

Confronting two-sex demographic models with data

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Abstract. Most population dynamics models explicitly track the density of a single sex. When the operational sex ratio can vary, two-sex models may be needed to understand and predict population trajectories. Various functions have been proposed to describe the relative contributions of females and males to recruitment, and these functions can differ qualitatively in the patterns that they generate. Which mating function best describes the dynamics of real populations is not known, since alternative two-sex models have not been confronted with experimental data. We conducted the first such comparison, using laboratory populations of the bean beetle *Callosobruchus maculatus*. Manipulations of the operational sex ratio and total density provided strong support for a demographic model in which the birth rate was proportional to the harmonic mean of female and male densities, and females, males, and their offspring made unique contributions to density dependence. We offer guidelines for transferring this approach to other, less tractable systems in which possibilities for sex ratio manipulations are more limited. We show that informative experimental designs require strong perturbations of the operational sex ratio. The functional form of density dependence (saturating vs. over-compensatory) and the relative contributions of each sex to density dependence can both determine in which direction and at which population densities such perturbations would be most informative. Our experimental results and guidelines for design strategies promote synthesis of two-sex population dynamics theory with empirical data.

Key words: demography; density dependence; dioecy; experimental design; mating function; mating system; population dynamics; sex.

INTRODUCTION

Most models of population dynamics consider the density of a single sex. One-sex approaches are often appropriate for hermaphroditic organisms, including most plants. They may also be appropriate for dioecious organisms, including most animals, if the sex ratio of individuals available for mating (operational sex ratio) is constant and perfectly tracks the birth sex ratio, in which case no information is gained by explicitly accounting for both sexes. However, in nature operational sex ratios can be highly variable (Hardy 2002). Many common processes can generate this variation and cause departures from the birth sex ratio, including: sex differences in demographic rates (Jenouvrier et al. 2010, Shelton 2010a, b); sex-specific interactions with parasites or pathogens (Miller et al. 2007, Harrison et al. 2010); sex-biased dispersal behavior (Ranta et al. 1999, Veran and Beissinger 2009, Miller et al. 2011); sex-specific phenology (Calabrese and Fagan 2004, Calabrese et al. 2008); sex ratio distortion by uni-parentally transmitted symbionts (Engelstädter and Hurst 2009, Himler et al. 2011); sex-selective harvesting in exploited populations (Coleman et al. 1996, Milner et al. 2007); and demographic stochasticity, especially in small popula-

tions (Engen et al. 2003, Lee et al. 2011). When the operational sex ratio is subject to variation, the application of one-sex models to dioecious organisms—a common practice—requires the likely unrealistic assumption that availability of males has no influence on female fertility (Mysterud et al. 2002, Rankin and Kokko 2007). Demographic models that explicitly account for both sexes may be a better alternative.

Various two-sex demographic functions have been proposed, mostly members of the weighted power means family (Hadeler 1989). These functions, which we call “mating functions,” predict the density of matings based on females only, males only, the minimum of female and male densities, and the weighted, geometric, and harmonic means of female and male densities (Miller et al. 2011). Mating functions are multiplied by a per-mating birth rate (λ) to give the numbers of births at low density, and can be combined with density-dependent terms to predict realized recruitment under higher density conditions (Table 1). Mating functions were developed in the context of human demography (i.e., “marriage functions”; Iannelli et al. 2005) but are now widely used in the study of non-human populations, including social mating systems ranging from polyandry to monogamy to polygyny (Rosen 1983, Caswell and Weeks 1986, Caswell 2001, Kot 2001).

Theoretical work indicates that different mating functions can yield qualitatively different population

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TABLE 1. Candidate two-sex demographic models and fits to *Callosobruchus maculatus* recruitment data.

