LETTER

Sex and stochasticity affect range expansion of experimental invasions

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Abstract

Understanding and predicting range expansion are key objectives in many basic and applied contexts. Among dioecious organisms, there is strong evidence for sex differences in dispersal, which could alter the sex ratio at the expansion's leading edge. However, demographic stochasticity could also affect leading-edge sex ratios, perhaps overwhelming sex-biased dispersal. We used insects in laboratory mesocosms to test the effects of sex-biased dispersal on range expansion, and a simulation model to explore interactive effects of sex-biased dispersal and demographic stochasticity. Sex-biased dispersal created spatial clines in the sex ratio, which influenced offspring production at the front and altered invasion velocity. Increasing female dispersal relative to males accelerated spread, despite the prediction that demographic stochasticity would weaken a signal of sex-biased dispersal. Our results provide the first experimental evidence for an influence of sex-biased dispersal on invasion velocity, highlighting the value of accounting for sex structure in studies of range expansion.

Keywords

Biological invasion, *Callosobruchus maculatus*, demographic stochasticity, demography, dioecy, sex ratio, spatial population dynamics.

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INTRODUCTION

The boundaries of species' ranges are dynamic, now more than ever. Global climate change is leading to colonisation of new environments and range shifts (Crozier & Dwyer 2006); reintroduction programmes promote the spread of threatened species into formerly occupied habitat (Tinker *et al.* 2008); and, the transport of non-indigenous organisms to novel environments often leads to their establishment and expansion, with significant ecological and economic impacts (Pimentel *et al.* 2000). We refer to scenarios in which populations expand their geographical ranges into previously unoccupied areas as 'biological invasions'.

Population biologists have a developed a large body of theory for the spread of biological invasions. Many invasion models couple local population growth with a probability distribution (or 'kernel') of individual dispersal distances (Skellam 1951; Kot *et al.* 1996; Okubo & Levin 2002; Hastings *et al.* 2005). Under many conditions, the interplay of local demography and dispersal generates a travelling wave that is 'pulled' along by propagule production at the leading edge, where low-density conditions may allow for rapid population growth. This body of theory provides a framework for estimating the velocity of expansion and its sensitivities to local demography and dispersal parameters (Neubert & Caswell 2000; Caswell *et al.* 2003), a toolkit on which applied studies have come to rely (e.g., Jongejans *et al.* 2008; Miller & Tenhumberg 2010). However, nearly all theoretical and empirical studies of biological invasions have tracked the density of only one sex (females only or females and males combined). The application of one-sex invasion theory to dioecious species (most animals) is complicated by the fact that dispersal is often sex biased, with females and males moving different distances (reviewed in Miller *et al.* 2011).

Sex-biased dispersal is potentially important because it can generate a spatial cline in the sex ratio, from the core of the range to the low-density leading edge. Skew in the sex ratio should be strongest in habitat patches at the leading edge of the wave (where the farther-dispersing sex will be over-represented), precisely the region that most strongly affects the velocity of spread (Kot *et al.* 1996). If local population growth is sensitive to skew in the sex ratio, then sex-biased dispersal will alter rates of propagule production at the invasion's leading edge and can therefore be expected to influence the dynamics of range expansion. It is often assumed that population growth is female-dominant and not sensitive to variation in the availability of males, but intuition and evidence suggest otherwise (Caswell & Weeks 1986; Rankin & Kokko 2007; Miller & Inouye 2011). Recent theoretical developments for two-sex invasions indicate that accounting for sex-biased dispersal can significantly modify expectations for the velocity of range expansion, relative to traditional one-sex approaches (Miller *et al.* 2011). Failure to account for sex differences in movement can lead to inaccurate predictions for range expansion, even if average dispersal behaviour is well known.

Despite advances in theory and suggestive patterns in the literature, we lack direct empirical tests for the role of sex-biased dispersal in range expansion. One potential source of discrepancy between theoretical expectations and empirical patterns of two-sex invasions is demographic stochasticity arising from the discreteness of individual organisms. Effects of demographic stochasticity may be manifest in local demography, dispersal or both (Melbourne & Hastings 2009). First, demographic stochasticity in local demography can generate variance in propagule production and sex ratio, leading to variation in the availability of propagules for dispersal. Second, demographic stochasticity in dispersal occurs when individual propagules "sample" from a distribution of dispersal distances. Low-probability kernel tails, so important in deterministic spread models, may go unsampled during a given bout of dispersal. In fact, we should expect this random sampling to generate skewed sex ratios in leading-edge patches even without deterministic differences

in underlying kernels because rare events are unlikely to be sampled evenly by both sexes. Furthermore, where deterministic sex differences in dispersal occur they are often modest (Miller *et al.* 2011), suggesting that effects of sex biases may be masked by noisy sampling from kernel tails. Demographic stochasticity is known to reduce average invasion speeds (Snyder 2003) and increase variance (Melbourne & Hastings 2009), but its interaction with sex-biased dispersal has not been explored. Whether inherent noisiness in local population growth and/or dispersal would overwhelm the expected signal of sex-biased movement remains an open and important question.

