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Local extinctions promote co-existence of semelparous and iteroparous life histories

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ABSTRACT

We studied the evolution of semelparity (reproducing once per lifetime) and iteroparity (reproducing repeated times in subsequent breeding seasons) using numerical simulations. In particular, we were interested in the conditions enabling long-term persistence of the two strategies in a given population system. Our general approach was to simulate a semelparous and an iteroparous population in a spatially structured system where dispersing individuals link habitable sub-units together. The local dynamics of each sub-unit was subjected to demographic stochasticity. It appears that demographic stochasticity and local extinction processes may enhance the long-term co-existence of semelparity and iteroparity. The key for co-existence of the two life histories is as follows. First, the population is set into a spatially structured context. Second, demographic stochasticity prevents local population dynamics reaching steady-state equilibria and creates strategy-specific local extinctions. These vacancies will be occupied by dispersing individuals of semelparous and iteroparous life histories. Without the joint action of these elements, the co-existence of the two life histories would become impossible.

Keywords: co-existence, Cole's paradox, iteroparity, life history, semelparity, stochasticity.

INTRODUCTION

Cole (1954) initiated research on differences in relative fitness between reproducing only once (semelparity) and several times per lifetime (iteroparity). Cole's (1954) theoretical treatment suggested that semelparous organisms should exceed the fitness level of iteroparous organisms with only a small additional effort. This expectation, under the 'Darwinian fitness maximization research programme', is contradicted by most natural species being iteroparous. This problem is known as 'Cole's paradox'.

Charnov and Schaffer (1973) made a correction for the fact that juvenile mortality is often different from adult mortality. Later, Bulmer (1985) realized that previous treatments of Cole's paradox had not considered density dependence affecting the dynamics of populations. He introduced density dependence to act on juvenile survival rate. Bulmer (1994)

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derived the inequality $b_I/b_S + P_A < 1$ (where P_A is adult survival rate and b_I and b_S are the offspring numbers for iteroparous and semelparous breeding strategies, respectively; our notation follows Ranta *et al.*, 2000b) to predict the conditions when a semelparous population cannot be invaded by an iteroparous mutant. Here, semelparity and iteroparity can show long-term co-existence, but semelparity is still a winning strategy over a rather wide part of the parameter space (as defined by v and P_A in the Bulmer inequality; but see also Ranta *et al.*, 2000a,b). Ranta *et al.* (2000b) extended the investigation of the relative fitness merits of iteroparity and semelparity into a spatially structured system. They divided the population into several semi-independent sub-populations that are linked by dispersal of individuals. In this system, the co-existence of the two life-history strategies was shown to be possible for a very broad range of parameter combinations. This co-existence is possible because spatial linkage via dispersing individuals takes the population dynamics of semelparous breeders into the range of non-stable fluctuations. Elsewhere, it has been shown that non-linear population dynamics enhance long-term persistence (over thousands of generations) of iteroparity and semelparity as life histories (Ranta *et al.*, 2000a).

With the spatially extended version of the evolution of life histories problem, we conclude that invasion by a rare mutant strategy is possible in the range defined by the Bulmer inequality. Thus, co-existence of the two life-history strategies is possible (Ranta *et al.*, 2000b). However, despite our refinement, there remain parameter combinations when only one of the two strategies is an evolutionarily stable strategy (ESS; Maynard Smith, 1982). With stable dynamics and the Bulmer inequality ($b_I/b_S + P_A < 1$) holding, a rare iteroparous mutant cannot invade a resident population of semelparous breeders when juvenile survival, P_J, is less than 0.51. When iteroparity is the resident common strategy and semelparity is the mutant invader, the criterion for non-successful invasion is slightly more complex (Fig. 1).