Model	Mating function (numerator)	Density dependence (denominator)	Equation	K	ΔAIC	w
1	female dominance	unstructured	$N_{t+1} = \frac{\lambda F_t}{1 + (bN_t)^\gamma}$	4	383.7	<0.0001
2	female dominance	sex-structured	$N_{t+1} = \frac{\lambda F_t}{1 + (b_F F_t)^{\gamma_F} + (b_M M_t)^{\gamma_M}}$	6	3.6	0.14
3	minimum	unstructured	$N_{t+1} = \frac{\lambda \times \min(F_t, M_t)}{1 + (bN_t)^\gamma}$	4	302.4	<0.0001
4	minimum	sex-structured	$N_{t+1} = \frac{\lambda \times \min(F_t, M_t)}{1 + (b_F F_t)^{\gamma_F} + (b_M M_t)^{\gamma_M}}$	6	309.4	<0.0001
5	geometric mean	unstructured	$N_{t+1} = \frac{\lambda h \sqrt{F_t h^{-1} M_t}}{1 + (bN_t)^\gamma}$	5	88.4	<0.0001
6	geometric mean	stage-structured	$N_{t+1} = \frac{\lambda h \sqrt{F_t h^{-1} M_t}}{1 + (b_N N_t)^{\gamma_N} + (b_O \sqrt{F_t h^{-1} M_t})^{\gamma_O}}$	7	76.9	<0.0001
7	geometric mean	sex-structured	$N_{t+1} = \frac{\lambda h \sqrt{F_t h^{-1} M_t}}{1 + (b_F F_t)^{\gamma_F} + (b_M M_t)^{\gamma_M}}$	7	77.5	<0.0001
8	geometric mean	sex- and stage-structured	$N_{t+1} = \frac{\lambda h \sqrt{F_t h^{-1} M_t}}{1 + (b_F F_t)^{\gamma_F} + (b_M M_t)^{\gamma_M} + (b_O \sqrt{F_t h^{-1} M_t})^{\gamma_O}}$	9	47.6	<0.0001
9	weighted mean	unstructured	$N_{t+1} = \frac{\lambda h (a F_t h^{-1} + [1 - a] M_t)}{1 + (bN_t)^\gamma}$	6	114.3	<0.0001
10	weighted mean	stage-structured	$N_{t+1} = \frac{\lambda h (a F_t h^{-1} + [1 - a] M_t)}{1 + (b_N N_t)^{\gamma_N} + (b_O (a F_t h^{-1} + [1 - a] M_t))^{\gamma_O}}$	8	61.7	<0.0001
11	weighted mean	sex-structured	$N_{t+1} = \frac{\lambda h (a F_t h^{-1} + [1 - a] M_t)}{1 + (b_F F_t)^{\gamma_F} + (b_M M_t)^{\gamma_M}}$	8	16.4	<0.0001
12	weighted mean	sex- and stage-structured	$N_{t+1} = \frac{\lambda h (a F_t h^{-1} + [1 - a] M_t)}{1 + (b_F F_t)^{\gamma_F} + (b_M M_t)^{\gamma_M} + (b_O (a F_t h^{-1} + [1 - a] M_t))^{\gamma_O}}$	10	69.1	<0.0001
13	harmonic mean	unstructured	$N_{t+1} = \frac{\lambda h \frac{2F_t h^{-1} M_t}{F_t h^{-1} + M_t}}{1 + (bN_t)^\gamma}$	5	178.2	<0.0001
14	harmonic mean	stage-structured	$N_{t+1} = \frac{\lambda h \frac{2F_t h^{-1} M_t}{F_t h^{-1} + M_t}}{1 + (b_N N_t)^{\gamma_N} + \left(b_O \frac{2F_t h^{-1} M_t}{F_t h^{-1} + M_t} \right)^{\gamma_O}}$	7	11.6	<0.0001
15	harmonic mean	sex-structured	$N_{t+1} = \frac{\lambda h \frac{2F_t h^{-1} M_t}{F_t h^{-1} + M_t}}{1 + (b_F F_t)^{\gamma_F} + (b_M M_t)^{\gamma_M}}$	7	39.6	<0.0001
16	harmonic mean	sex- and stage-structured	$N_{t+1} = \frac{\lambda h \frac{2F_t h^{-1} M_t}{F_t h^{-1} + M_t}}{1 + (b_F F_t)^{\gamma_F} + (b_M M_t)^{\gamma_M} + \left(b_O \frac{2F_t h^{-1} M_t}{F_t h^{-1} + M_t} \right)^{\gamma_O}}$	9	0.0	0.85

Notes: For all models, the number of parameters (K) includes the standard deviation of the Gaussian likelihood function (σ). ΔAIC is the difference between each AIC value and the minimum of the model set; w is the AIC weight. Variables are: N_t, initial density; N_{t+1}, density in the next generation; λ, per-mating birth rate; F, number of females; M, number of males; a, parameter that weights the contributions of females and males; b, parameter that controls the per capita contribution to density dependence (greater values correspond to lower maximum recruitment); γ, parameter describing the shape of the recruitment function; h, harem size. The density-dependent parameters b and γ are subscripted to specify females (F), males (M), and offspring (O). Model 16 (in boldface type) received the majority of support from the data.

dynamics (Bessa-Gomes et al. 2010). For example, the harmonic mean function (often regarded as the most realistic) can stabilize population dynamics for a monogamous mating system, relative to a female-dominant function, but the stabilizing effect is weaker for a polygynous mating system (Lindstrom and Kokko 1998, Ranta et al. 1999). Similarly, the effects of sex-biased dispersal on the spread of biological invasions can depend sensitively on the choice of mating function because it influences the rate of propagule production at the invasion's leading edge, where the operational sex ratio can be strongly skewed (Miller et al. 2011).

Given that the functional form can have significant dynamical consequences, population biologists have long recognized a need for studies that compare the fits of alternative mating functions to empirical data (Keyfitz 1972, McFarland 1972, Caswell and Weeks 1986, Lindstrom and Kokko 1998, Caswell 2001, Miller et al. 2011). This has been attempted for humans, but the human operational sex ratio is not sufficiently variable to distinguish among competing two-sex models (Keyfitz 1972). To our knowledge, no studies of non-human organisms have confronted alternative mating functions with data. Furthermore, there has been little discussion in the demography literature about experimental designs that would provide the most discriminatory power. How much variation in the operational sex ratio is necessary to distinguish among mating functions? Are female- and male-biased sex ratios equally informative? At what population density or densities are sex ratio manipulations most useful? Answers to such questions would promote synthesis of two-sex theory with data and advance our abilities to understand and manage the population dynamics of dioecious organisms.