This study was designed to evaluate the role of sex-biased dispersal in range expansion using the bean beetle *Callosobruchus maculatus* (F.) (Coleoptera: Chrysomelidae), a laboratory model species. We first quantified sex differences in beetle dispersal and the influence of sex ratio variation on population growth. We then tested the effects of sex-biased dispersal on the velocity of range expansion by manipulating the relative dispersal distances of females and males as they expanded their range through replicated landscapes. Finally, we used a two-sex invasion model to ask whether demographic stochasticity would swamp a deterministic signal of sex-biased dispersal. We also used the model to examine how effects of demographic stochasticity can propagate through the invasion process to generate variability in spread rates, and whether dispersal bias would amplify or dampen variance in spread. Our results demonstrate the potential for sex-biased dispersal to influence the mean and variance of invasion velocity, highlighting the value of accounting for sex structure in studies of range expansion. However, the results also suggest that demographic stochasticity can dampen this influence.

MATERIALS AND METHODS

Study system

Callosobruchus maculatus is an agricultural pest and a model organism in ecology and evolution. Gravid females deposit eggs on seeds of cultivated legumes (Fabaceae). Larvae burrow into beans, pupate and emerge as adults; the egg-to-adult developmental period is *c.* 32 days under our incubator conditions (27.5 °C and a 16 : 8-h photoperiod). The adult lifespan is *c.* 1 week and adults do not need to eat. Adult females can be readily distinguished from males by their size (larger), coloration (darker, more patterned elytra) and shape (wider). Our populations were reared exclusively on mung beans (*Vigna radiata*).

Parameter estimation

Dispersal
We quantified post-natal dispersal through one-dimensional arrays consisting of 41 Petri dishes ('patches') filled with 5 g of mung beans and connected by 1 cm of tubing. We tested for sex differences in dispersal by releasing newly emerged (0- to 48-h old) beetles in the centre of the array. Locations were recorded 24 h following release. We observed a total of 435 and 429 dispersal events for females and males respectively. The experiment included beetle releases from a range of sex ratios and densities as part of a separate study to quantify the contingencies of dispersal on these local conditions. For this study, we focus on overall sex differences, which were consistent across sex ratios and densities. For analysis,

we first explored the fits of alternative discrete probability distributions to the data, pooled across sexes, using Akaike's Information Criterion (AIC) as a measure of fit (Burnham & Anderson 2002). We found that a negative binomial distribution provided the best fit and proceeded to ask whether neither, either or both parameters of the negative binomial (mean and dispersion) were sex-specific. We quantified support for these hypotheses using ΔAIC and AIC weights (proportional weight of evidence in favour of each candidate model).

Local demography
We conducted experiments to quantify the influence of sex ratio variation on local population dynamics. We assigned populations (reared in square Petri dishes on 5 g of beans) to treatments that varied across a response surface, crossing initial density (2–192 beetles) and sex ratio (0.1–0.9 proportion female). Each of 48 density–sex ratio combinations was replicated five or more times for a total of 244 populations. Crossing sex ratio with density allowed us to quantify sex-specific contributions to low-density growth rates and density-dependent regulation. We focus here on low-density growth rates, as they determine the trajectories of newly colonised locations at the front of an invasion wave. We compared the fits of 16 candidate models, including a female-dominant (null) model and various two-sex models that have been proposed in the literature. See Miller & Inouye (2011) for further information on the experimental design and data analysis. To characterise the primary sex ratio, we compared the fits of binomial and beta-binomial distributions to observed counts of female and male offspring from each experimental population.

Invasion experiment

We integrated dispersal and local demography to examine experimentally how sex-biased dispersal affects range expansion. The experiment included three dispersal treatments: male-biased dispersal, no dispersal bias and female-biased dispersal. Each treatment was replicated six times for a total of 18 independent invasions, each of which ran for nine generations. We discretised the life cycle into local population growth (32 days) and dispersal (1 day) phases. During the dispersal phase, we implemented the assigned dispersal treatments manually. For each beetle, a random dispersal distance was drawn from the kernel(s) assigned to that replicate. Kernels were based on the beetle dispersal data. In the experiments described above (Parameter estimation: Dispersal), beetle dispersal was found to be dependent on the local sex ratio. Yet, the primary sex ratio was unbiased (Results), suggesting limited opportunity for sex ratio-dependent post-natal dispersal under realistic conditions. For the invasion experiment, we therefore used kernels that were fit to the subset of data where the sex ratio of released beetles was unbiased (92 female and 88 male dispersal events).