Ranta *et al.* (2000b) did not include any ingredients other than a spatially structured population system with dispersing individuals linking the sub-units together. Here we explore further the parameter space shown in Fig. 1 for which Ranta *et al.* (2000b) found no potential for co-existence between semelparity and iteroparity. We explore here the consequences of demographic stochasticity (e.g. Shaffer, 1981, 1987; Ginzburg *et al.*, 1982; Burgman *et al.*, 1993; Lande, 1993) on the co-existence of the two life-history strategies, semelparity and iteroparity. We follow Shaffer (1981, 1987) by accepting that stochastic demographic factors may operate via chance realizations of individual probabilities of death and reproduction in a finite (small) population. The stochasticity may arise from local external perturbations acting on births and deaths or because, for example, all mature individuals in a local unit are of the same sex. To examine the significance of demographic stochasticity on the co-existence of semelparity and iteroparity, we adopted a spatially structured system. In this setting, dispersal becomes the key element to revitalize a local unit that has gone extinct due to demographic stochasticity.

LIFE HISTORIES AND DEMOGRAPHIC STOCHASTICITY IN A SPATIALLY STRUCTURED SYSTEM

Bulmer's (1994) model for temporal dynamics of semelparous and iteroparous reproducers is as follows:

$$N_S(k+1) = P_J(N_S, N_I) b_S N_S(k) \quad (1)$$

$$N_I(k+1) = [P_J(N_S, N_I) v b_S + P_A] N_I(k) \quad (2)$$

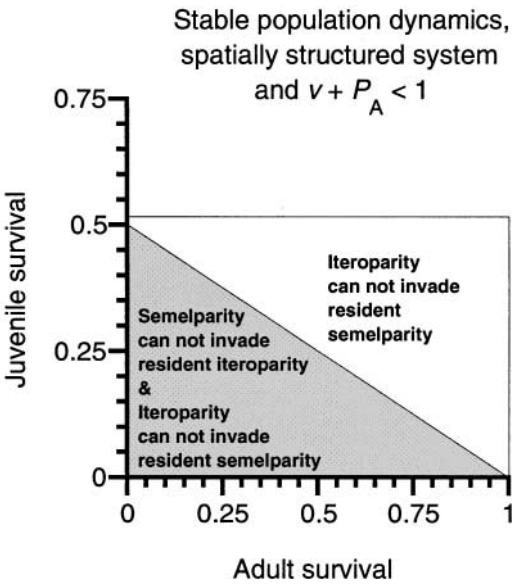

Fig. 1. Juvenile and adult survival rates that do not permit co-existence of semelparity and iteroparity in a spatially subdivided population. The search is done with stable population dynamics in the range of parameter values where the Bulmer inequality ($b_I/b_S + P_A < 1$; P_A = adult survival rate; b_I and b_S = number of offspring for iteroparous and semelparous breeding strategies respectively) is true. The white triangle delimits the area where iteroparity cannot invade a system where semelparity is resident; the shaded triangle is for the cases where a rare mutant (either semelparity or iteroparity) cannot invade a resident strategy (either iteroparity or semelparity). Simplified from Ranta *et al.* (2000b).

with

$$P_J = p_j \exp(-\alpha(b_S N_S(k) + v b_S N_I(k))) \tag{3}$$

Here, N is population size after dispersal, k is years and b_S is the number of offspring for semelparous breeders. The number of offspring produced by iteroparous breeders is $b_I = v b_S$, where $v > 0$, but often $0 < v < 1$. The proportion of offspring surviving the first year is P_J, and P_A is the adult survival rate of iteroparous breeders ($0 < P_J < 1$ and $0 < P_A < 1$, $P_J < P_A$). In this system, density dependence acts via juvenile survival (Bulmer, 1994); the term p_j is the maximum juvenile survival in the absence of competition from other juveniles. The parameter α is a scaling coefficient affecting the maximum values N can achieve (here $\alpha = 0.1$).

To incorporate spatial structure and dispersal linkage into the population renewal process, we write

$$N_{S,i}(k) = (1 - m_S)N_{S,i}(k) + \bar{m}_S \bar{N}_S(k) \tag{4}$$

$$N_{I,i}(k) = (1 - m_I)N_{I,i}(k) + \bar{m}_I \bar{N}_I(k) \tag{5}$$

where m is the strategy-specific proportion ($0 \le m \le 1$) of individuals leaving their natal patch i and N is the average strategy-specific population size taken over all i patches at time k. Thus, our spatial structure is implicit (Allen *et al.*, 1993; Heino *et al.*, 1997).