Our study had two primary objectives. First, we experimentally manipulated operational sex ratios in laboratory populations of the bean beetle *Callosobruchus maculatus* (Coleoptera: Bruchidae) and compared the fits of alternative two-sex demographic models to recruitment data. Laboratory organisms offer great potential for elucidating two-sex population dynamics due to the ease of controlled, replicated perturbations to the operational sex ratio. However, for non-model organisms in the field, including threatened species for which an understanding of two-sex demography may be critical (e.g., Milner-Gulland et al. 2003), experimental perturbations may be significantly more difficult, expensive, and limited by ethical concerns. Therefore, our second objective was to identify optimal strategies, given practical constraints, for data collection and experimental design that maximize the strength of inference regarding the functional form of two-sex demography. We suggest that time series data from populations near equilibrium will be inadequate for identifying mating functions, but describe experimental manipulations that are likely to distinguish among competing functional forms. Thus, we provide a novel analysis of two-sex population dynamics using a laboratory model system,

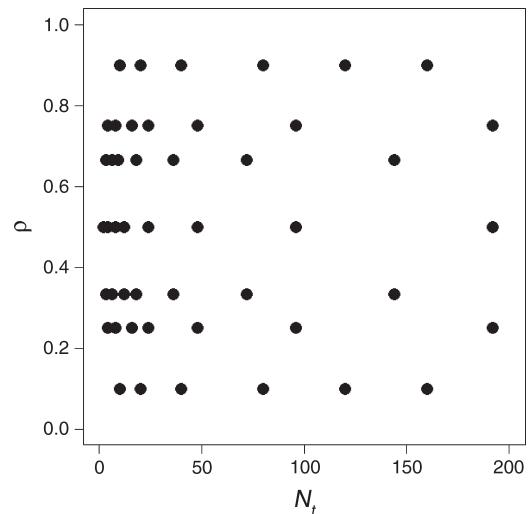


FIG. 1. Response surface for two-sex bean beetle demography experiments. Points represent combinations of initial density (N_t , beetles/dish) and sex ratio (ρ , proportion female). Each point was replicated with four or five experimental populations.

and offer guidelines for transferring this approach to other, less-tractable systems.

METHODS AND RESULTS

Experimental methods

Callosobruchus maculatus (Coleoptera: Bruchidae) is a stored grain pest and a laboratory model species in ecology and evolution (e.g., Fox 1993a, Bonsall et al. 2002). Gravid females deposit eggs on seeds of various cultivated legumes (Fabaceae) (Janzen 1977). Larvae burrow into beans, pupate, and emerge as adults; the egg-to-adult developmental period is 30–35 d under our incubator conditions (27.5°C and a 16 h:8 h photoperiod, Percival I-36VL; Percival Scientific, Perry, Iowa, USA). The adult lifespan is approximately one week and adults do not need to eat. Adult sexes can be readily distinguished by their size (females are larger), color, and patterning on their elytra. Our stock populations were reared exclusively on mung beans (*Vigna radiata*).

The mating functions we compared (Table 1) differ only in the nature of frequency-dependence; they are all linear with respect to total population density. We therefore could have fit models to data in which the sex ratio varied but total density was held constant, i.e., a substitutive design. However, substitutive designs are known to be a poor approach for model selection and parameter estimation (Inouye 2001). We therefore quantified bean beetle population dynamics across a response surface, where the axes were operational sex ratio (ρ), which ranged from 10% to 90% female, and total population density (N_t), which ranged from 2 to 192 adult beetles (Fig. 1). We assume direct correspondence between the adult sex ratio and the operational sex ratio (i.e., all adults are available for mating), which

is supported by the fact that both sexes can mate multiply (Arnqvist et al. 2005). The response variable (the third dimension of the surface) was beetle recruitment in the next generation (N_{t+1}). We distributed treatments across the response surface (with the constraint that female and male densities were assigned integer values) but concentrated treatments near the low end of the density gradient to capture the transition from exponential to density-dependent recruitment. Each treatment was replicated four or five times for a total of 244 experimental populations.

Each population was introduced to a square Petri dish with 5 g of mung beans and stored in an incubator. We initiated populations with adult beetles that were 6–36 h old; we assumed that these beetles were virgins, however some matings may have occurred before the experiments were initiated. All beetles used to initiate populations were reared under similar densities, so our analysis does not include any effects of larval density on adult reproductive performance. After 7 days, individuals of the parental generation (N_t) were removed. After 35 days, females and males of the next generation (N_{t+1}) were counted.

Model selection and analysis

Our first step was to identify the appropriate density-dependent model structure for beetle population dynamics. We compared the fits of three common density-dependent recruitment models to the pooled data ($N = F + M$; where F is number of females and M is number of males): the Ricker model, $N_{t+1} = \lambda N_t \exp(-bN_t)$ (Ricker 1954), the Beverton-Holt model, $N_{t+1} = \lambda N_t / (1 + bN_t)$ (Beverton and Holt 1957), and a generalized form of Beverton-Holt, $N_{t+1} = \lambda N_t / (1 + [bN_t]^\gamma)$ (Shepherd 1982). All functions include a parameter b , which controls the per capita contribution to density dependence (greater values correspond to lower maximum recruitment). The generalized Beverton-Holt function can exhibit a range of dynamical behavior depending on the value of γ (Shepherd 1982). When $\gamma < 1$ recruitment (N_{t+1}) increases monotonically as initial density (N_t) increases. When $\gamma = 1$, the model reduces to the Beverton-Holt model in which recruitment asymptotes as initial density increases, reflecting a fixed amount of space or resources available for new recruits. When $\gamma > 1$, the function is humped and recruitment decreases with increasing initial density past the recruitment peak (classic over-compensatory Ricker dynamics), reflecting interference or aggression among individuals at high density. Thus, the shape of the recruitment function is rooted in the natural history of the organism.

