Sex in space: population dynamic consequences

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Sex, so important in the reproduction of bigametic species, is nonetheless often ignored in explorations of the dynamics of populations. Using a growth model of dispersal-coupled populations we can keep track of fluctuations in numbers of females and males. The sexes may differ from each other in their ability to disperse and their sensitivity to population density. As a further complication, the breeding system is either monogamous or polygamous. We use the harmonic mean birth function to account for sex-ratio-dependent population growth in a Moran–Ricker population renewal process. Incorporating the spatial dimension stabilizes the dynamics of populations with monogamy as the breeding system, but does not stabilize the population dynamics of polygamous species. Most notably, in populations coupled with dispersal, where the sexes differ in their dispersal ability there are rarely stable and equal sex ratios. Rather, a two-point cycle, four-point cycle and eventually complex behaviour of sex-ratio dynamics will emerge with increasing birth rates. Monogamy often leads to less noisy sex-ratio dynamics than polygamy. In our model, the sex-ratio dynamics of coupled populations differ from those of an isolated population system, where a stable 50:50 sex ratio is achievable with equal density-dependence costs for females and males. When sexes match in their dispersal ability, the population dynamics and sex-ratio dynamics of coupled populations collapse to those of isolated populations.

Keywords: sexual reproduction; spatially structured populations; sex ratio dynamics; bifurcation; polygamy

1. INTRODUCTION

A curious feature in population ecology is that the significance of males in affecting the dynamics of populations is largely overlooked (e.g. Royama (1992), Gotelli (1995) and Hastings (1997) for textbook examples). Also, various views exist about how males affect population dynamics. The most explicit—though often implicitly assumed—view is that any population has enough potent males to fertilize all sexually virile females. Accordingly, one has to keep track of only the dynamics of female numbers. The few studies that explicitly focus on the consequences of sexual reproduction on population dynamics inarticulately refer to the dynamics of populations in isolation (Das Gupta 1972; Schoen 1983; Dash & Cressman 1988; Caswell & Weeks 1986; Doebeli & Koella 1994; Johnson 1994; Castillo-Chavez & Huang 1995; Ruxton 1995; Doebeli 1996, 1997; Lindström & Kokko 1998).

Differing views have emerged on the significance of sex in population dynamics: (i) sex stabilizes the dynamics (Doebeli & Koella 1994; Ruxton 1995; Doebeli 1996); (ii) sex does not necessarily stabilize the dynamics (Lindström & Kokko 1998); and (iii) sex has no effect on population dynamics (Castillo-Chavez & Huang 1995). One obvious reason for these disagreeing views is the use of various approaches in different studies. Briefly, reduced propensity to complex dynamics in two-sex models has been observed in models with a

mix of different genotypes (Doebeli & Koella 1994; Ruxton 1995; Doebeli 1996); polygyny and demographic sex differences become important if the males' role in reproduction and density dependence are considered directly (Lindström & Kokko 1998). Castillo-Chavez & Huang's (1995) view originates from a comparison of analytical solutions for one- and two-sex logistic models, where pair formation is governed by the Haderler *et al.* (1988) model. There is, however, one unifying aspect in the research on the consequences of sexual reproduction on population dynamics: the focus has been on dynamics of isolated populations. This is in striking contrast with other aspects of contemporary theory on population dynamics where the domain centre has shifted to study many populations coupled by dispersal of individuals. The aim is to unravel how dispersal in spatially set populations affects the emerging population dynamics (Hassell *et al.* 1991, 1994; Bascompte & Solé 1995; Perry 1995; Ranta *et al.* 1995, 1997; Ranta & Kaitala 1997; Kaitala & Ranta 1998).

In simulations and analyses of spatial population dynamics, dispersal has been reported to either change or not change the stability properties of the local populations (e.g. Vance 1984; González-Andujar & Perry 1993; Ruxton 1993; Rohani *et al.* 1996). In nature, an important stabilizing factor may be, for example, mortality during dispersal. Furthermore, more complicated patterns arise in a spatial context, such as spatial autocorrelation and spatial synchrony (Ranta & Kaitala 1997), which may be

connected with the phenomenon referred to as spatial self-organization of population dynamics (Kaitala & Ranta 1998).

