

# Delayed female reproduction in equilibrium and chaotic populations

VEIJO KAITALA<sup>1\*</sup>, TAPIO MAPPE<sup>2</sup> and HANNU YLÖNEN<sup>2</sup>

<sup>1</sup>*University of Helsinki, Department of Population Biology and Systematics, Box 17, FIN-00014 Helsinki, Finland and Helsinki University of Technology, Systems Analysis Laboratory, Otakaari 1, FIN-02150 Espoo, Finland*

<sup>2</sup>*Evolutionary Ecology Unit, Department of Biology and Konnevesi Research Station, University of Jyväskylä, PO Box 35, FIN-40351 Jyväskylä, Finland*

## Summary

Behavioural and life history polymorphisms are often observed in animal populations. We analyse the timing of maturation and reproduction in risky and resource-limited environments. Field and laboratory evidence suggests that female voles and mice, for example, can adjust their breeding according to the level of risk to their own survival and to survival probabilities and recruitment of young produced under different environmental conditions. Under risky or harsh conditions breeding can be postponed until later in the current breeding season or even to the next breeding season. We develop a population dynamics and life history model for polymorphism in reproduction (co-existence of breeding and non-breeding behaviours) of females in an age-structured population, with two temporally distinct mating events within the breeding season. We assume that, after overwintering, the females can breed in spring and again in summer or they can delay breeding in spring and breed in summer only. Young females born in spring can either mature and breed in summer or stay immature and postpone breeding over the winter to the next breeding season. We show that an evolutionarily stable breeding strategy is either an age-structured combination of pure breeding behaviours (old females breed and young delay maturity) or a mixed breeding behaviour within age-classes (a fraction of females breed and the rest of the age class postpones breeding). Co-occurrence of mixed reproductive behaviour in spring and summer within a single breeding season is observed in fluctuating populations only. The reproductive patterns depend on intraspecific, possibly interspecific, and ecological factors. The density dependence (e.g. social suppression) and predation risk are shown to be possible evolutionary mechanisms in adjusting the relative proportions of the different but co-existing reproductive behaviours.

*Keywords:* delayed reproduction; evolutionarily stable strategy; life history polymorphism; population dynamics; chaos

## Introduction

Life history theory assumes that reproduction is costly. In the absence of reproductive costs iteroparous animals should mature at the earliest possible age and then reproduce as often as possible (Roff, 1992). The reproductive costs are often divided into the two categories of physiological and ecological (Reznick, 1992). The physiological costs are well characterized as the trade-off in the energy allocation between growth and reproduction in animals with indeterminate growth. The ecological costs are due to external factors, such as predation risk or intra- and interspecific competition, which decrease the survival of breeding animals or their breeding success. The social dimension in the reproductive costs, that is, the possibility that breeding behaviour is partly regulated by interactions between conspecific individuals, has not

\* To whom correspondence should be addressed at: Helsinki University of Technology, Systems Analysis Laboratory, Otakaari 1, FIN-02150 Espoo, Finland.

been considered theoretically in the literature (but see Wasser and Barash, 1983; Bujalska, 1990; Ferrière and Clobert, 1992).

In many populations of microtines, breeding behaviour appears to be dimorphic such that one fraction of females breed while another fraction delays breeding. Experimental studies as well as field observations in the deer mice *Peromyscus maniculatus* (Fairbairn, 1977) and in the bank vole *Clethrionomys glareolus* (Ylönen, 1989; Nordahl, 1993; Korpimäki *et al.*, 1994; Ylönen and Ronkainen, 1994; Koskela and Ylönen, 1995) suggest that some females can suppress breeding in the middle of the breeding season or delay maturation or reproduction to the end of the breeding season or over the winter. Obviously, females attempt to adjust the timing of breeding to variation in intraspecific competition and/or predation risk, the factors that are supposed to affect the reproductive costs.

In the present paper we study the evolutionary question of delayed maturation and reproduction in an age-structured population in animals that live in a seasonal environment and that may reproduce twice within the breeding season. We develop a population dynamics and life history model to analyse the question of whether partially delayed breeding in females could be a mixed evolutionarily stable life history strategy and under which environmental conditions it could be expected. By a mixed breeding strategy we mean that one can observe two different types of breeding behaviours within the same age class. In our modelling techniques we combine behavioural options or life history traits with non-linear population dynamics models (Kaitala *et al.*, 1989, 1993; Kaitala, 1990; Kaitala and Getz, 1995). This modelling approach is an effective alternative in analysing dimorphic or polymorphic behaviours or life histories in evolutionary modelling studies.