For the male-biased treatment, we drew random dispersal values from the sex-specific kernels fit to the observed dispersal data (which showed significant male bias; Results). For the female-biased treatment, we switched the sexes assigned to the kernels such that females were dispersed according to the fitted male kernel, and vice versa. For the unbiased treatment, we generated an average kernel and applied it to both sexes. Experimental treatments therefore differed in the relative dispersal distances of females and males, but maintained a constant mean kernel; in the hypothetical scenario

where individuals could not be sexed, these treatments would appear identical. By randomly sampling from dispersal distributions, our manual dispersal treatments retained the demographic stochasticity inherent in natural dispersal.

We initiated each replicate invasion with 43 females and 43 males (expected equilibrium population size and sex ratio) and tracked the spread of the invasion wave in one direction only (the 'right' half of symmetric expansion). Left-dispersing beetles were discarded. We assumed that left-dispersing beetles would contribute negligibly to right-travelling wave fronts; simulations (not shown) supported this assumption. Given the labour-intensive nature of the treatments (in total, we dispersed 51 829 beetles by hand), we maintained each replicate at a manageable size by eliminating habitat patches more than 16 patches behind the farthest consecutively occupied patch; this cut-off is twice the 95th percentile of observed dispersal distances.

Analysis of invasion experiments

To combine information from multiple generations of independent replicates, we standardised all patches, for each replicate in each generation, with respect to its distance from the front. The front was defined as the farthest patch in which local density equalled or exceeded a threshold value (analogous to a detection threshold for organisms in the field). Because invasion waves are expected to achieve a constant shape under many conditions (Kot *et al.* 1996), the particular value of the density threshold should not affect our estimates of wave speed as long as it is below the equilibrium local density. We found that varying the density threshold had no influence on our conclusions; we present results based on a threshold of five individuals.

First, we examined whether and how local sex ratios following dispersal varied with distance from the invasion front and if the spatial cline differed among dispersal treatments. We used a generalised linear model with a binomial link function in R version 2.13.1 (R Core Development Team 2011) to test whether the sex ratio (proportion female) varied from the core to the front, and whether the spatial pattern differed across dispersal treatments. We used AIC to compare two models in which the distance dependence of the local sex ratio was constant or differed among treatments.

Second, we examined whether the local population growth rate (N_{t+1}/N_t) varied with distance from the invasion front. Examination of the data indicated nonlinear variation in growth rate across the distance gradient. We therefore fit generalised additive models (GAM) to $\log(y + 1)$-transformed data using the 'gam' function (package mgcv). We used AIC to compare two GAMs in which the distance dependence of population growth was constant or differed among treatments.

Finally, we tested the effects of dispersal treatment on the velocity of expansion using a mixed-effects linear model with invasion replicate as a random effect nested within the fixed effect of treatment. We quantified velocity as the net displacement of the invasion front from one dispersal phase to the next (patches per generation). We dropped the velocity estimates for generation 1 of all invasion replicates, as the initial conditions were far from a stable wave shape. Visual inspection of the data suggested that transient dynamics had begun to dissipate by generation 2 (Fig. S1). Replicate was treated as a random effect because invasion speeds across generations but within replicates were likely non-independent (due to

genetic founder effects, for example). The untransformed velocity data conformed well to model assumptions. We used AIC to compare models in which invasion speed was constant or differed among treatments.

Two-sex invasion model

We used a two-sex invasion model to explore the consequences of sex-biased dispersal beyond the levels included in our invasion experiments and to quantify the influence of multiple sources of demographic stochasticity on mean and variance of invasion speed. We used a discrete-space version of the model developed in Miller *et al.* 2011, where $F(x)_t$ and $M(x)_t$ give the densities of females and males, respectively, in patch x at time t:

$$
\begin{aligned}
F(x)_{t+1} &= \sum_{i=1}^{N} K_F(|x-y|) g\big(F(y)_t, M(y)_t\big)\phi \\
M(x)_{t+1} &= \sum_{i=1}^{N} K_M(|x-y|) g\big(F(y)_t, M(y)_t\big)(1-\phi)
\end{aligned} \tag{1}
$$

$K(x)$ is the sex-specific dispersal kernel, $g(F,M)$ is the function for local two-sex demography, ϕ is the primary (birth) sex ratio (proportion female) and the spatial domain consists of patches (i) 1 through N. We used negative binomial distributions for the sex-specific kernels, where sex-specific mean and dispersion parameters were varied, but constrained so that the population mean kernel under a primary 50 : 50 sex ratio was constant and matched the experimental system. We used the following functional form for two-sex demography:

$$
g(F_t, M_t) = \frac{Rb \frac{2F_t b^{-1} M_t}{F_t b^{-1} + M_t}}{1 + (b_F F_t)^{\gamma_F} + (b_M M_t)^{\gamma_M} + \left(b_O \frac{2F_t b^{-1} M_t}{F_t b^{-1} + M_t}\right)^{\gamma_O}}, \tag{2}
$$

where R is the per-mating birth rate, b is the 'harem size' or number of female mates per males (Caswell & Weeks 1986) and b and γ control the strength and form of density dependence respectively. Density-dependence parameters are subscripted to indicate unique contributions of females, males and offspring (O), the latter being approximated by a pair formation term (because larvae developing inside beans cannot be directly censused). This demographic function was identified as the best fit by a model selection analysis (Miller & Inouye 2011, Results).

