.007. In contrast, the sex ratio is strongly affected by the number of foundresses, with a less female-biased sex ratio being favoured as the patch size increases (Fig. 2c, dashed lines).

### Budding dispersal

We now consider that, when females disperse to new patches, they do so with patch mates ('budding dispersal'; Haldane, 1932; Pollock, 1983; Goodnight, 1992; Gardner & West, 2006; Lehmann *et al.*, 2006). We assume that, after mating, females form groups (buds) of size  $n$  at random within their patch, and that each group either remains on the focal patch with probability  $1 - d_B$  or else it disperses to a random patch elsewhere in the population with probability  $d_B$ . After dispersal, density-dependent regulation leaves one randomly chosen group on each patch. We also allow for some random exchange of females between patches after density-dependent regulation: with probability  $m$  a female migrates, in which case she is repositioned in a random space vacated by another migratory individual, and with probability  $1 - m$  she remains in her patch. Incorporating this migration into the model facilitates synthesis with the computer simulations of Avilés (1993) and the mathematical analysis of Gardner & West (2006). With these assumptions, the fitness of juvenile males and females can be written as:

$$w_f = (1 - x) \left\{ (1 - d_B) \frac{1}{(1 - d_B)K(1 - y) + d_B K(1 - z)} + d_B \frac{1}{K(1 - z)} \right\}, \tag{8}$$

and

$$w_m = x \frac{1 - y}{y} \left\{ (1 - d_B) \frac{1}{(1 - d_B)K(1 - y) + d_B K(1 - z)} + d_B \frac{1}{K(1 - z)} \right\}. \tag{9}$$

Note that the fitness functions are identical to those derived for the individual dispersal model, except that the individual dispersal parameter  $d_i$  has been replaced with the budding dispersal parameter  $d_B$ . Thus, following the same procedure as before, we obtain a convergence stable sex ratio of:

$$z^* = \frac{c_m(r_S - r_M)}{c_f(r_D - (1 - d_B)^2 r_F) + c_m(r_S - (1 - d_B)^2 r_M)}, \quad (10)$$

where, again, the only difference from the model of the previous section is the replacement of  $d_I$  with  $d_B$ . Restricting our attention to haploidy and diploidy, so that the class reproductive values are  $c_f = c_m = 1/2$ , relatedness to offspring is  $r_D = r_S = r_O$  and relatedness to random same-patch juveniles is  $r_F = r_M = r_P$ , eqn 10 again reduces to eqn 4, which we reproduce here as eqn 11 for ease of reference:

$$z^* = \frac{1 - r}{2(1 - ar)}, \quad (11)$$

where relatedness is  $r = r_P/r_O$  and the intensity of local resource competition is  $a = (1 - d_B)^2$ . Because eqn 11 is identical – as it is written – to eqn 4, we see that relatedness and localized resource competition impact upon the sex ratio in the same way in both the individual dispersal and budding dispersal models: higher relatedness favours a more female-biased sex ratio (Fig. 1a), and stronger competition favours a less female-biased sex ratio (Fig. 1b).

The difference between the two models lies in how relatedness and competition emerge (and become associated) as a consequence of the rate and pattern of dispersal. For the purposes of calculating within-patch relatedness, the migration of females after density-dependent regulation in the budding dispersal model plays the same role as dispersal prior to density-dependent regulation in the individual dispersal model, hence we can simply write  $m$  where we see  $d_I$  in eqn 5 to yield relatedness for the budding dispersal model:

$$r = \frac{1}{n - (n - 1)(1 - m)^2}. \quad (12)$$

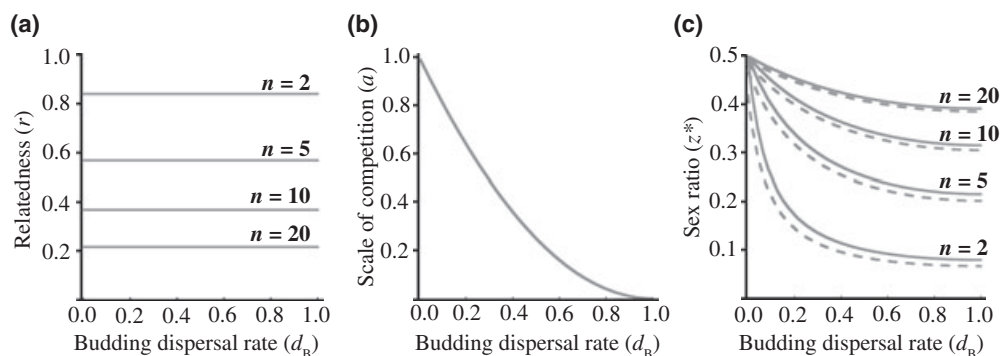
Hence, relatedness is a decreasing function of female migration after density-dependent regulation, but is unaffected by the rate of budding dispersal (Fig. 3a).