There is plenty of evidence that in many animal species, females and males differ in their dispersal rate and distances dispersed (Cockburn *et al.* 1985; Matter 1996; Alonso *et al.* 1998). Also, data exist to indicate that females and males may differ in their demography. In polygynous, sexually size-dimorphic species, males often suffer a higher mortality risk than females (Clinton & LeBoeuf 1993; Anholt 1997; Jorgenson *et al.* 1997), while in monogyny, sex differences are often less severe and more variable (Berger & Cunningham 1995; Cooch *et al.* 1996; Gaillard *et al.* 1997).

Against this background we are motivated to implement a model on sexual reproduction into a spatial context. Simply, our question is: how do spatial dynamics affect the dynamics of two-sex populations? To do this we shall make use of the Moran–Ricker type of model, used by Lindström & Kokko (1998) when studying the consequences of sexual reproduction on single-population stability. We shall assume a large number of subpopulations that are coupled via dispersing individuals. The mating system is either monogamy or polygamy. In our analyses, there are sex-correlated differences in dispersal rate and vulnerability to density-dependent population processes.

2. SPATIALLY IMPLICIT MODEL ON SEXUAL REPRODUCTION

We shall focus on sexual reproduction and sex-ratio dynamics in spatially structured populations coupled via dispersal. To track temporal changes in the two-sex population dynamics, we write

$$\begin{aligned}\tilde{X}_{F,i,t} &= (1 - m_F)X_{F,i,t} + m_F \bar{X}_{F,t}, \\ \tilde{X}_{M,i,t} &= (1 - m_M)X_{M,i,t} + m_M \bar{X}_{M,t}\end{aligned}\quad (1a)$$

and

$$X_{\bullet,i,t+1} = f_{\bullet}(\tilde{X}_{F,i,t}, \tilde{X}_{M,i,t}). \quad (1b)$$

Here $X_{F,i,t}$ is the number of female and $X_{M,i,t}$ is the number of male individuals in the i th population at time t . The symbol $\bullet$ refers either to females or males. A given sex-specific proportion $m_{\bullet}$ of individuals leave the natal population which also receives immigrants from the other populations in the system, $\bar{X}_{\bullet,t}$ is the mean density of females or males taken over all populations at time t (cf. Allen *et al.* 1993), and $\tilde{X}_{\bullet}$ is the population size after dispersal. The dependency of the number of births (B), population size and sex ratio is taken after the harmonic mean birth function (Caswell & Weeks 1986), which is modified to incorporate polygyny

$$B(X_{F,i}, X_{M,i}) = \frac{2kX_{F,i}X_{M,i}}{X_{F,i}h^{-1} + X_{M,i}}. \quad (2)$$

The total number of offspring per female is k , when $h = 1$ we have monogyny, while $h > 1$ refers to polygyny (for more details, see Caswell & Weeks 1986; Lindström & Kokko 1998). For the population renewal function $f_{\bullet}$ we shall use the Moran–Ricker dynamics

$$\begin{aligned}X_{F,i,t+1} &= 0.5B(\tilde{X}_{F,i,t}, \tilde{X}_{M,i,t})\exp[-\mu_F(\tilde{X}_{F,i,t} + \tilde{X}_{M,i,t})], \\ X_{M,i,t+1} &= 0.5B(\tilde{X}_{F,i,t}, \tilde{X}_{M,i,t})\exp[-\mu_M(\tilde{X}_{F,i,t} + \tilde{X}_{M,i,t})].\end{aligned}\quad (3)$$

In this equation, sex-specific density-dependent responses are taken care of by the parameter $\mu_{\bullet}$. In essence our population renewal process—depending on both population size and sex ratio—is the same as recently used by Lindström & Kokko (1998). The refinement comes from the coupling of several subpopulations.