To incorporate demographic stochasticity into the population renewal process, we replace $X_{S,i}(k+1)$ and $X_{I,i}(k+1)$, where $X = \exp(N)$, by $X_{S,i}(k+1) = \text{normal}\,[X_{S,i}(k+1), \sigma]$ and $X_{I,i}(k+1) = \text{normal}\,[X_{I,i}(k+1), \sigma]$. That is, $N_{S,i}(k+1)$ and $N_{I,i}(k+1)$ are drawn from random numbers obeying a log-normal distribution with parameters $N_{S,i}(k+1)$ or $N_{I,i}(k+1)$ and σ. When $N_{S,i}(k+1) \leq 0$ or $N_{I,i}(k+1) \leq 0$, we set $N_{S,i}(k+1) = 0$ or $N_{I,i}(k+1) = 0$. This is one way to incorporate local extinctions due to demographic stochasticity. The values of σ we used ranged from 0.1 to 5.0. We shall, however, report results for $\sigma = 1.0$, as our main conclusions are not affected by the value of σ (when it is in this range). More realistic assumptions can be made in different contexts; for example, the variance could be assumed to be density dependent.

From equation (1), Bulmer (1994) derived the inequality $v + P_A < 1$, showing when invasion by semelparous breeders is not possible. For the inequality to hold, the population dynamics has to be stable (Bulmer, 1994). Equation (1) is a modification of the Ricker equation with $r = \ln(\lambda)$, where $\lambda_S = P_J b_S$ and $\lambda_I = (P_J v b_S + P_A)$. It is well known that the Ricker equation yields stable dynamics when $1 < r \leq 2$ (May, 1974, 1975, 1976). Thus, in what follows, we take $r < 2$ to remain within the range where the emerging population dynamics is stable and the Bulmer inequality holds. Ranta *et al.* (2000a) have shown that the dynamics of semelparous breeders become unstable at a lower growth rate than those of iteroparous breeders, since the fitness sensitivity of the semelparous reproductive strategy to environmental fluctuations affecting juvenile survival is higher than the sensitivity of the iteroparous reproductive strategy. Thus, we ensured that $r_S < 2$.

A list of the constraints in our analysis is as follows: $r_S < 2$ (stable dynamics), $v + P_A < 1$ (Bulmer inequality, co-existence of semelparity and iteroparity is not possible in a non-structured system), and P_J and p_j in the shaded area in Fig. 1 (co-existence not possible in a spatially structured population system). We further assume demographic stochasticity in action as described above. We use a system of 100 population sub-units in an implicit space. They were initialized with random numbers from a uniform distribution between 0 and 1 with both life-history strategies. After 10,000 generations of competition for the same resources, the co-existence of the two life histories in the system of the n sub-units was scored from the final 1000 generations. We set the dispersing fraction for semelparity and iteroparity to be equal: $m_S = m_I = 0.05$ [we experimented with a range of m (0.01–0.5); our main conclusions, however, remain the same, regardless of the value of m].

RESULTS

In general, our results can be summarized by stating that long-term persistence of the two life-history strategies is possible – given demographic stochasticity and dispersal of individuals – in a spatially structured population system. Given also the constraints (stable dynamics, Bulmer inequality holds), co-existence is possible over the entire range of adult and juvenile survival rates (Fig. 1), which did not allow co-existence without demographic stochasticity (Ranta *et al.*, 2000b). The possible ranges of feasible parameter values (juvenile survival, adult survival and offspring numbers for semelparity and iteroparity) are given in Fig. 2 (the panels in this figure are based on close to 6000 parameter combinations). Note, however, that the parameter values are not independent of each other, as might be assumed from Fig. 2, but are strictly regulated by the constraints listed above.