We used eqns (1) and (2) to conduct a simulation experiment that crossed the presence/absence of demographic stochasticity in local population growth with stochasticity in dispersal for a total of four treatments. Demographic stochasticity in local population growth was modelled by drawing a Poisson random variable where the mean was equal to the deterministic prediction for total recruitment. Then, offspring were assigned as females or males by drawing a random variable from a beta-binomial distribution fit to primary sex ratio data (Results). To model demographic stochasticity in dispersal, each propagule sampled a dispersal distance (number of patches) from the assigned kernel. In simulations with deterministic demography and stochastic dispersal, the expected number of propagules was rounded to the nearest integer. For each treatment, we simulated spread for a range of sex-specific kernels, at and exceeding observed levels of bias, for 50 generations and calculated the mean per-generation velocity excluding the first five generations of transient dynamics. To quantify the influence of sex-biased dis-

persal on variability in spread rates, we calculated the coefficient of variation (CV) across generations of spread.

RESULTS

Sex-biased dispersal

Beetle dispersal through one-dimensional spatial arrays was significantly sex-biased (Fig. 1). A negative binomial kernel with sex differences in mean and dispersion parameters provided the best fit to the dispersal data (AIC weight = 0.99) and the kernel with no sex differences was not supported (AIC weight < 0.001, ΔAIC = 47.8). Males had a greater mean dispersal distance than females and the difference in dispersion indicates that their kernel had a longer tail. Model selection results for the subset of data based on dispersal from an unbiased sex ratio (used to generate manual dispersal kernels) were qualitatively identical, with the null model receiving no support (AIC weight < 0.002) and sex-specific mean and dispersion providing the best fit (AIC weight = 0.6). Sex-specific dispersal parameters are given in Table S1.

Sex-structured local population growth

A model including both sexes fit beetle population growth data better than a one-sex, female-dominant model (see Miller & Inouye 2011 for complete model selection results). The functional form is given in eqn (2) (AIC weight of this model > 0.8) and the maximum likelihood parameter estimates are provided in Table S1. Because we are primarily interested in low-density dynamics, we derived from eqn (2) the dependence of the low-density population growth rate, $g'(F_t = 0, M_t = 0)$, on the population sex ratio (proportion female) (Fig. 2). The low-density growth rate increased with female relative abundance until reaching a threshold sex ratio (74% female) and then declined. Extreme skew in the sex ratio (< 2.7% and > 99.6% female) was predicted to cause declining (< 1) population growth rates.

The primary sex ratio did not deviate from 1 : 1 (the confidence intervals included 0.5). However, a beta-binomial distribution provided a modestly better fit than a binomial distribution
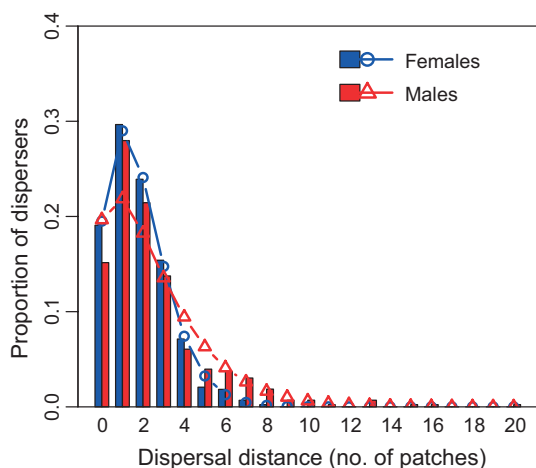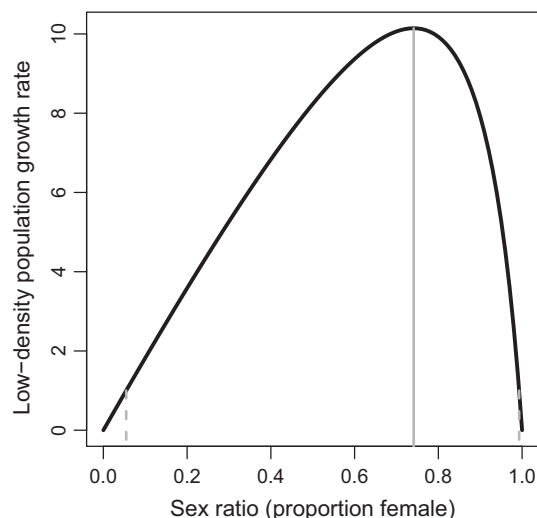

Figure 2 Effect of population sex ratio (proportion female) on the geometric, low-density population growth rate based on parameter estimates from sex-ratio manipulation experiments (Table S1). Solid grey line indicates the sex ratio that maximises low-density population growth and dashed grey lines indicate sex-ratio thresholds for positive population growth.