We evaluated these alternatives using the Akaike information criterion (AIC). We used a Gaussian likelihood function and estimated the standard deviation (σ) of the data as a free parameter. We calculated Δ AICs and AIC weights (w), which sum to one and give the proportional weight of evidence in favor of each candidate model (Burnham and Anderson 2002). The

generalized Beverton-Holt model received the vast majority of support from the data ($w = 0.99$). We therefore proceeded to ask which mating function provided the best fit to the data within this density-dependent context.

We quantified the fits of five candidate mating functions that have been proposed in the literature (Caswell 2001, Kot 2001). Model descriptions and equations are given in Table 1. We did not include a male-dominant model ($N_{t+1} = \lambda M_t$) because it is biologically unrealistic for *C. maculatus* and we wished to keep the set of candidate models small. All models share the parameter λ , the low-density number of births per individual (for functions in which a single sex dominates) or per “union” (for functions in which both sexes contribute). In addition, the weighted mean function includes the parameter a , which weights the contributions of females and males. The two-sex mating functions (geometric mean, weighted mean, harmonic mean) can be generalized to represent non-monogamous social mating systems by scaling female density by the “harem size” (h). Values of h less than, equal to, and greater than one can be interpreted to represent polyandry, monogamy, and polygyny, respectively. The low-density birth rate then represents the number of offspring per harem and is multiplied by harem size (λh).

In addition to testing alternative mating functions, the response surface design (Fig. 1) allowed us to examine the possibility of interactions between sex ratio dependence and density dependence. We combined each mating function with up to four alternative forms of generalized Beverton-Holt density dependence (Table 1). For all mating functions, we considered models in which density dependence was unstructured or sex-structured (explicit terms for females and males). For the two-sex mating functions, we included two additional possibilities in which offspring (larval) density was added to the unstructured or sex-structured parental terms. While we did not quantify larval densities (larvae develop inside beans), we used the mating terms, which are proportional to larval densities, as proxies; this allowed us to introduce stage structure into the models. Thus, we considered a total of 16 candidate models (Table 1). We evaluated model fit using Δ AIC and AIC weights (w), as above. In all models, the one, two, or three density dependent terms were allowed to take on unique values for the parameters b (which controls the overall strength of the density dependent effect) and γ (which controls the form of the effect [e.g., saturating vs. over-compensatory]).

The model with the harmonic mean mating function and unique contributions to density dependence by females, males, and offspring (model 16) provided the best fit to the data (Table 1). AIC weights indicate that this model received the majority of support ($w_{16} = 0.85$). Fig. 2 shows the recruitment data and the model prediction using the maximum-likelihood parameter

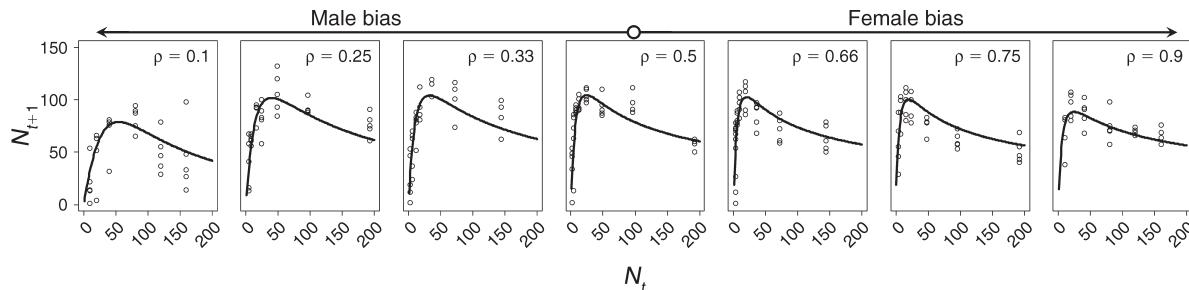


FIG. 2. Bean beetle data (points) and predictions of the best-fitting two-sex model (lines) initial density (N_t , beetles/dish) vs. density in the next generation (N_{t+1}).

estimates (Table 2). The model prediction is a surface in N_t vs. ρ space; the lines in Fig. 2 represent slices of the surface that was fit over continuous variation in ρ . The maximum-likelihood estimate for harem size ($\hat{h} = 8.19$ female mates/male) indicates that *C. maculatus* is polygynous. Accordingly, the low-density population growth rate (slope of the recruitment surface near $N_t = 0$) is maximized at a strongly female-biased operational sex ratio (74% female). Bean beetles are expected to achieve positive population growth rates under operational sex ratios ranging from 2.7% to 99.6% female. We caution that the high upper limit of tolerable female bias may be due to mating by some females prior to the initiation of our experiments. This would also tend to positively bias our harem size estimate, though strong polygyny is consistent with our behavioral observations and with prior work on this species (e.g., Fox 1993b).

The parameter estimates indicate that the density-dependent effect of females was stronger than that of males ($\hat{b}_F = 0.062$, $\hat{b}_M = 0.015$; 95% CI's did not overlap). The form of the female effect was saturating ($\hat{\gamma}_F = 1.08$; 95% CI included 1.0), consistent with the idea that females are limited by suitable oviposition sites, whereas the effect of males was overcompensatory ($\hat{\gamma}_M = 2.38$; 95% CI did not include 1.0). Thus, increasing the density of males but not females decreases the number of recruits, consistent with known negative effects of multiple matings on female fitness (Crudginton and Siva-Jothy 2000, Arnqvist et al. 2005). The density-dependent exponent for offspring ($\hat{\gamma}_O = 1.44$) also indicates over-compensatory effects, possibly driven by interference competition and/or cannibalism among larvae within beans (e.g., Ishii and Shimada 2008).