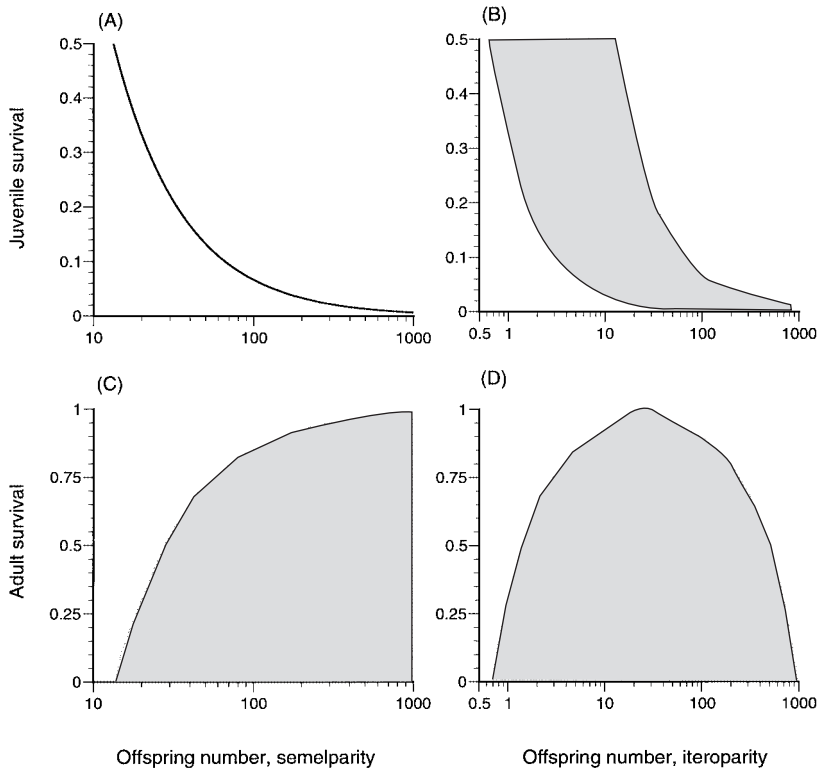

Fig. 2. Juvenile survival and adult survival rates versus number of offspring for semelparity and iteroparity. These parameter values permit long-term co-existence of semelparity and iteroparity as life histories in a spatially subdivided population. Demographic stochasticity may cause local extinctions of the two strategies but dispersing individuals, coupling the sub-units together, can rescue later on the extinct units.

To illustrate the kind of dynamics emerging for semelparity and iteroparity, we randomly selected one set of parameter value combinations from among those enabling co-existence. The dynamics of semelparity and iteroparity for these values are illustrated in Fig. 3. The key to the co-existence of the two life histories is as follows. First, the population is set into a spatially (implicit) structured context. Second, demographic stochasticity permits stable dynamics to emerge, and also creates – due to local extinctions – strategy-specific vacancies in the system. Finally, these vacancies will become eliminated via dispersing individuals of semelparity or iteroparity life histories. Without the joint action of these elements, co-existence of the two life histories would be impossible.

DISCUSSION

Demographic stochasticity – the independence of the birth and death processes within a population – has received most attention in the field of conservation biology, where the main concern is that such stochasticity can lead to extinction of small isolated populations