In our study we used the simplest class of models that included delayed reproduction as a behavioural option in an age-structured population. We assume two temporally distinct mating events within a single breeding season. Furthermore, we consider an age-structured population, formed by relatively short-lived (maximally two breeding seasons and a non-breeding season in between) animals. We assume in particular that, after overwintering, the females can breed in spring and again in summer or they can delay breeding in spring and breed in summer only. Young females born in spring can either mature and reproduce in summer or stay immature and postpone breeding over the winter to the next breeding season. Our approach is restricted to females as, due to long pregnancy and lactation times, this sex should be more vulnerable in risky environments when breeding. Male maturation should only be dependent on the frequency of receptive females and on the density of conspecific old males.

Our purpose is not to develop an exact model for population dynamics of microtines in this paper (although the age structure and the mating system is conceptually close to those observed, for example, in *P. maniculatus* and *C. glareolus*). Instead, our purpose is to develop a theory to understand the possible evolutionary mechanisms that are capable of maintaining polymorphic breeding behaviour in animals. The particular mechanism that we have in mind is frequency-dependent selection, that is, the fitnesses of individuals behaving in different ways are assumed to depend on the frequencies of the behaviour chosen by the other individuals in a local population. We propose that density dependence (social suppression of maturation and breeding; see e.g. Bujalska, 1973), predation risk (e.g. selective predation towards females in breeding condition; see e.g. Cushing, 1985) and other social factors (e.g. recruitment of young produced; see Fairbairn, 1977) are possible factors that regulate frequency-dependent selection.

We next derive a general dynamic model for delayed reproduction in an age-structured population that reproduces twice during a breeding season. In the third section we analyse the evolutionarily stable (ES) breeding strategies. We first confine ourselves to an analytical equilibrium analysis. We show that when the population level remains constant, an ES breeding

strategy is either an age-structured combination of pure breeding behaviours (old females breed and young delay maturity) or a mixed breeding behaviour within age classes (a fraction of young females breed during the summer of their birth and the rest of the age class delay maturity, or a fraction of overwintered females delay breeding in spring). However, extensive population fluctuations are a rule in microtines (e.g. Henttonen, 1987; Hansson and Henttonen, 1988) and, hence, we also consider ES breeding behaviours in fluctuating populations. We show that breeding systems, including the possibility of delayed reproduction, can resist population invasion by breeding systems that lack these options. Furthermore, the breeding strategies may depend on the population density or predation pressure in a very complicated way.

### **Modelling the population dynamics and breeding behaviour**

We next develop a basic model for studying delayed reproduction in age-structured populations. In particular, we are interested in life histories that are characterized by partially delayed breeding strategies. By a partially delayed breeding strategy we mean that in a population there are two different and distinguishable reproductive behaviours within a single age class. Such a dimorphism can be observed in the timing of maturation of the young or in delayed breeding among individuals of reproductive age. For example, partially delayed maturation occurs when a fraction of individuals mature at a certain time and the other fraction of the same cohort will mature later in different environmental conditions. We first confine ourselves to an analytical analysis of deterministic equilibria of the population dynamics. We then analyse ES breeding strategies in fluctuating populations.

We consider a population of animals which reproduces seasonally twice a year. Assume that, within a year, the first offspring are produced by overwintered females in early spring and the second litter is produced later during the summer. Thus, in our model, the breeding season includes the spring and the summer of the same year. For simplicity, the two reproductive events are assumed to be non-overlapping such that there are two distinct breedings, one in spring and one in summer.

Assume that the spring-born offspring have the following options for maturation and breeding:

- (1) The offspring born in spring either mature early, breed during the year of their birth and die, or they mature late, delaying breeding to the next year.
- (2) The offspring born in summer delay breeding obligatorily to the next breeding season.

Assume further that the overwintered individuals have an option to delay breeding from spring to late summer. The overwintered individuals either breed in spring and, if still alive, later during the summer and die, or they pass breeding in spring, breed once later in summer and die. Note that the overwintered population is composed of both the spring-born individuals that have delayed maturity over the summer and the summer-born individuals.