Above, we found that the intensity of localized competition in the budding dispersal model is given by the same expression as for the individual dispersal model, but with individual dispersal rate being replaced by the budding dispersal rate:  $a = (1 - d_B)^2$ . Hence, competition is a decreasing function of budding dispersal rate, and is unaffected by migration after density-dependent regulation (Fig. 3b).

Although relatedness and competition are both determined by the individual dispersal rate in the first model, they are decoupled in the second model, with relatedness being determined by female migration after density-dependent regulation and competition being determined by budding dispersal before density-dependent regulation. Expressing the within-patch relatedness ( $r$ ) and intensity of local resource competition ( $a$ ) in terms of model parameters ( $n$ ,  $d_B$  and  $m$ ), and substituting into eqn 11, obtains a convergence stable sex ratio of:

$$z^* = \frac{n - 1}{2n} \frac{n(1 - (1 - m)^2)}{(n - 1)(1 - (1 - m)^2) + 1 - (1 - d_B)^2}, \quad (13)$$

which is a decreasing function of the budding dispersal rate – i.e. budding dispersal promotes a female bias. Furthermore, the sex ratio is an increasing function of the migration rate of individuals after density-dependent regulation and an increasing function of the number of foundresses (Fig. 3c, solid lines; Avilés, 1993). Assuming full budding dispersal ( $d_B = 1$ ), we find that a vanishingly small allocation to males is favoured in the limit of low migration ( $z^* \rightarrow 0$  as  $m \rightarrow 0$ ) and also that the sex ratio asymptotes towards one half with increasingly large numbers of foundresses ( $z^* \rightarrow 1/2$  as  $n \rightarrow \infty$ ). However, we also recover Avilés' (1993) simulation result that substantial female bias is favoured, even with very large numbers of foundresses, provided that between patch migration is sufficiently low [ $z^* \approx mn/(1 + 2mn)$  if  $m \ll 1$ ,  $n \gg 1$  and  $mn$  is on the order of 1] – for example, one male for every two females if there is an average of one migrant foundress per patch. Note that,



**Fig. 3** Budding dispersal and the sex ratio. (a) Within-group relatedness ( $r$ ) as a function of budding dispersal rate ( $d_B$ ), for varying patch size ( $n = 2, 5, 10$  &  $20$ ). (b) Scale of competition ( $a$ ) as a function of budding dispersal rate ( $d_B$ ). (c) The convergence stable sex ratio ( $z^*$ ) as a function of budding dispersal rate ( $d_B$ ), for varying patch size ( $n = 2, 5, 10$  &  $20$ ) and a fixed rate of migrant exchange ( $m = 0.1$ ). Bold lines represent the convergence stable sex ratio for haploids and diploids, dashed lines represent the convergence stable sex ratio for haplodiploids.

evaluating eqn 13 at  $d_B = m = d_I$  exactly recovers eqn 6 of the individual dispersal model.

Again, the situation is somewhat more complicated for haplodiploids, whose peculiar biology ( $c_f \neq c_m$ ,  $r_D \neq r_S$  and  $r_F \neq r_M$ ) means that the sex ratio of eqn 10 cannot be reduced to the more simple form of eqn 11. In this case, the convergence stable sex ratio is given by:

$$z^* = \frac{n-1}{2n} \frac{4n - (n-1)(1-m)^2 - 2}{4n - (n-1)(1-m)^2 - 1} \times \frac{n(1 - (1-m)^2)}{(n-1)(1 - (1-m)^2) + 1 - (1-d_B)^2}, \quad (14)$$

(mathematical details are given in the Appendix). Here, the convergence stable sex ratio is strongly affected by the rate of budding dispersal, a higher budding dispersal rate favouring a more female-biased sex ratio (Fig. 3c, dashed lines). Conversely, the sex ratio is predicted to be less female biased as the rate of migration after density-dependent regulation increases, and as the number of foundresses increases (Fig. 3c, dashed lines; Avilés, 1993). Again, for complete budding dispersal ( $d_B = 1$ ) we find that a vanishingly low proportion of males is favoured as the migration rate approaches zero ( $z^* \rightarrow 0$  as  $m \rightarrow 0$ ), that a sex ratio of one half is favoured in the limit of a large number of foundresses ( $z^* \rightarrow 1/2$  as  $n \rightarrow \infty$ ), and that even if patches are founded by large numbers of foundresses a substantial female bias can be favoured provided that migration is sufficiently rare [ $z^* \approx mn/(1+2mn)$  if  $m \ll 1$ ,  $n \gg 1$  and  $mn$  is on the order of 1]. Finally, note that eqn 7 of the individual dispersal model is recovered by evaluating eqn 13 at  $d_B = m = d_I$ .