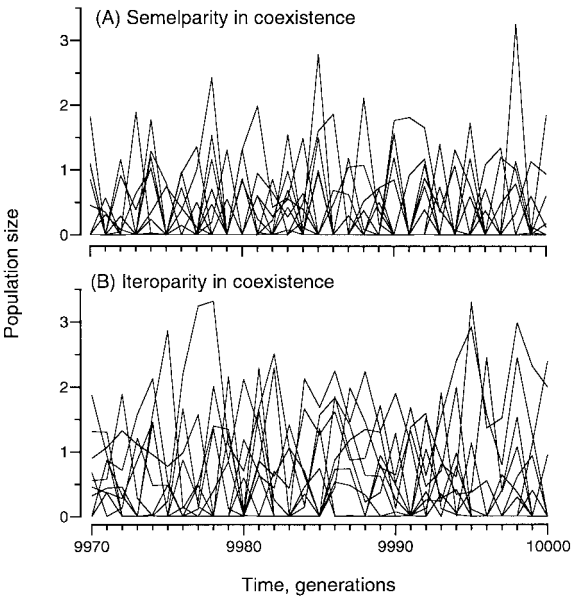

Fig. 3. An example of population dynamics of semelparous and iteroparous breeders (10 randomly selected populations for each life-history type) during the final 30 generations of their co-existence. For this example, the parameter values used ($P_A = 0.53$, $P_J = 0.083$, $b_S = 80$, $b_I = 32$) were drawn at random from the parameter space in Fig. 2 ($m = 0.05$). During the 10,000 generations simulated, local sub-units with semelparity went extinct 490,272 times; the corresponding number for iteroparity was 358,716. During the period shown, the median number of extinct semelparity sub-units was 45 time units; the corresponding figure for iteroparity was 37.

(Gabriel and Bürger, 1992; Kokko and Ebenhard, 1996). It has been concluded, therefore, that demographic stochasticity is important only in small populations. Several recent publications investigating the wider role of demographic stochasticity on the evolution of cooperation (Doebeli *et al.*, 1997), on the dynamics of host–parasitoid spatial systems (Wilson and Hassell, 1997) and on the invasibility of polyploids in plants (Rodriguez, 1996) have suggested that this conclusion should be relaxed.

The effect of demographic stochasticity on the evolution of life histories has rarely been addressed. One of the few studies to deal with this topic is that by Fox (1993). In the tradition of Cole (1954), Murphy (1968), Gadgil and Bossert (1970), Bryant (1971) and Charnov and Schaffer (1973), Fox (1993) assumed that a specific environment favours a certain life-history strategy. Fox studied a modified Cole-Charnov-Schaffer model with demographic stochasticity that assumed equal growth rate by annuals and perennials. From an analysis of variance on the dynamics of annual and perennial populations that are under demographic stochasticity, Fox concluded that only a miniscule part of the difference between the strategies is due to demographic stochasticity; the main reason for the difference in the dynamics between these two life-history strategies is the greater number of descendants of the annuals. Fox concluded that demographic stochasticity plays a minor role in shaping life-history evolution, as it does not appear to favour a specific life-history type under neutral conditions (that is, $\lambda_a = \lambda_p$).

Fox (1993) further stated that, when demographic calculations are restricted to integers, then annuals do not suffer as much from integer truncation as perennials. However, the co-existence equilibria that can be reached using integer arithmetic are unstable equilibria. Deviations from such equilibria can result in the fixation of the perennial. In addition to the deterministic model and the integer arithmetic model, Fox (1993) also considered a third, stochastic model, which assumed survival not as a rate as in the two previous models but as a probability function. The results with this model did not deviate crucially from those of the deterministic model. There is, however, an important difference: annuals occasionally get fixed in the population system. This means that, if placed into a spatial structure with moderate dispersal, Fox's stochastic model might also predict long-term persistent co-existence of annuals and perennials.

In our study of the conditions under which a semelparous population can co-exist with an iteroparous population, the problem was approached by placing the semelparous and iteroparous populations into a spatially implicit structure, linking subpopulations through dispersal. Based on the results of previous studies (Ranta *et al.*, 2000a,b), we conclude that long-term persistent co-existence between the two reproductive strategies over thousands of generations is possible when the intrinsic rate of increase exceeds a value of 2, and thus creates non-equilibrium population dynamics. We also believe that spatial structure can enable co-existence of the two reproductive strategies when both populations, if isolated, show stable dynamics. Here, we have shown that demographic stochasticity, or the resulting occasional extinctions of subpopulations, enables the two reproductive strategies to co-exist, even when spatial structure alone would not have produced long-term co-existence. The stochastic model, if mean transitions of the noise from zero are not allowed, is stable with the origin as an attractor. In the time spans studied, the stochastic systems may have arrived at a quasi-static distribution from which extinction takes extremely long times. This would be akin to a deterministic model predicting eventual exclusion but having such long transients that co-existence effectively occurs. The definition of co-existence, therefore, is dependent on the time scales studied.

Here, co-existence under demographic stochasticity was achieved in all the parameter ranges in which co-existence was not possible in a spatial setting only, indicating the importance of demographic stochasticity in the evolution of competing life-history types.

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