Interestingly, the harmonic mean mating function provided a poor fit to the data when the density dependent term was unstructured or structured by only sex or stage (Table 1). In fact, had we considered only models with unstructured density effects we would have identified the geometric mean function as the best fit, and had we considered only models with sex-structured density effects we would have identified the female dominant function as the best fit. Thus, there was an interaction between density and sex ratio dependence such that accurate characterization of density depen-

dence was essential for identifying the appropriate mating function.

Fitting two-sex models to time series data

The response surface experimental design (Fig. 1) provided information-rich data that facilitated unambiguous inference about the functional form of two-sex demography for *C. maculatus*. The controlled and replicated (and hence rather luxurious) perturbations that we were able to conduct are not possible for most field systems. Rather, time series of female and male densities are more likely to be the data available for natural populations (e.g., Mysterud et al. 2002, Ewen et al. 2011). We therefore asked how likely one would be to accurately characterize two-sex population dynamics using time series in which population densities fluctuate near equilibria and sex ratio variation is due to demographic stochasticity.

To answer this question, we used the best-fitting model and maximum-likelihood parameter estimates (Tables 1, 2) to simulate a stochastic time series of bean beetle population dynamics, starting at the expected equilibrium size (85 beetles). Parameter values were drawn randomly from uniform distributions encompassing the 95% confidence intervals (Table 2); intervals were estimated holding all other parameters constant at their point estimates (Hilborn and Mangel 1997). We incorporated demographic stochasticity by drawing

TABLE 2. Maximum-likelihood estimates and 95% confidence intervals (CI) for *C. maculatus* demographic parameters.

Parameter	Point estimate	95% CI
λ	18.47	18.03–18.98
h	8.19	7.93–8.47
b_F	0.062	0.054–0.07
b_M	0.015	0.013–0.0164
b_O	0.63	0.61–0.65
γ_F	1.08	0.95–1.23
γ_M	2.38	1.92–2.97
γ_O	1.44	1.41–1.48

Notes: The best-fit model was the harmonic mean mating function with sex- and stage-structured density dependence (Model 16 in Table 1). The density-dependent parameters b and γ are subscripted to specify females (F), males (M), and offspring (O).

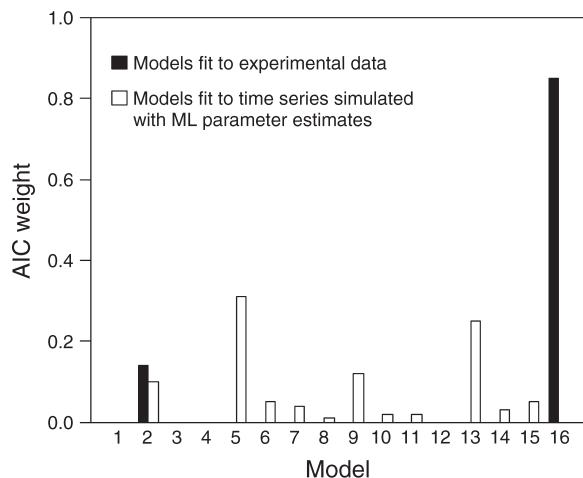


FIG. 3. AIC weights of 16 candidate models (Table 1) fit to recruitment data from the response surface experiment (solid bars) or to time series data that were simulated with the best-fitting model (16 in Table 1) and maximum-likelihood (ML) parameter estimates (Table 2) (open bars).

values for total population size each generation from a Poisson distribution with mean and variance equal to the deterministic model prediction (N_{t+i}). We distributed total density between the sexes according to a beta-binomial distribution with parameters fit to the bean beetle data: probability of female = 0.49 (the confidence interval overlapped 0.5, indicating an unbiased birth-sex ratio) and overdispersion parameter = 431.6. The beta-binomial distribution provided a modestly better fit to the sex ratio data than a binomial distribution ($\Delta\text{AIC} = 1.4$).

We fit the full set of models (Table 1) to 20 generations of simulated data; our conclusions are not particularly sensitive to time series duration. We found that time series data provided insufficient information to differentiate among models or accurately identify the “true” mating function (Fig. 3). Eight models made up the 95% confidence set (defined as $\sum_i w_i \leq 0.95$, summing from the largest to smallest w_i , Burnham and Anderson 2002) and the harmonic mean function with female, male, and offspring density effects—the model that generated the data—was not among these (it was ranked 12th). Thus, at realistic population sizes demographic stochasticity provided insufficient variation to reveal the underlying dynamical structure.