## Discussion

We have derived analytical results for a model of sex ratio evolution in a group-structured population characterized by budding dispersal. Previously, theoretical understanding of this problem has been based upon the results of numerical simulations (Avilés, 1993). In line with Avilés' (1993) simulation study, we have found that budding dispersal favours female-biased sex allocation, with the convergence stable sex ratio (proportion male) decreasing as the rate of budding dispersal increases. This is in contrast to the astonishing result that the sex ratio is unaffected by the rate of individual dispersal in a purely viscous population (Bulmer, 1986; Frank, 1986a; Taylor, 1988). A low rate of individual dispersal results in a high within-patch relatedness, which favours a more female-biased sex ratio (Frank, 1985), but it also results in a high degree of kin competition, which favours a less female-biased sex ratio (Frank, 1986a,b), and these effects cancel exactly or approximately, giving no net impact of individual dispersal upon sex ratio evolution (Bulmer, 1986; Frank, 1986a; Taylor, 1988). The difference

with budding dispersal is that it reduces the extent to which the offspring of patch-mates compete for resources, which promotes a more female-biased sex ratio, and by keeping relatives together as they disperse, it allows a high relatedness to be maintained, which also promotes a more female-biased sex ratio. In other words, budding decouples the competition and relatedness consequences of dispersal (Gardner & West, 2006).

We have also examined the impact of other demographic parameters upon sex allocation. We have found that an increased number of adult females reproducing on a patch favours a reduced female-biased sex ratio, owing to a corresponding reduction in within-patch relatedness (Hamilton, 1967; Avilés, 1993). Following Avilés (1993; see also Gardner & West, 2006), we have also examined the impact of exchange of individuals after dispersal and density-dependent regulation, and have found that an increased exchange of individuals also favours a reduced female-biased sex ratio, again owing to a reduction in within-patch relatedness. Importantly, we have recovered Avilés' (1993) interesting result that even very large groups can be expected to exhibit strongly female-biased sex ratios, provided that the rate of exchange of individuals between groups is sufficiently low – as is the case in social spiders. For example, in the limit of large group size, and only one migrant per group per generation, the sex ratio corresponds to two females for every male.

We have taken a kin selection approach to the problem of budding dispersal and the sex ratio. Previously, this problem has been tackled using a multilevel selection approach. Indeed, Avilés (1993) suggested that the female-biased sex ratios of social spiders could not be explained by kin selection, and emphasized the need for selection between groups. However, at a formal level, the multilevel selection approach to social evolution is equivalent to the kin selection approach; any analysis of multilevel selection can always be translated into an equivalent kin selection analysis and, provided that the analyses are performed correctly, these will not lead to conflicting predictions (Hamilton, 1975; Grafen, 1984; Wade, 1985; Frank, 1986b, 1998; Queller, 1992b; Bourke & Franks, 1995; West *et al.*, 2007). Despite this equivalence, it is often easier to solve biological problems using kin selection methodology, for instance because multilevel selection theory is difficult to apply to class-structured populations (West *et al.*, 2008). This is the situation for the present problem of budding dispersal and the sex ratio, which appears complicated when viewed from a multilevel selection perspective – and hence has previously been tackled using numerical simulation methods, which provide only limited insight – but which is easily resolved if approached from a kin selection perspective.

This study has clarified the use (and, in particular, the complementarity) of 'open' model vs. 'closed'

model approaches to social evolution theory (Gardner & West, 2006). Eqn 4, repeated as eqn 11, describes the dependence of the convergence stable sex ratio ( $z^*$ ) upon within-group relatedness ( $r$ ) and local resource competition ( $a$ ), without specifying how these two determinants are themselves associated and how they emerge as a consequence of population demographic assumptions. This open model approach allows a general overview – here it applies equally to the individual dispersal and budding dispersal models – but it lacks in concreteness. In contrast, eqns 6 and 13 show explicitly how sex ratio depends upon more tangible population parameters, such as number of foundresses per patch ( $n$ ), and dispersal/migration rates ( $d_I$ ,  $d_B$  and  $m$ ). This closed model approach allows for more specific, quantitative predictions, but lacks in generality as it is dependent on particular model assumptions. Put another way, whereas the closed model approach tells us precisely what sex ratio to expect, the open model approach helps us conceptualize why the sex ratio takes the value that it does, and how to generalise from the findings of specific models to yield deeper insights about the fundamental processes driving sex ratio evolution.