(ΔAIC = 1.4), indicating some overdispersion in the primary sex ratio (Miller & Inouye 2011).

Invasion experiments

We evaluated the effects of sex-biased dispersal on beetle range expansion by applying male-biased, unbiased and female-biased dispersal treatments to replicated invasions. Like natural dispersal, manual dispersal, combined with local population growth, generated travelling invasion waves (Fig. 3).

We found clinal variation in local sex ratio with respect to distance from the invasion front. The interiors of the experimental ranges were close to a 1 : 1 sex ratio but, approaching the low-density fronts, variance in local sex ratio increased (Fig. 4a). The mean direction of sex ratio bias varied among dispersal treatments (ΔAIC = 66.8, AIC weight of model with treatment effect > 0.99), as expected: males were over-represented at the invasion fronts under male-biased dispersal, females were over-represented at the invasion fronts under female-biased dispersal and the unbiased dispersal treatment was intermediate. However, the strong stochastic variation in sex ratio and the relatively weak differences in fitted distance-dependent sex ratios were striking (Fig. 4a).

The local per capita growth rates varied across the spatial cline from the core of the range to the leading edge (Fig. 4b), and the pattern of clinal variation differed among treatments (ΔAIC = 189.9, AIC weight of model including treatment effect > 0.99). For all treatments, local per capita growth rates increased from the core of the ranges outwards as the strength of density dependence declined along the wave fronts. However, population growth rates did not increase monotonically. Rather, they peaked near the invasion front then declined, and the spatial pattern of decline differed among treatments (Fig. 4b).

Finally, we examined how the spatial pattern of population growth along the invasion wave translated to the velocity of expansion. We found that *C. maculatus* invasion speed was strongly influ-

Figure 1 Results of dispersal trials and fitted negative binomial dispersal kernels (blue circles: females, red triangles: males). Bars indicate proportions of 435 female and 429 male dispersal events. See Table S1 for kernel parameter values.
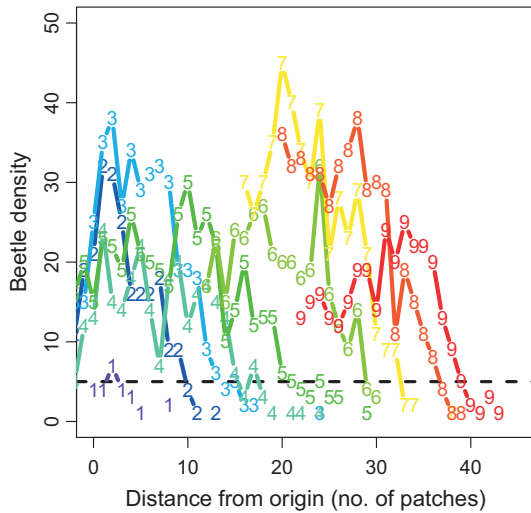
Figure 3 Example of a travelling invasion wave. Solid lines show sequential generations, indicated with numbers, from one bean beetle invasion replicate. The dashed horizontal line represents the density threshold (five beetles) for identifying the invasion front. The front is defined for each generation as the farthest patch in which beetle density was equal to or exceeded the threshold density.

Figure 5 Experimental results for the effects of sex-biased dispersal on invasion speed. Boxes show the inner quartiles of the distributions of invasion speed, whiskers extend to the 5 and 95 percentiles and the black bar indicates the median. Dispersal treatment strongly affected invasion speed despite the constant mean dispersal kernel across treatments (ΔAIC = 6.03, Akaike's Information Criterion (AIC) weight of treatment effect = 0.95).

enced by dispersal treatment (ΔAIC = 6.03, AIC weight of model including treatment effect = 0.95). Shifting dispersal from male biased to female biased accelerated beetle range expansion (Fig. 5). Tests of the parameter estimates (*post hoc t*-tests) indicated that the female- and male-biased treatments different significantly ($P < 0.05$) from each other, but neither differed significantly from the unbiased treatment.