Strategic allocation of experimental effort

The weak inferences provided by time series data indicate a need for experimental perturbations. Unfortunately, the practical challenges of manipulating sex ratios and/or densities can be substantial, especially in the field. We therefore asked if there are regions of the sex-ratio–density surface that provide more information than others and should be prioritized for experimental perturbation. To answer this question, we calculated the predictions of competing models across the response

surface, given similar parameter values. Regions of the surface where models are most divergent provide the greatest potential for differentiating among them. We quantified divergence by calculating the mean of all pairwise differences of model predictions across the response surface. The larger the mean difference, the more informative the position on the surface. In an earlier study, Inouye (2001) investigated response surface designs based on the geometric mean of model divergence. The geometric mean gives greater weight to small differences than the arithmetic mean; if any two models predict the same value at a particular point on the surface, the geometric mean for the entire set of models will equal zero at that point, whereas the arithmetic mean weights small and large divergences equally. Given our goal of producing general guidelines for experimental designs, the geometric mean was deemed too conservative a measure of discriminatory power. For example, the female-dominant and minimum mating functions are identical under male-biased sex ratios, which would lead to zero geometric mean divergence for half of the response surface, even if the remaining functions strongly diverge in this region of the surface. However, the arithmetic mean can still mask potentially useful information about particular pairs of mating functions. We therefore present results for pairwise divergences in Appendix A and we highlight important results below.

To generalize our recommendations, we evaluated whether and how experimental strategies for characterizing two-sex dynamics should change under different scenarios of density dependence. We combined the mating functions with the generalized Beverton-Holt model of density-dependence, as in Table 1. First, we considered two alternative forms of unstructured density dependence ($b_F = b_M > 0$): saturating ($\gamma_F = \gamma_M = 1$) and overcompensatory ($\gamma_F = \gamma_M = 2$). Second, we examined the consequences of unique female and male density effects, including equal strengths ($b_F = b_M$) but sex-specific forms ($\gamma_F = 2, \gamma_M = 1$), and sex-specific strengths ($b_F > b_M$) but equal saturating ($\gamma_F = \gamma_M = 1$) and overcompensatory ($\gamma_F = \gamma_M = 2$) forms. Other parameters were held constant to provide a standard equilibrium population size; changing the equilibrium has no influence on our conclusions. Here we present results for a monogamous mating system ($h = 1$). We show results for polygyny ($h > 1$) in Appendix B and describe key differences between mating systems below. For simplicity, we did not include density dependent effects of offspring. As in our case study, we excluded the male-dominant function because it is unrealistic for most dioecious organisms. Note that unlike the simulated time series (Fig. 3) there is no “true” model in this analysis, and we consider predictions for only a single generation of recruitment, a realistic constraint for many ecological experiments.

This analysis yielded three key results. First, near an unbiased operational sex ratio ($\rho = 0.5$) predictions of

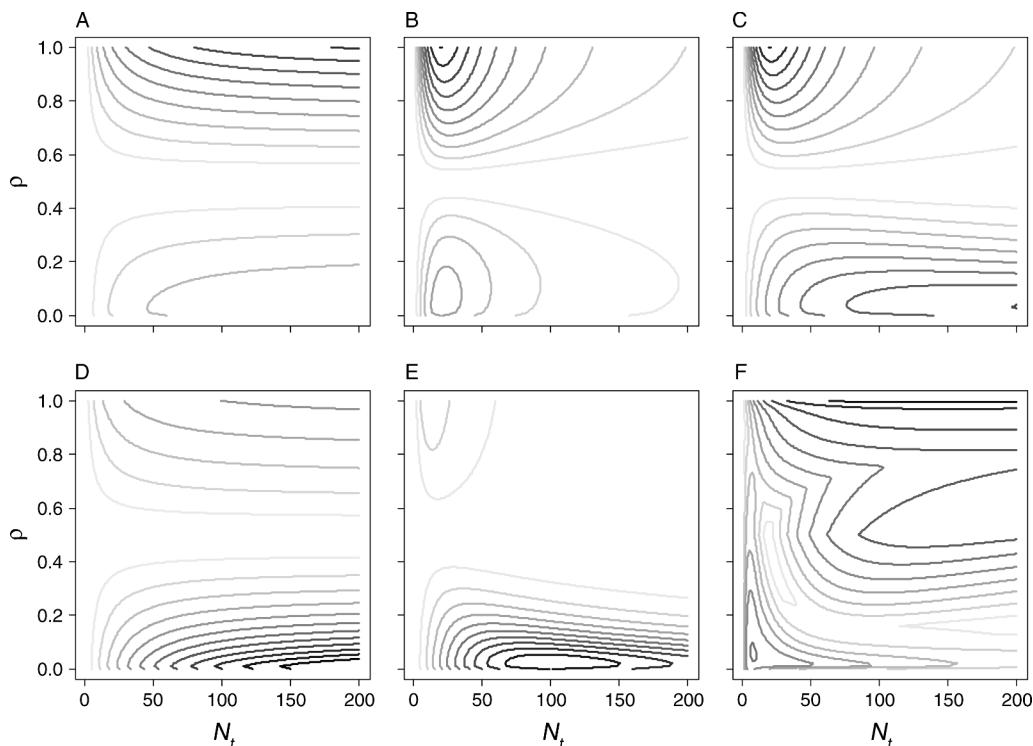


FIG. 4. Mean pairwise divergence among five alternative mating functions (Table 1) over a density (N_t)–sex ratio (ρ , proportion female) recruitment surface. Lines represent surface contours, and darker colors represent greater mean divergence. Regions of high model divergence provide the greatest potential for differentiating among candidate models using empirical data and should therefore be prioritized for experimental treatments. (A, B) Unstructured density dependence. Panels show cases where population growth is a saturating (A; $\gamma_F = \gamma_M = 1$) or humped (B; $\gamma_F = \gamma_M = 2$) function of density, with females and males contributing equally to population regulation ($b_F = b_M = 0.05$). (C–E) Sex-structured density dependence. Females and males differ in the form of density dependence (C; $\gamma_F = 2$, $\gamma_M = 1$, $b_F = b_M = 0.05$) or in the strength of density dependence ($b_F = 0.09$, $b_M = 0.01$) with saturating (D; $\gamma_F = \gamma_M = 1$) or humped (E; $\gamma_F = \gamma_M = 2$) forms. (F) Mean divergence surface based on bean beetle parameters (Table 2). The parameter b controls the per capita contribution to density dependence (greater values correspond to lower maximum recruitment), and γ describes the shape of the recruitment function. Subscript F denotes females, and M denotes males.