With all these elements incorporated, we have parameters accounting for how density-dependent processes affect females and males, as well as how large a fraction of the focal female and male population is dispersing from their natal site, plus a parameter accounting for the mating system. Hence, the number of different parameter combinations easily becomes infinitely large. Here we have restricted ourselves to a very limited number of them. The number of female offspring k per fertilized female ranges from 1 to 40 as we wish our model to cover a range from limited breeders to (almost) explosive breeders. The parameter k serves also as the bifurcation parameter.

We assumed that only one sex disperses, $m_M = 0.2$, or that one sex disperses less than the other sex, $m_F = 0.05$, $m_M = 0.2$. By taking the parameter $h = 1$ or $h = 3$, we have either monogamy or (modest) polygamy. With these parameter combinations sex-specific density-dependent responses may be equal, $\mu_F = \mu_M = 1$. When $\mu_M = 1.2\mu_F$, the effects are stronger for the dispersing sex ($m_M = 0.2$, $m_F = 0.05$); with $m_M = 0.2$, $m_F = 0$ and $\mu_F = 1.2\mu_M$, the costs are higher for the sex not dispersing. When selecting $m_M = 0.2$, $m_F = 0.05$ and $\mu_M = 1.2\mu_F$, the density-dependent costs are higher for the sex dispersing more (with $\mu_F = 1.2\mu_M$ the situation is reversed). This all means that in total we have 12 differing parameter combinations for the coupled population system with implicit spatial structure.

Our simulations were done with a total of 100 populations. They were initiated for female numbers drawn from uniformly distributed random numbers from the interval (0.5, 2). Initial male numbers per population were set to $X_{M,i,1} = X_{F,i,1} + \epsilon_i$, where ϵ_i are the uniform random numbers from the interval (−0.05, 0.05). Thus, our populations were initiated with a slightly biased 50:50 ratio of the sexes. Our rationale here is that in nature, populations, even from places with matching resource availability, are rarely invariant in size. Also, when scoring the sex ratio in natural populations a 50:50 ratio is rarely met exactly, even in most monogamous species. Here we define sex ratio as females/(females + males). The data to be displayed were sampled by randomly selecting one population out of the 100 as the focal one. For the focal population initial values were held constant for all values of k . We let the system run for 1000 generations and displayed the next 100 generations in the bifurcation graphs.

The high number of parameter combinations explains why, at this stage of our research, we would like to limit ourselves to a spatially implicit system (Allen *et al.* 1993). Making the model spatially explicit would call for more parameters (e.g. sex-specific parameters for

dispersing distance, proportion or density dependence of individuals dispersing, and mortality during dispersal). Experimentation shows that the major features emerging (see below) in the spatially implicit model are also retained in a spatially explicit version of the current model. However, as we would like to compare how incorporating space affects the emerging population dynamics and sex-ratio dynamics, we shall compare our results with a single-population version of the sexual reproduction model (Lindström & Kokko 1998).

3. RESULTS

Our reference point is how sexual reproduction affects population dynamics and sex-ratio dynamics in a single, isolated population. The bifurcation diagrams for both monogamy and polygamy indicate that a 50:50 sex ratio emerges over the entire range of the reproductive parameter k used (figure 1). However, this presupposes that there are matching costs of density dependence for females and males. If the costs differ, sex-ratio dynamics evolve from stable dynamics via a two-point cycle to higher-order periodic dynamics to complex dynamics (figure 1). The fuzziness in sex-ratio dynamics commences with smaller values of k when the mating system is polygamy as compared to monogamy.