Our aim has been to provide an illustrative overview of how and why budding dispersal impacts upon sex ratio, and to form conceptual links with the theory of social evolution in viscous populations more generally. For this reason, we have considered a generic model with relatively broad applicability, and a range of inheritance modes, whilst explicitly neglecting biological details particular to individual taxa. For example, Avilés' (1993) simulation study allowed for multiple generations between social spider dispersal events (see also Frank, 1987), which has not been considered in the present study. We also assumed a system of monandry in order to simplify relatedness calculations, and we highlight the possibility that other mating systems might give rise to quantitatively different predictions. Finally, we have assumed complete maternal control of sex, yet there may be scope for evolutionary conflicts of interests between (and even within) individual family members in this respect (Beukeboom *et al.*, 2001; Wild & West, 2009). Sex allocation is one of the few topics in evolutionary biology where researchers can reasonably aim for a quantitative – rather than just a qualitative – fit between theoretical prediction and empirical data (West, 2009), so extension of the basic theory to allow for more complex models, tailored to the particular biology of specific taxa, represents an important avenue for future research.

## Acknowledgments

We thank Kevin Foster and Stu West for discussion and comments on the manuscript. AG is funded by the Royal Society, AA was funded by BBSRC, and JA is supported

by PDBC-IGC and is funded by FCT (SFRH/BD/33206/2007).

## References

- Avilés, L. 1993. Interdemic selection and the sex ratio: a social spider perspective. *Am. Nat.* **142**: 320–345.
- Beukeboom, L.W., de Jong, T.J. & Pen, I. 2001. Why girls want to be boys. *BioEssays* **23**: 477–480.
- Bourke, A.F.G. & Franks, N.R. 1995. *Social Evolution in Ants*. Princeton University Press, Princeton, NJ.
- Bulmer, M.G. 1986. Sex ratio theory in geographically structured populations. *Heredity* **56**: 69–73.
- Christiansen, F.B. 1991. On conditions for evolutionary stability for a continuously varying character. *Am. Nat.* **138**: 37–50.
- Eshel, I. & Motro, U. 1981. Kin selection and strong evolutionary stability of mutual help. *Theor. Popul. Biol.* **19**: 420–433.
- Falconer, D.S. 1981. *Introduction to Quantitative Genetics*, 2nd edn. Longman, New York.
- Frank, S.A. 1985. Hierarchical selection theory and sex ratios II: on applying the theory, and a test with fig wasps. *Evolution* **39**: 949–964.
- Frank, S.A. 1986a. The genetic value of sons and daughters. *Heredity* **56**: 351–354.
- Frank, S.A. 1986b. Hierarchical selection theory and sex ratios I: general solutions for structured populations. *Theor. Popul. Biol.* **29**: 312–342.
- Frank, S.A. 1987. Demography and sex ratio in social spiders. *Evolution* **41**: 1267–1281.
- Frank, S.A. 1997. Multivariate analysis of correlated selection and kin selection, with an ESS maximization method. *J. Theor. Biol.* **189**: 307–316.
- Frank, S.A. 1998. *Foundations of Social Evolution*. Princeton University Press, Princeton, NJ.
- Gardner, A. & West, S.A. 2006. Demography, altruism, and the benefits of budding. *J. Evol. Biol.* **19**: 1707–1716.
- Goodnight, K.F. 1992. The effect of stochastic variation on kin selection in a budding-viscous population. *Am. Nat.* **140**: 1028–1040.
- Grafen, A. 1984. Natural selection, kin selection and group selection. In: *Behavioural Ecology: An Evolutionary Approach* (J.R. Krebs & N.B. Davies, eds), pp. 62–84. Blackwell Scientific Publications, Oxford.
- Grafen, A. 1985. A geometric view of relatedness. *Oxf. Surv. Evol. Biol.* **2**: 28–89.
- Haldane, J.B.S. 1932. *The Causes of Evolution*. Longmans, New York.
- Hamilton, W.D. 1964. The genetical evolution of social behaviour I & II. *J. Theor. Biol.* **7**: 1–52.
- Hamilton, W.D. 1967. Extraordinary sex ratios. *Science* **156**: 477–488.
- Hamilton, W.D. 1971. Selection of selfish and altruistic behaviour in some extreme models. In: *Man and Beast: Comparative Social Behavior* (J.F. Eisenberg & W.S. Dillon, eds), pp. 57–91. Smithsonian Press, Washington.
- Hamilton, W.D. 1975. Innate social aptitudes of man: an approach from evolutionary genetics. In: *Biosocial Anthropology* (R. Fox, ed.), pp. 133–155. Wiley, New York.
- Kümmerli, R., Gardner, A., West, S.A. & Griffin, A.S. 2009. Limited dispersal, budding dispersal and cooperation: an experimental study. *Evolution*, doi: 10.1111/j.1558-5646.2008.00548.x.