The reproductive season is followed by an overwintering period. We assume that overwintering survival is independent of density.

In the present model we do not need to take into account the effect of the timing of maturation on overwintering survival since there are only immature individuals in the overwintering population. It would be possible to extend the model such that the spring-born females that mature early and reproduce during the summer of their birth may survive over the winter and reproduce during the following summer. This extension would not affect our main conclusions but would complicate the notation considerably.

*Breeding strategies*

Consider the individuals born during the previous season. Assume that some of the individuals choose to breed in spring and the rest of the individuals delay breeding to the summer. We define here the breeding strategy of the overwintered individuals as the fraction,  $f^1$ , of the individuals delaying breeding to the late summer.

Consider next the offspring produced during spring by the breeding fraction  $1 - f^1$ . Assume that some of the individuals who are siblings choose to mature and breed early during the same summer and the rest of the siblings delay their breeding to the next summer. Then the breeding strategy of the individuals born in spring is defined here as the fraction  $f^0$  of the offspring of an individual, i.e. siblings, delaying their maturity to the next summer.

This type of a strategy is a mixed strategy and can be interpreted as the probability that an individual chooses either the early-breeding or late-breeding behaviour. All the individuals are assumed to be phenotypically and genotypically identical. Defining the strategy as a fraction or probability of choosing between two options has the advantage that each newborn individual among the same litter has the same expected lifetime fitness.

*Breeding dynamics within a year*

We first develop a model for the dynamics of delayed reproduction within a single year (see Fig. 1). For the purposes of the subsequent analyses, we then present the dynamic version of the model (see below). We shall study the breeding strategies of females only and make a simplifying assumption that the reproductive behaviour of males does not affect the reproduction of females. Furthermore, all density-dependent effects are assumed to depend on the number of females only.

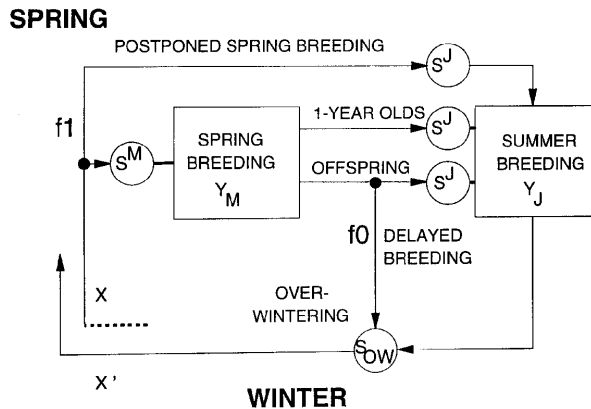


Figure 1. The dynamics of delayed reproduction within a year. The population reproduces twice a year, first in spring and then in summer. The population size of identical overwintered females prior to the breeding season is  $X$ . An overwintered female may choose to breed in spring, in which case her survival rate prior to summer breeding is  $s^M$ , and again in summer, in which case her survival rate prior to summer breeding is  $s^J$ . Alternatively, an overwintered female may pass breeding in spring and breed in summer, in which case her survival prior to summer breeding is  $s^J$ . The fraction of the females that pass breeding in spring is denoted as  $f^1$ . An offspring born in spring may either mature and breed during the summer of her birth, in which case her survival prior to summer breeding is  $s^J$  and die, or she may delay breeding, overwinter and breed during the next season once or twice. The fraction of the spring-born females that delay breeding is denoted as  $f^0$ . The overwintering survival rate is  $s_{ow}$ . The density-dependent per capita reproductive successes in spring and in summer are  $Y_M$  and  $Y_J$ , respectively. The population size after the next overwintering period is  $X'$ .

The reproductive seasons are separated from each other by overwintering or diapause periods. Let  $X$  denote the total population size of identical females after the overwintering period and let  $X^M$  and  $X^J$  denote, respectively, the total sizes of the female parent populations reproducing in spring ( $M = \text{March–May}$ ) and in summer ( $J = \text{June–July}$ ). Further, let  $x^M$  and  $x^J$  denote the sizes of the offspring populations born in spring and in summer.