It is an interesting finding that in a system with dispersal-coupled populations the emerging stability of the population dynamics is largely dependent on the mating system (figures 2 and 3). In monogamous systems the population bifurcation graphs are much less noisy than with polygamy, or even in a system with an isolated population (figure 1). With polygamy in coupled populations the bifurcation graphs for population size are rather complex and the level of complexity is dependent on the dispersal process as well as on the penalties due to density-dependent reactions. For example, if both sexes disperse ($m_M = 0.2$, $m_F = 0.05$) and the penalty of density dependence is higher for the less-dispersing sex ($\mu_F = 1.2\mu_M$), a rather stable two-point population dynamics emerges for a wide range of parameter values of k (figure 3*d*(iii)). When the costs of density dependence are higher in the more dispersing sex, a far more complicated fuzziness in the population dynamics emerges (figure 3*d*(ii)).

Sex-ratio dynamics (as a function of k) very much echo the pattern of variation in population size bifurcation (figures 2 and 3). The most notable observation is that in dispersal-coupled populations there is rarely a stable and equal sex ratio if the two sexes differ in their predisposition to migrate. The coupled system often yields two-point cycles in the sex ratio, especially in monogamy, with a wide range of values of k (figure 2). In polygamy, towards larger values of k , sex-ratio dynamics assume complex chaotic fluctuations (figure 3).

Let us remember here that we have experimented with a great number of parameter value combinations. The results of those experiments, however, largely matched those reported in figures 2 and 3. Perhaps the most notable difference being that if the sexes match in their dispersal ability, the dynamics of coupled populations collapse to those of an isolated population.

Figure 1. Bifurcation diagrams of the Moran-Ricker dynamics of explicit sexual reproduction in an isolated population. Left-hand panels (i, ii) display population size variation while right-hand panels (iii, iv) give sex-ratio dynamics. Monogamous (a) and polygamous (b) breeding systems are treated separately.

4. DISCUSSION

The current results suggest that sexual reproduction, especially polygyny and demographic sex differences, provide a plausible explanation for complex population dynamics in spatially structured populations. Thus, the main result echoes the earlier conclusions by Lindström & Kokko (1998). However, as it has been argued that dispersal may also stabilize local population dynamics in a patchy population (Gonzalez-Andujar & Perry 1993), the result is not self-evident. The exact nature of dispersal as a stabilizing factor largely depends on the model details, as recently summarized by Paradis (1997). In the current study, sexual reproduction may be a more important determinant of the local dynamics than dispersal, as the general propensity of 'common pool' dispersal models (such as equation (1)) in patchy population systems is to stabilize local dynamics (Heino *et al.* 1997).

An interesting feature in the results is the difference between monogamous and polygamous mating systems. A likely explanation is the variation in the population sex

Figure 2. Bifurcation diagrams for dispersal-coupled populations with explicit sexual reproduction (Moran–Ricker renewal) and monogamy as the breeding system. Population size variation (*a, c*) and sex-ratio variation (*b, d*) are displayed against a wide range of parameter values of *k*. Sex-specific dispersal rates (m_F, m_M) are (*a, b*) $m_M = 0.2, m_F = 0$; (*c, d*) $m_M = 0.2, m_F = 0.05$. Density-dependency values (μ_F, μ_M) as used in the simulations are (i) $\mu_M = \mu_F$; (ii) $\mu_M = 1.2\mu_F$; (iii) $\mu_F = 1.2\mu_M$.

ratio induced by dispersal and the consequences of this sex-ratio variation to local population growth rate. If the number of births occurring in the population at a given time is given by the harmonic mean birth function (equation (2)), the optimal sex ratio for population growth is given by $X_F = X_M/\sqrt{h}$, where X_F and X_M refer to the number of females and males, and h is the average harem size (Caswell & Weeks 1986). In monogamy the population growth peaks at a 50:50 sex ratio. However, in a polygamous system the number of females present becomes relatively more important than the number of males for population growth. Therefore, increased male mortality or deviations from a 50:50 sex ratio influence the population growth rate less than in a monogamous mating system.