- Lehmann, L., Perrin, N. & Rousset, F. 2006. Population demography and the evolution of helping behaviors. *Evolution* **60**: 1137–1151.
- Pollock, G.B. 1983. Population viscosity and kin selection. *Am. Nat.* **122**: 817–829.
- Price, G.R. 1970. Selection and covariance. *Nature* **227**: 520–521.
- Queller, D.C. 1992a. Does population viscosity promote kin selection? *Trends Ecol. Evol.* **7**: 322–324.
- Queller, D.C. 1992b. Quantitative genetics, inclusive fitness, and group selection. *Am. Nat.* **139**: 540–558.
- Taylor, P.D. 1988. Inclusive fitness models with two sexes. *Theor. Popul. Biol.* **34**: 145–168.
- Taylor, P.D. 1992. Altruism in viscous populations – an inclusive fitness model. *Evol. Ecol.* **6**: 352–356.
- Taylor, P.D. 1996. Inclusive fitness arguments in genetic models of behaviour. *J. Math. Biol.* **34**: 654–674.
- Taylor, P.D. & Frank, S.A. 1996. How to make a kin selection model. *J. Theor. Biol.* **180**: 27–37.
- Taylor, P.D., Wild, G. & Gardner, A. 2007. Direct fitness versus inclusive fitness: how shall we model kin selection? *J. Evol. Biol.* **20**: 296–304.
- Wade, M.J. 1985. Soft selection, hard selection, kin selection and group selection. *Am. Nat.* **125**: 61–73.
- West, S.A. 2009. *Sex Allocation*. Princeton University Press, Princeton, NJ.
- West, S.A., Pen, I. & Griffin, A.S. 2002. Cooperation and competition between relatives. *Science* **296**: 72–75.
- West, S.A., Griffin, A.S. & Gardner, A. 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J. Evol. Biol.* **20**: 415–432.
- West, S.A., Griffin, A.S. & Gardner, A. 2008. Social semantics: how useful has group selection been? *J. Evol. Biol.* **21**: 374–385.
- Wild, G. & West, S.A. 2009. Genomic imprinting and sex allocation. *Am. Nat.* **173**: E1–E14.
- Wilson, D.S., Pollock, G.B. & Dugatkin, L.A. 1992. Can altruism evolve in purely viscous populations. *Evol. Ecol.* **6**: 331–341.
- Wright, S. 1931. Evolution in mendelian populations. *Genetics* **16**: 97–159.

## Appendix

### Convergence stable sex ratio

Here we determine the convergence stable sex ratio for haploid, diploid and haplodiploid populations. We use notation consistent with the individual dispersal model, but the derivation applies equally to the budding dispersal model if  $d_I$  is replaced with  $d_B$  throughout. We begin by noting that the average fitness of all juvenile females is found by evaluating eqn 1 at  $x = y = z$ , to obtain  $\bar{w}_f = 1/K$ . Hence, the relative fitness of the focal female's daughter, expressed as a fraction of the average for her class, is  $w_f/\bar{w}_f$ , or:

$$W_f = (1-x) \left\{ (1-d_I) \frac{1}{(1-d_I)(1-y) + d_I(1-z)} + d_I \frac{1}{1-z} \right\}. \quad (\text{A1})$$

Similarly, the average fitness of juvenile males is found by evaluating eqn 2 at  $x = y = z$ , to obtain  $\bar{w}_m = 1/K$ , and

the relative fitness of the focal female's son, expressed as a fraction of the average for his class, is  $w_m/\bar{w}_m$ , or:

$$W_m = x \frac{1-y}{y} \left\{ (1-d_I) \frac{1}{(1-d_I)(1-y) + d_I(1-z)} + d_I \frac{1}{1-z} \right\}. \quad (\text{A2})$$