Simulation experiments

Simulations of stochastic, two-sex range expansion yielded three main results. First, in the absence of any demographic stochasticity,
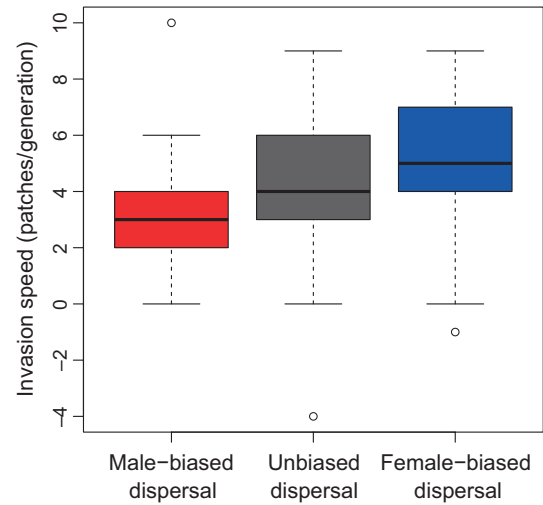
invasion speeds increased with increasing female bias in dispersal, consistent with experimental results (Fig. 6a). However, invasion speed was predicted to peak near the level of female-biased dispersal included in our experiment and further dispersal bias in favour of females was predicted to reduce rates of spread. Second, demographic stochasticity affected the responsiveness of spread rates to sex biases in dispersal (Fig. 6a). Demographic stochasticity operating only in local population growth modestly reduced invasion speeds relative to non-stochastic predictions, but did not substantially alter the shape of the response to variation in dispersal bias. In contrast, demographic stochasticity in dispersal strongly reduced invasion speeds overall and weakened the influence of
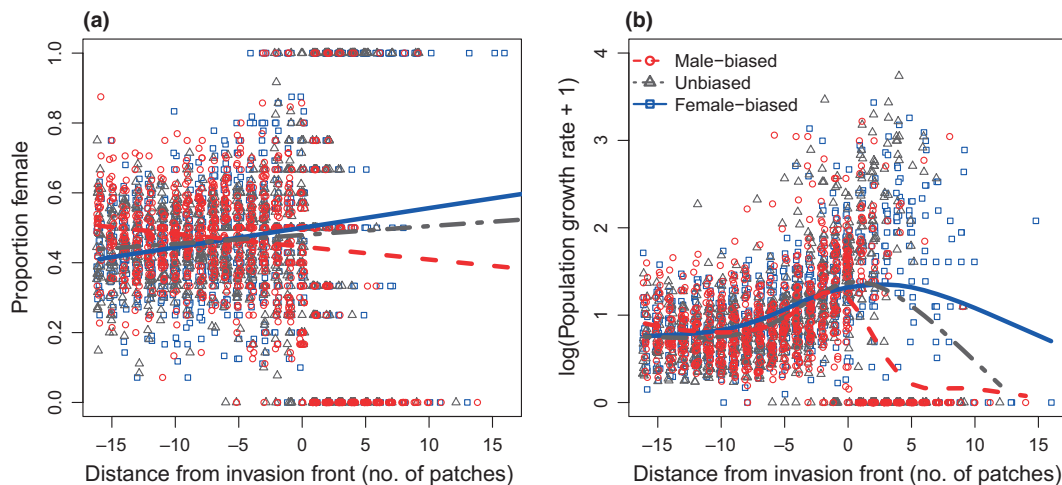

Figure 4 (a) Variation in local sex ratio (proportion female) with respect to distance from the invasion front (see Fig. 3). Points show observed values for male-biased (red circles), unbiased (grey triangles) and female-biased (blue squares) dispersal treatments. Dashed, short-long dashed and solid lines show the respective fitted binomial models. (b) Variation in the local per capita population growth rate (new beetles per colonising beetle) with respect to distance from the invasion front. Point and line types as in (a). Lines show fitted generalised additive models.

dispersal bias (a shallower slope of the response function near zero dispersal bias), whether or not local demography was also stochastic. Over the range of our dispersal treatments, there was little expected influence of sex-biased dispersal on mean rates of spread (a change of less than one patch per generation).

Finally, sex-biased dispersal increased the coefficient of variation (CV) of invasion speed from generation to generation, particularly when combined with demographic stochasticity in dispersal (Fig. 6b). Like mean invasion speed, the effect on CV increased as dispersal became increasingly sex biased. Over the range of our dispersal treatments, there was little predicted effect of sex-biased dispersal on the CV of invasion speed, consistent with experimental results. The observed CV's were 0.5, 0.54 and 0.51 for the male-biased, unbiased and female-biased treatments respectively.

DISCUSSION

Despite a long history of work on the interaction of dispersal and demography in driving spatial spread, population sex structure has rarely been considered in this context. Ignoring sex structure may be justifiable if the sexes do not differ in dispersal (in which case, the sex ratio does not vary systematically through space), or if local demography is truly female-dominant (in which case, male dispersal is unimportant). However, these assumptions are rarely tested, and growing evidence for sex-biased dispersal (Greenwood 1980; Clarke et al. 1997; Beirinckx et al. 2006; Miller et al. 2011) and sex ratio-dependent population growth (Mysterud et al. 2002; Milner-Gulland et al. 2003; Milner et al. 2007; Rankin & Kokko 2007; Miller & Inouye 2011) calls into question the adequacy of one-sex approaches for studying range expansion by dioecious organisms.

We tracked the cascading effects of sex-biased dispersal from spatial clines in sex ratio to spatial clines in population growth to overall rates of spread, against a backdrop of demographic stochasticity.