models with alternative mating functions are all too similar to be reliably differentiated (Fig. 4), consistent with our time series analysis (Fig. 3) and previous findings (Keyfitz 1972). Perturbations of the operational sex ratio are essential for differentiating among mating functions. When both sexes contribute equally to density dependence, female-biased perturbations ($\rho > 0.5$) are on average more informative (Fig. 4A, B). However, examination of all pairwise differences (Appendix A) indicates that the greater value of female-biased experiments is driven solely by the female-dominant function, which diverges most strongly from other models at highly female-biased sex ratios (where other mating functions predict low recruitment due to scarcity of males). Also, while stronger perturbations generally lead to greater mean divergence (Fig. 4A, B), the geometric and harmonic mean functions cannot be differentiated at sex ratios too near $\rho = 0$ and $\rho = 1$ because both predict recruitment failure at these extremes (Appendix A).

Our second result is that the form of density dependence should influence experimental strategies

for detecting the functional form of two-sex demography. Predictions of alternative mating functions diverge most when expected recruitment (N_{t+1}) is greatest. A given difference between mating functions always yields a proportional difference in population growth rate, and thus the greatest absolute recruitment difference is at the initial density that maximizes recruitment. When recruitment is a saturating function of density ($\gamma = 1$; Fig. 4A) higher initial densities differentiate more strongly among mating functions, however the information provided by greater densities asymptotes. When recruitment is a humped function of density ($\gamma > 1$; Fig. 4B), the predictions of alternative mating functions are most different at initial densities corresponding to the peak of the recruitment curve (at $N_t = 20$ in this example).

The third key result is that sex-specific contributions to density dependence, such as we found for *C. maculatus*, influence the relative value of female- vs. male-biased sex ratio perturbations and the densities at which these should be conducted (Fig. 4C–E). When the sexes differ in the form of density effect, different directions of sex ratio perturbation may be most

informative at different densities (Fig. 4C). Skew toward the sex with a saturating effect is asymptotically more informative at higher densities, whereas skew toward the sex with an over-compensatory effect is most informative at its recruitment peak. Manipulating the sex ratio by addition of the “saturating” sex may be the safer strategy, since it would be easy to miss the mark of the “over-compensatory” sex’s recruitment peak. Also, observation error may complicate model selection at low population densities. When the sexes differ in the strength of their density effects, over-representation of the more weakly regulating sex (lower b) will generally be more informative than over-representation of the more strongly regulating sex (Fig. 4D, E). This is true under both forms of density dependence for the reasons described above (greater recruitment allows for greater divergence). However, if only perturbations in favor of the more strongly regulating sex (females in Fig. 4) are possible, the optimal density for these perturbations depends upon the shape of the recruitment curve (Fig. 4D, E). While we have focused a monogamous mating system ($h = 1$), our general recommendation to prioritize the initial densities that maximize recruitment applies to non-monogamous systems as well. With all else equal, polygyny tends to increase the relative value of male-biased perturbations because two-sex functions behave similarly to the female-dominant function as harem size increases (Appendix B; see also Miller et al. 2011).

When the sexes differ in both the strength and form of density dependence, patterns of mating function divergence are difficult to distill into general guidelines, particularly when combined with non-monogamous mating systems; the information content of different regions of the surface depends upon the particular parameter combinations. To illustrate this point, we used the fitted bean beetle parameters (Table 2) to generate a divergence surface (Fig. 4F). The most informative region of the surface was strong female bias at high density, which likely reflects the saturating density effects of females and the deviation between female-dominant and two-sex functions when males are rare. The next most informative region was strong male bias at low density, which likely reflects the over-compensatory density effects of males and the greater value of male-biased treatments due to polygyny.

To test the utility of the model divergence approach, we performed a post hoc re-analysis of the bean beetle data, dividing the full data set into four subsets: greater or less than equilibrium sex ratio ($p^* = 0.5$) and greater or less than equilibrium density ($N^* = 85$). We re-fit all candidate models (Table 1) to each data subset and found that the female-biased, high-density subset was the only one to recover the “true” mating function (the one identified by the full data set) as the best fit, and the male-biased, low-density subset provided the second most support. While there is clearly an element of circularity to this reanalysis (we conducted the experiment to estimate the parameters to generate the

divergence surface to design the experiment!), the results nonetheless inspire confidence that model divergence is a useful measure of discriminatory power, and that qualitative impressions of behavior and natural history can help guide strategies for efficient experimental designs.

We have emphasized information-rich regions of the response surface that should be prioritized for experiments that focus exclusively on mating functions. However, it is also useful to include representation from other regions for more accurate estimation of density dependent population dynamic processes. Maximum-likelihood confidence intervals based on the female-biased / high-density subset for λ (24.96–27.78) and h (11.58–12.44) were in the ballpark of the full data set (Table 2), but given the much smaller range of initial densities in the data subset it is not surprising that results differed somewhat. We expect that having some representation from multiple regions of the surface will help constrain parameter values such that the “true” mating function would be more likely to be identified.