Consider a locus  $G$  that controls sex ratio, and denote the genic value of a gene drawn from this locus from a focal juvenile by  $g$ . Further, denote the additive genetic 'breeding' value (Price, 1970; Falconer, 1981; Grafen, 1985) for the sex ratio strategy of this individual's mother by  $\tilde{g}$ , the average breeding value of all the adult females in the juveniles patch by  $\bar{g}'$  and the average breeding value of the population by  $\bar{g}$ . Natural selection favours those genes that are associated with increased fitness; the appropriate definition of fitness in a sex structured population is  $W = c_f W_f + c_m W_m$ , where  $W_f$  and  $W_m$  are the fitness of females and males, respectively, expressed relative to the average for their sex; and  $c_f$  and  $c_m$  are the class reproductive values of females and males respectively (Taylor, 1996; Taylor & Frank, 1996; Frank, 1997, 1998; Taylor *et al.*, 2007). Assuming vanishing genetic variation, the direction of natural selection acting upon the average breeding value of the population is given by the sign of:

$$\frac{dW}{dg} = c_f \frac{dW_f}{dg_f} + c_m \frac{dW_m}{dg_m}, \quad (\text{A3})$$

where, for clarity, we have subscripted an individual's genic value  $g$  with  $f$  or  $m$  if it is female or male, respectively; and all derivatives are evaluated at the population average  $g = g_f = g_m = \bar{g}$  (Taylor, 1996; Taylor & Frank, 1996; Frank, 1997, 1998; Taylor *et al.*, 2007).

The first derivative on the RHS of eqn A3 describes the impact of the value of a gene drawn from a juvenile female on that individual's relative fitness, which is mediated by (i) the correlation between her genic value and her mother's breeding value, the correlation between her mother's breeding value and her mother's sex ratio strategy, and the correlation between her mother's sex ratio and her own relative fitness; and (ii) the correlation between her genic value and the average breeding value of adult females on her patch, the correlation between the average breeding value of adult females on her patch and the average sex ratio strategy of her patch, and the correlation between the average sex ratio strategy of her patch and her relative fitness, i.e.:

$$\frac{dW_f}{dg_f} = \frac{\partial W_f}{\partial x} \frac{dx}{d\tilde{g}} \frac{d\tilde{g}}{dg_f} + \frac{\partial W_f}{\partial y} \frac{dy}{d\bar{g}'} \frac{d\bar{g}'}{dg_f} = \left( \frac{\partial W_f}{\partial x} p_D + \frac{\partial W_f}{\partial y} p_F \right) \gamma, \quad (\text{A4})$$

where  $p_D$  is the coefficient of consanguinity between an adult female and her juvenile daughter;  $p_F$  is the coefficient of consanguinity between an adult female and a random juvenile female on the same patch; and the

mapping between genotype and phenotype is  $dx/d\tilde{g} = dy/d\tilde{g}' = \gamma$ .

We can perform the analogous expansion for the second derivative on the RHS of eqn A3:

$$\frac{dW_m}{dg_m} = \frac{\partial W_m}{\partial x} \frac{dx}{d\tilde{g}} \frac{d\tilde{g}}{dg_m} + \frac{\partial W_m}{\partial y} \frac{dy}{d\tilde{g}'} \frac{d\tilde{g}'}{dg_m} = \left( \frac{\partial W_m}{\partial x} p_S + \frac{\partial W_m}{\partial y} p_M \right) \gamma, \quad (\text{A5})$$

where  $p_S$  is the coefficient of consanguinity between an adult female and her juvenile son; and  $p_M$  is the coefficient of consanguinity between a random adult female and a random juvenile male on the same patch. Substituting eqns A4 and A5 into eqn A3, the condition for an increase in the population average sex ratio strategy is:

$$c_f \left( \frac{\partial W_f}{\partial x} p_D + \frac{\partial W_f}{\partial y} p_F \right) + c_m \left( \frac{\partial W_m}{\partial x} p_S + \frac{\partial W_m}{\partial y} p_M \right) > 0. \quad (\text{A6})$$

Finally, using eqns A1 and A2 to calculate the appropriate partial derivatives, and dividing both sides of inequality (A6) by the consanguinity for a focal adult female to herself ( $p_I$ ), the condition for increase becomes:

$$c_f \left( -\frac{1}{1-z} r_D + \frac{(1-d_1)^2}{1-z} r_F \right) + c_m \left( \frac{1}{z} r_S - \frac{1-z(1-d_1)^2}{z(1-z)} r_M \right) > 0, \quad (\text{A7})$$

where  $r_D = p_D/p_I$  is the relatedness of a mother and daughter from the perspective of the mother;  $r_F = p_F/p_I$  is the relatedness of a random adult female and random juvenile female from the same patch, from the perspective of the former;  $r_S = p_S/p_I$  is the relatedness of a mother and son from the perspective of the mother; and  $r_M = p_M/p_I$  is the relatedness of a random adult female and a random juvenile male from the same patch, from the perspective of the former. Setting the LHS of condition (A7) to zero, and solving for  $z = z^*$ , yields an equilibrium sex ratio given by eqn 3 in the main text. The derivative of the LHS of condition (A7) with respect to  $z$  is negative for all  $r_F < r_D$  and  $r_M < r_S$ , hence this equilibrium sex ratio is globally convergence stable (Eshel & Motro, 1981; Christiansen, 1991; Taylor, 1996).