Since this is a first step in introducing sexual reproduction into the modelling of spatial population dynamics, a host of questions remain unanswered. The consequences of density-dependent versus density-independent dispersal as well as distance-dependent dispersal on population dynamics are largely unexplored. Also, as suggested by Lindström & Kokko (1998), the partly controversial results attained with models considering either population demography or phenotypic variation (Doebeli & Koella 1994; Ruxton 1995; Doebeli 1996) cannot be explained without models accounting for both aspects. This is naturally the case with spatial models as well. Finally, there remains the possibility that different dispersal strategies evolve and coexist in a spatially structured population (Holt & McPeck 1996; Doebeli & Ruxton 1997).

Figure 3. Bifurcation diagrams for dispersal-coupled populations with explicit sexual reproduction (Moran–Ricker renewal) and polygamy as the breeding system. Population size variation (*a*, *c*) and sex-ratio variation (*b*, *d*) are displayed against a wide range of parameter values of *k*. Sex-specific dispersal rates (m_F , m_M) are (*a*, *b*) $m_M = 0.2$, $m_F = 0$; (*c*, *d*) $m_M = 0.2$, $m_F = 0.05$. Density-dependency values (μ_F , μ_M) as used in the simulations are (i) $\mu_M = \mu_F$; (ii) $\mu_M = 1.2\mu_F$; (iii) $\mu_F = 1.2\mu_M$.

Population dynamic consequences of such phenomena are currently not known.

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REFERENCES

- Allen, J. C., Schaffer, W. M. & Rosko, D. 1993 Chaos reduces species extinction by amplifying local population noise. *Nature* **364**, 229–232.
- Alonso, J. C., Martin, E., Alonso, J. A. & Morales, M. B. 1998 Proximate and ultimate causes of natal dispersal in the great bustard *Otis tarda*. *Behav. Ecol.* **9**, 243–252.
- Anholt, B. R. 1997 Sexual size dimorphism and sex-specific survival in adults of the damselfly *Lestes disjunctus*. *Ecol. Entomol.* **22**, 127–132.
- Bascompte, J. & Solé, R. V. 1995 Rethinking complexity: modelling spatiotemporal dynamics in ecology. *Trends Ecol. Evol.* **10**, 361–366.
- Berger, J. & Cunningham, C. 1995 Predation, sensitivity and sex: why female black rhinoceroses outlive males. *Behav. Ecol.* **6**, 57–64.
- Castillo-Chavez, C. & Huang, W. 1995 The logistic equation revisited: the two-sex case. *Math. Biosci.* **128**, 299–316.
- Caswell, H. & Weeks, D. E. 1986 Two-sex models: chaos, extinction, and other dynamic consequences of sex. *Am. Nat.* **128**, 707–735.
- Clinton, W. L. & LeBoeuf, B. J. 1993 Sexual selection's effects on male life history and the pattern of male mortality. *Ecology* **74**, 1884–1892.