There was a powerful influence of demographic stochasticity on the sex ratio of leading-edge patches (Fig. 4a). Following dispersal, female-only and male-only patches were common near the leading edges, regardless of dispersal treatment, particularly at the low-density fronts where patches were colonised by one or few individuals. Nonetheless, a signature of sex-biased dispersal on local population growth was detectable, with female-biased dispersal treatments maintaining positive growth rates in patches at and beyond the invasion front (Fig. 4b). The treatment-induced shift in patterns of population growth along the invasion wave due to the sex ratio dependence of population growth (Fig. 2) explains the positive effect of female-biased dispersal on bean beetle invasion speed (Fig. 5).

The positive effect of shifting dispersal from male biased to female biased was predicted by general theory (Miller et al. 2011), was well matched by deterministic simulations (Fig. 6a), and was arguably unsurprising: populations move more quickly as females, the regenerative sex, disperse farther, until the point where negative effects of male limitation exceed positive effects of female dispersal. However, we also found that demographic stochasticity can dampen the influence of dispersal bias and shift the conditions causing peak invasion speed (Fig. 6a). In contrast to deterministic expectations, dispersal bias on the order of our experimental treatments, acting in concert with demographic stochasticity, was predicted to have only a weak effect on mean invasion speed. In this light, our experimental results are surprising. Demographic stochasticity was operating in our experiment and should have clouded the signal of deterministic sex differences in movement; yet, we detected this signal. We suspect that the mismatch is due to misspecification of local population growth in leading-edge patches with highly skewed sex ratios. Our two-sex demography function predicts extinction of female-only patches (Fig. 2; this property is used as a criterion for 'good' two-sex functions: Ianelli et al. 2005).
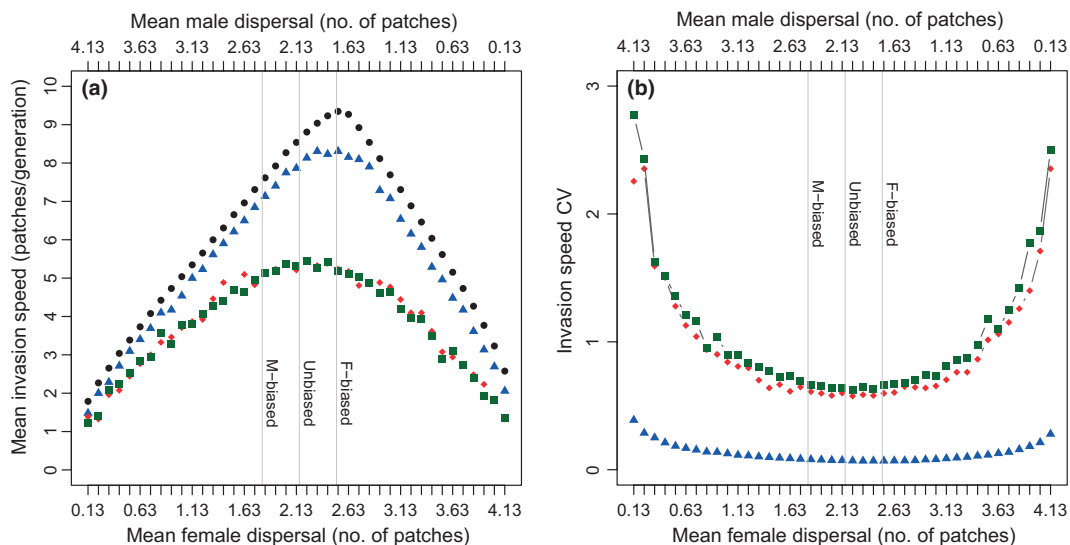

Figure 6 (a) Simulation results for the mean invasion speed (patches/generation) in relation to sex-biased dispersal and different sources of demographic stochasticity (no stochasticity: black circles; stochasticity in local population growth only: blue triangles; stochasticity in dispersal only: red diamonds; stochasticity in both: green squares). The top and bottom horizontal axes vary female and male mean dispersal distance; these run in opposite directions to hold constant the population mean. The dispersion parameters also covary with the means (not shown). The vertical lines correspond to experimental treatments. (b) Simulation results for the coefficient of variation (CV) of invasion speed, corresponding to the means shown in (a). Layout and symbology are identical to (a).

However, the 24-h dispersal period provided brief mating opportunities for females that subsequently colonised female-only patches. In fact, 78.5% of lone females in leading-edge patches produced some offspring, although their fertility (mean = 9.06 offspring) was significantly lower than that of females with one mate (mean = 16.6; t = 4.96, df = 94.7, P < 0.001). Thus, non-zero fertility of female-only patches at the invasion front likely boosted invasion speeds of female-biased replicates relative to model predictions. Mating opportunities prior to colonisation of leading-edge patches may be a mechanism of general significance that can modify rates of spread and not just an idiosyncrasy of our experimental design.