## Relatedness

Here we derive the consanguinity and relatedness coefficients for haploid, diploid and haplodiploid populations. We use notation appropriate to the individual dispersal model, but the calculations apply equally to the budding dispersal model if  $d_1$  is replaced with  $m$  throughout.

### Haploidy

We focus on the inbreeding coefficient  $f$ , which is the average consanguinity of mating partners, and hence it is also the average consanguinity of opposite and same sex juveniles within a patch. At equilibrium, in a neutral population, the consanguinity of two juveniles randomly

chosen from the same patch is given by the probability that they have the same mother ( $1/n$ ) times the consanguinity of full siblings ( $1/2 + 1/2f$ ), plus the probability that they have different mothers  $[(n-1)/n]$  times the probability that the mothers (and hence also the fathers) derive from the same patch  $[(1-d_1)^2]$  times the consanguinity for two juveniles randomly drawn from the same patch ( $f$ ), i.e.:

$$f = \frac{1}{n} \left( \frac{1}{2} + \frac{1}{2}f \right) + \frac{n-1}{n} (1-d_1)^2 f. \quad (\text{A8})$$

Solving eqn A8 for  $f$  obtains:

$$f = \frac{1}{2n-1-2(n-1)(1-d_1)^2}. \quad (\text{A9})$$

The consanguinity of an adult female with a random juvenile sharing her patch is  $p_P = f$ , and the consanguinity of an adult female with one of her offspring is given by  $p_O = 1/2 + 1/2f$ . Using the solution (A9), the within-patch relatedness  $r = p_P/p_O$  is given by eqn 5 in the main text.

### Diploidy

Again we focus on the coefficient of inbreeding,  $f$ . At equilibrium in a neutral population this is equal to the probability that two random juveniles on the same patch share the same mother ( $1/n$ ) times the consanguinity for full siblings ( $1/2(1/2 + 1/2f) + 1/2f$ ) plus the probability that they do not share the same mother  $[(n-1)/n]$  times the probability that their mothers (and hence also their fathers) derive from the same patch  $[(1-d_1)^2]$  times the consanguinity of two random juveniles drawn from the same patch ( $f$ ), i.e.:

$$f = \frac{1}{n} \left( \frac{1}{2} \left( \frac{1}{2} + \frac{1}{2}f \right) + \frac{1}{2}f \right) + \frac{n-1}{n} (1-d_1)^2 f. \quad (\text{A10})$$

Solving eqn A10 for  $f$  obtains:

$$f = \frac{1}{4n-3-4(n-1)(1-d_1)^2}. \quad (\text{A11})$$

As before, the consanguinity of an adult female with a random juvenile sharing her patch is  $p_P = f$ , and the consanguinity of an adult female with one of her offspring is given by  $p_O = 1/2(1/2 + 1/2f) + 1/2f$ . Using the solution (A11), the within-patch relatedness  $r = p_P/p_O$  is once again given by eqn 5 in the main text.

### Haplodiploidy

We continue to denote the consanguinity of mating partners by  $f$ , and this is also the average consanguinity of opposite-sex juveniles sharing the same patch. In addition, we now denote the average consanguinity of two juvenile females sharing the same patch by  $\phi$ , and the average consanguinity of two juvenile males sharing the same patch by  $\mu$ . The consanguinity of two opposite-sex juvenile patch mates is given by the probability that they share the same mother ( $1/n$ ) times the consanguinity of

full sibs (with probability  $\frac{1}{2}$  the juvenile female derives her gene from her mother, as does the juvenile male, in which case the consanguinity is  $\frac{1}{2} + \frac{1}{2}f$ , and with probability  $\frac{1}{2}$  the juvenile female derives her gene from her father, and the juvenile male, from his mother, in which case the consanguinity is  $f$ ) plus the probability that they do not share the same mother  $[(n - 1)/n]$  times the probability that their mothers (and hence also the juvenile female's father) derive from the same patch  $[(1 - d_1)^2]$  times the consanguinity of the parents from which their genes originated (with probability  $\frac{1}{2}$  this is the juvenile female's mother and the juvenile male's mother, in which case consanguinity is  $\phi$ , and with probability  $\frac{1}{2}$  this is the juvenile female's father and the juvenile male's mother, in which case consanguinity is  $f$ ), i.e.:

$$f = \frac{1}{n} \left( \frac{1}{2} \left( \frac{1}{2} + \frac{1}{2}f \right) + \frac{1}{2}f \right) + \frac{n-1}{n} (1 - d_1)^2 \left( \frac{1}{2} \phi + \frac{1}{2}f \right). \tag{A12}$$