- Cockburn, A., Scott, M. P. & Scotts, D. J. 1985 Inbreeding avoidance and male-biased dispersal in *Antechinus* spp (Marsupialia: Dasyuridae). *Anim. Behav.* **33**, 908–915.
- Cooch, E. G., Lank, D. B. & Cooke, F. 1996 Intraseasonal variation in the development of sexual size dimorphism in a precocial bird: evidence from the lesser snow goose. *J. Anim. Ecol.* **65**, 439–450.
- Das Gupta, P. 1972 On two-sex models leading to stable populations. *Theor. Popul. Biol.* **3**, 358–375.
- Dash, A. T. & Cressman, R. 1988 Polygamy in human and animal species. *Math. Biosci.* **88**, 49–66.
- Doebeli, M. 1996 Quantitative genetics and population dynamics. *Evolution* **50**, 532–546.
- Doebeli, M. 1997 Genetic variation and persistence of predator–prey interactions in the Nicholson–Bailey model. *J. Theor. Biol.* **188**, 109–120.
- Doebeli, M. & Koella, J. C. 1994 Sex and population dynamics. *Proc. R. Soc. Lond. B* **257**, 17–23.
- Doebeli, M. & Ruxton, G. D. 1997 Evolution of dispersal rates in metapopulation models: branching and cyclic dynamics in phenotype space. *Evolution* **51**, 1730–1741.
- Gaillard, J.-M., Boutin, J.-M., Delorme, D., Van Laere, G., Duncan, P. & Lebreton, J.-D. 1997 Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia* **112**, 502–513.
- González-Andujar, J.-L. & Perry, J. N. 1993 The effect of dispersal between chaotic and non-chaotic populations within a metapopulation. *Oikos* **66**, 555–557.
- Gotelli, N. J. 1995 *A primer of ecology*. Sunderland, MA: Sinauer.
- Hadeler, K. P., Waldstätter, R. & Wörz-Busekros, A. 1988 Models for pair-formation in bisexual populations. *J. Math. Biol.* **26**, 635–649.
- Hassell, M. P., Comins, H. N. & May, R. M. 1991 Spatial structure and chaos in insect population dynamics. *Nature* **353**, 255–258.
- Hassell, M. P., Comins, H. N. & May, R. M. 1994 Species coexistence and self-organizing spatial dynamics. *Nature* **370**, 290–292.
- Hastings, A. 1997 *Population biology*. New York: Springer.
- Heino, M., Kaitala, V., Ranta, E. & Lindström, J. 1997 Synchronous dynamics and rates of extinction in spatially structured populations. *Proc. R. Soc. Lond. B* **264**, 481–486.
- Holt, R. M. & McPeck, M. A. 1996 Chaotic population dynamics favors the evolution of dispersal. *Am. Nat.* **148**, 709–718.
- Johnson, S. D. 1994 Sex ratio and population stability. *Oikos* **69**, 172–176.
- Jorgenson, J. T., Festa-Bianchet, M., Gaillard, J. M. & Wishart, W. D. 1997 Effects of age, sex, disease, and density on survival of bighorn sheep. *Ecology* **78**, 1019–1032.
- Kaitala, V. & Ranta, E. 1998 Traveling wave dynamics and self organization in a spatio-temporally structured population. *Ecol. Lett.* **1**, 186–192.
- Lindström, J. & Kokko, H. 1998 Sexual reproduction and population dynamics: the role of polygyny and demographic sex differences. *Proc. R. Soc. Lond. B* **265**, 483–488.
- Matter, S. F. 1996 Interpatch movement of the red milkweed beetle, *Tetraopes tetraophthalmus*—individual responses to patch size and isolation. *Oecologia* **105**, 447–453.
- Paradis, E. 1997 Metapopulations and chaos: on the stabilizing influence of dispersal. *J. Theor. Biol.* **186**, 261–266.
- Perry, D. A. 1995 Self-organizing systems across scales. *Trends Ecol. Evol.* **10**, 241–244.
- Ranta, E. & Kaitala, V. 1997 Travelling waves in vole population dynamics. *Nature* **390**, 456.
- Ranta, E., Kaitala, V., Lindström, J. & Lindén, H. 1995 Synchrony in population dynamics. *Proc. R. Soc. Lond. B* **262**, 113–118.
- Ranta, E., Kaitala, V. & Lundberg, P. 1997 Population variability in space and time: the dynamics of synchronous population fluctuations. *Science* **278**, 1621–1623.
- Rohani, P., May, R. M. & Hassell, M. P. 1996 Metapopulations and equilibrium stability: the effects of spatial structure. *J. Theor. Biol.* **181**, 97–109.
- Royama, T. 1992 *Analytical population dynamics*. London: Chapman & Hall.
- Ruxton, G. D. 1993 Linked populations can still be chaotic. *Oikos* **68**, 347–348.
- Ruxton, G. D. 1995 Population models with sexual reproduction show a reduced propensity to exhibit chaos. *J. Theor. Biol.* **175**, 595–601.
- Schoen, R. 1983 Relationships in a simple harmonic mean two-sex fertility model. *J. Math. Biol.* **18**, 201–211.
- Vance, R. R. 1984 The effect of dispersal on population stability in one-species, discrete-space population growth models. *Am. Nat.* **123**, 230–254.