Our goal in the analysis of model divergence is not to provide field-ready experimental designs. Rather, we hope to stimulate thought and discussion about how the details of density dependence can be exploited for the sake of inference about mating functions. To this end, we provide code in the open-source software R that will generate mean divergence and pairwise divergences among mating functions across the response surface (Supplement). We suggest that experimenters use this code to identify experimental design strategies based on what is already known about their systems, and explore the consequences of variation in parameters that are unknown.

DISCUSSION

We present the first analysis of competing two-sex demographic models based on experimental perturbations of the operational sex ratio. Our results provide strong support for the harmonic mean mating function as an appropriate framework for characterizing two-sex population dynamics. Bean beetles experience maximal population growth at a strongly female-biased operational sex ratio and were expected to maintain positive growth rates at sex ratios greater than 99% female. Females clearly drive population dynamics but the superior fit of the harmonic mean function over the female-dominant function indicates that males do matter, even for a highly polygynous species. The harmonic mean mating function is widely regarded as the best (or least flawed) mating function (Caswell 2001, Bessa-Gomes et al. 2010). Our results bolster theoretical studies whose conclusions rest on the assumption that this function adequately describes the dynamics of two-sex populations (e.g., Lindstrom and Kokko 1998, Ranta et al. 1999, Miller et al. 2007). However, more studies that confront alternative two-sex models with data are needed to determine if empirical support for the

harmonic mean function is widespread. Finally, our experimental design allowed us to characterize complex density-dependent processes that were structured by both sex and life stage. The results suggest that two-sex models with sex-specific forms of density dependence may be a useful way to study the population-dynamic consequences of sexual conflict.

Another motivation for this study was to identify efficient strategies for analyses of two-sex demography in less tractable systems. We found that strong perturbations of the sex ratio (of greater magnitude than expected due to demographic stochasticity) are essential for identifying underlying contributions of both sexes to population dynamics. Lack of evidence for sex ratio effects based on time series data (e.g., Ewen et al. 2011) should be interpreted cautiously. This problem is akin to “density vagueness” (Strong 1986), where natural fluctuations around density equilibria can mask the role of density dependence in population dynamics; density manipulations are therefore required. Like the detection of density dependence, the contributions of both sexes to population dynamics may be better detected with short-term experiments (e.g., a single generation) than long-term observational data (Harrison and Cappuccino 1995).

Our results also indicate that the nature of density dependence should influence how short-term, two-sex experiments are designed. The potential for interactions between the effects of sex ratio and density, as were observed for *C. maculatus*, strongly argues for the use of response surface experimental designs (Inouye 2001). When practical constraints limit coverage of the response surface, combinations of sex ratio and density that yield the greatest number of recruits should be prioritized for experimental perturbation. If possible, two-sex demography experiments could be designed most efficiently using data from preliminary experiments that determine whether recruitment is a saturating or over-compensatory function of population density and whether the sexes differ in their density dependent effects. A priori knowledge of the strength, form, and sex specificity of density dependence would allow experimenters to weigh potential trade-offs in ability to discriminate among models against costs and logistical difficulty of manipulating population sizes, and decide whether sex ratio perturbations are best imposed by addition or removal of individuals. In cases where no preliminary data are available, natural history information may be a sufficient guide. For example, a sex that is limited by suitable nesting or oviposition space is likely to exhibit a saturating density effect, whereas a sex that engages in agonistic interactions is likely to exhibit an over-compensatory effect.

Although most mathematical models of population dynamics consider only a single sex, two-sex demography with an appropriate mating function can improve our understanding of many natural and managed populations. Due to potentially strong effects of biased

sex ratios at small population sizes, a better understanding of realistic mating functions can affect predictions about extinction risk and the importance of Allee effects (e.g., Lindstrom and Kokko 1998, Legendre et al. 1999, Bessa-Gomes et al. 2004, 2010, Lee et al. 2011) and the rate of spatial spread by invasive organisms (Miller et al. 2011). In addition to implications for managing species of conservation concern, knowing which mating functions are most appropriate can aid in management of harvested species; for example, in many ungulate populations and in some fisheries, harvesting pressures are much higher for males than females, leading to locally biased sex ratios that can affect population dynamics positively or negatively (e.g., Coleman et al. 1996, Kokko et al. 2001, Boukal et al. 2008). Finally, intentional sex ratio distortions have long been used in various attempts at insect pest control (Robinson 1983), but often without a framework that includes a well supported choice of mating functions. Studies on how to introduce transgenic constructs or symbiont-induced cytoplasmic incompatibility into insect populations can benefit from an explicit consideration of ways in which perturbed sex ratios affect population dynamics (e.g., Huang et al. 2009, Tortosa et al. 2010, Himler et al. 2011). Our recommendations for future experimental tests of mating functions will strengthen the dialogue between theory and empirical work in these diverse and important areas.

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APPENDIX A

Pairwise differences between mating functions (*Ecological Archives* E092-186-A1).

APPENDIX B

Experimental designs for non-monogamous mating systems (*Ecological Archives* E092-186-A2).

SUPPLEMENT

R code for generating model divergence surfaces (*Ecological Archives* E092-186-S1).