The average consanguinity of two juvenile females sharing the same patch is given by the probability that they share the same mother  $(1/n)$  times the consanguinity of full sisters  $(\frac{1}{4}(\frac{1}{2} + \frac{1}{2}f) + \frac{1}{2}f + \frac{1}{4})$  plus the probability that they do not share the same mother  $[(n - 1)/n]$  times the probability that their mothers (and hence also their fathers) derived from the same patch  $[(1 - d_1)^2]$  times the consanguinity of the parents from which their genes originated (with probability  $\frac{1}{4}$  they both derived their genes from their mothers, so consanguinity is  $\phi$ ; with probability  $\frac{1}{2}$  they derived their genes from opposite-sex parents, so consanguinity is  $f$ ; and with probability  $\frac{1}{4}$  they both derived their genes from their fathers, so consanguinity is  $\mu$ ), i.e.:

$$\phi = \frac{1}{n} \left( \frac{1}{4} \left( \frac{1}{2} + \frac{1}{2}f \right) + \frac{1}{2}f + \frac{1}{4} \right) + \frac{n-1}{n} (1 - d_1)^2 \left( \frac{1}{4} \phi + \frac{1}{2}f + \frac{1}{4} \mu \right). \tag{A13}$$

The consanguinity of two juvenile males sharing the same patch is given by the probability that they share the same mother  $(1/n)$  times the consanguinity of full

brothers  $(\frac{1}{2} + \frac{1}{2}f)$  plus the probability that they do not share the same mother  $[(n - 1)/n]$  times the probability that their mothers derived from the same patch  $[(1 - d_1)^2]$  times the average consanguinity of two juvenile females on the same patch  $(\phi)$ , i.e.:

$$\mu = \frac{1}{n} \left( \frac{1}{2} + \frac{1}{2}f \right) + \frac{n-1}{n} (1 - d_1)^2 \phi. \tag{A14}$$

Simultaneously solving eqns A12, A13 and A14, we obtain:

$$f = \frac{n}{n + (n - 1)(1 - (1 - d_1)^2)(3n + (n - 1)(1 - (1 - d_1)^2) + 1)}, \tag{A15}$$

$$\phi = \frac{2n + (n - 1)(1 - (1 - d_1)^2)}{2n + 2(n - 1)(1 - (1 - d_1)^2)(3n + (n - 1)(1 - (1 - d_1)^2) + 1)}, \tag{A16}$$

and

$$\mu = \frac{n + (n - 1)(1 - (1 - d_1)^2)}{n + (n - 1)(1 - (1 - d_1)^2)(3n + (n - 1)(1 - (1 - d_1)^2) + 1)}. \tag{A17}$$

From  $f$ ,  $\phi$  and  $\mu$ , we can calculate all of the other coefficients of consanguinity that are required in order to determine the convergence stable sex ratio. The consanguinity of an adult female to (i) herself is  $p_I = \frac{1}{2} + \frac{1}{2}f$ ; (ii) her daughter is  $p_D = \frac{1}{2}p_I + \frac{1}{2}f$ ; (iii) a random juvenile female on her patch is  $p_F = (1/n)p_D + ((n - 1)/n)(1 - d_1)^2(\frac{1}{2}\phi + \frac{1}{2}f)$ ; (iv) her son is  $p_S = p$  and (v) a random juvenile male on her patch is  $p_M = (1/n)p_S + ((n - 1)/n)(1 - d_1)^2\phi$ . Hence, we can calculate coefficients of relatedness, from the perspective of the adult female, for (i) her daughter ( $r_D = p_D/p_I$ ); (ii) a random juvenile female on her patch ( $r_F = p_F/p_I$ ); (iii) her son ( $r_S = p_S/p_I$ ) and (iv) a random juvenile male on her patch ( $r_M = p_M/p_I$ ). Substituting these into eqn 3, and setting  $c_f = 2/3$  and  $c_m = 1/3$ , we obtain eqn 7 of the main text.

Received 15 January 2009; revised 25 January 2009; accepted 26 January 2009