Laboratory studies are valuable for elucidating connections between demographic and dispersal mechanisms and patterns of range expansion, but they provide limited inference regarding the occurrence and importance of these processes in natural systems. However, sex-biased dispersal is common across invertebrate and vertebrate taxa (Miller *et al.* 2011) and its signature effect on patterns of range expansion – systematically skewed sex ratios at invasion fronts – has been documented in nature. For example, expanding populations of brown bears (*Ursus arctos*) in Finland (Kojola & Heikkinen 2006), Sweden (Swenson *et al.* 1998) and Croatia (Jerina & Adamic 2008) all showed significant over-representation of males at the low-density invasion fronts, reflecting known male-biased dispersal behaviour. While further field studies of sex-structured invasions are needed, available evidence suggests that the processes captured in our laboratory experiments operate in nature and merit greater attention.

The interaction of sex-biased dispersal and demographic stochasticity can affect not only mean rates of spread but also their variance (Fig. 6b). Melbourne & Hastings (2009) called attention to high variability in rates of spread and the challenges it poses to conservation and management. We found that sex-biased dispersal can increase variance in spread, particularly when sex differences are strong (stronger than our experimental treatments). The influence of dispersal bias on invasion variance suggests not only that predictability of spread may be fundamentally limited, as Melbourne and Hastings concluded, but also that these limitations may become more severe as dispersal becomes increasingly sex biased.

The finding that demographic stochasticity can dilute effects of sex-biased dispersal on range expansion when dispersal bias is low (Fig. 6) raises new questions: What is 'low' dispersal bias? And is dispersal bias in nature sufficiently 'low' that we rarely need to worry about it? To address these questions, we compared the sex differences in bean beetles, quantified as the log-ratio of male-to-female mean dispersal distance, to those observed in 65 other animal taxa described in Miller *et al.* (2011). We found that bean beetles are in the 60th percentile of the absolute value of dispersal bias (bias in either direction). This result suggests that bean beetles are rather ordinary and that sex-biased dispersal is often more extreme. Thus, we caution against using the noisiness of demographic stochasticity as license to ignore sex structure without first exploring the sensitivity of invasion speed to deviations from unbiased dispersal.

Dioecious organisms are vulnerable to local decline at the leading edges of expanding populations because low densities are associated with potential mate limitation (Engen *et al.* 2003). Previous simulation studies have shown that females and males dispersing into unoccupied areas may fail to locate one another, even if they share identical dispersal behaviour (Hopper & Roush 1993; South & Kenward 2001; Fagan *et al.* 2010). Density-dependent mate-location failure can be interpreted as a type of Allee effect (Gascoigne *et al.* 2009) and is well documented in low-density populations of invasive gypsy moths, for example (Tobin *et al.* 2007; Contarini *et al.* 2009; Robinet & Liebhold 2009). Allee effects due to mate location failure or other biological mechanisms can have a profound effect on spatial spread (Kot *et al.* 1996; Wang *et al.* 2002). Indeed, we found evidence for low-density mating failure in our experimental invasions, even in replicates without deterministic differences in female and male dispersal (Fig. 4b). In addition, sex-biased dispersal modified the locations of the peak and decline in population growth, with female-biased invasions best able to maintain increasing growth rates ahead of the front (pre-colonisation mating, discussed above, likely contributed to this). Thus, sex differences in use of space, whether deterministic or randomly realised, is a mechanism underlying mate-location failure and Allee effects, much like sex differences in use of time (Calabrese & Fagan 2004).

The potential for mate-location failure due to sex-biased dispersal raises exciting questions about the evolutionary ecology of sex-structured invasions. Sex-biased dispersal is hypothesised to be an adaptive response to inbreeding depression and local mate competition (Perrin & Mazalov 2000). However, selection on dispersal traits may vary across different parts of the range (Dytham 2009). The adaptive value of sex-biased dispersal depends upon dispersers encountering unrelated con-specifics in their new environment. While expanding into unoccupied territory, the farthest-dispersing individuals of the farther-dispersing sex face near-certain matelessness. This may select against sex-biased dispersal at invasion fronts and influence long-term rates of spread. There is growing appreciation for evolution of dispersal traits during range expansion and the influence of rapid evolution on the velocity of spread (Phillips *et al.* 2006; Travis *et al.* 2009), although sex-specific dispersal has not been considered in this context. The eco-evolutionary dynamics of sex-specific dispersal traits during range expansion are a potentially rich line of inquiry in need of further work.

In summary, our work suggests that one-sex approaches may often be inadequate for understanding and predicting the dynamics of range expansion by dioecious organisms. Dispersal is often sex biased and local demography is often sex ratio dependent. Our experiments provide the first empirical evidence for the interaction of these sex-structured processes during range expansion and its influence on the velocity of spread, revealing how average dispersal behaviour may lead us astray. However, demographic stochasticity can overwhelm the effects of small to moderate sex differences in movement. The tension between these results – sex-structure matters, except when it does not – poses challenges and opportunities for future work on range expansion.

AUTHORSHIP

TEXM and BDI designed and performed the research. TEXM analysed data and wrote the paper, with input from BDI.

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