We next assume that the survival of the reproductive individuals is mainly affected by predators specialized in chasing pregnant females. We assume in particular that the mortalities caused by predation occur prior to breeding. Let the survival rates of the pregnant females prior to spring and summer breedings be denoted as  $s^M$  and  $s^J$ , respectively. Note that we simplify the model here by assuming the same mortality for the 1-year-old and spring-born females. Further, we do not assume any other mortality factors in the model except winter mortality (see below).

### Spring

We further assume that fraction  $f^1$  of the overwintered individuals will delay reproduction in spring to make a terminal reproduction later in summer. Thus, the number of females passing spring breeding is

$$f^1 X \quad (1)$$

The total number of reproductive females that attempt to breed in spring includes fraction  $1 - f^1$  of the overwintered individuals. The actual breeding population in spring,  $X^M$ , is constituted of overwintered females that have chosen to breed in spring and have escaped the specialized predation. Thus, we have

$$X^M = (1 - f^1)s^M X \quad (2)$$

The total number of female offspring produced in spring is

$$x^M = X^M Y_M(X^M) \quad (3)$$

where  $Y_M(X^M)$  denotes the number of female offspring produced per female individual, when the breeding population size is  $X^M$ .

### Summer

Assume next that the female offspring born in spring either mature early and breed during the summer of their birth or delay maturation to the next reproductive season. By the definition of the maturation strategy, all new female offspring born in spring play the same strategy  $f^0$ , where  $f^0$  is the proportion of individuals that delay maturity to the next summer. Hence, a proportion  $(1 - f^0)$  of the female offspring mature and breed during the summer of their birth. The number of the spring-born females that delay maturity is

$$f^0 x^M \quad (4)$$

and the number of females that do not delay maturity is  $(1 - f^0)x^M$ .

The total number of reproductive females in summer during cycle  $k$  includes overwintered individuals (those which have reproduced once and survived the spring reproduction and those which have passed spring reproduction) and a fraction of newborn female individuals that mature early, that is

$$X^J = s^J [(1 - f^1)s^M X + f^1 X (1 - f^0) x^M] \quad (5)$$

The total number of offspring produced in summer is

$$x^J = X^J Y_J(X^J) \quad (6)$$

where  $Y_f(X^J)$  denotes the number of female offspring produced per female individual during summer breeding.

### Population dynamics model

We next present the population dynamics model which summarizes the population fluctuations in time. Assume that a constant fraction,  $s_{ow}$ , of the overwintering population survives to the following reproductive season and is alive at the beginning of the next reproductive season. Assuming the same overwintering survival for the offspring born in spring and summer, the number of overwintered females becomes

$$X^i = s_{ow} [f^0 x^M + x^J] \quad (7)$$

We finally assume that the per capita reproductive successes,  $Y_M(X^M)$  and  $Y_f(X^J)$ , are continuous and decreasing functions of the densities of the reproductive population sizes  $X^M$  and  $X^J$ , respectively. These assumptions are sufficient for deriving analytical conclusions of the properties of ES breeding strategies at an equilibrium population state.

The population dynamics under delayed breeding can be presented as a one-dimensional population model,

$$X^i = H(X; f^0, f^1)X \quad (8)$$

where the density-dependent population dynamics function  $H$  summarizes the assumptions made in Equations 2–7 and is given, after some algebra, as

$$H(X; f^0, f^1) = s_{ow} \{f^0(1 - f^1)s^M Y_M(X^M) + s^J[(1 - f^1)s^M + f^1 + (1 - f^0)(1 - f^1)s^M Y_M(X^M)]Y_f(X^J)\} \quad (9)$$

and  $X^M$  and  $X^J$  are given by Equations 2 and 5, respectively.

The population dynamics in Equations 8 and 9 represent the case in which there is only one phenotype present in the population. In order to emphasize the fact that the population dynamics depend on the behavioural options ( $f^0, f^1$ ) we have introduced them explicitly in the model notation.

### Analysis: evolutionarily stable strategies

We next turn to study the evolution of the reproductive systems in terms of the competition between different phenotypes.

The evolution of behavioural patterns and life history traits has been studied recently by applying three different measures of fitness which are assumed to be maximized by natural selection. A strategy (e.g. behaviour or life history trait) maximizing the lifetime production of offspring,  $R_0$  (Charlesworth, 1980), may also be an evolutionarily stable strategy (ESS) (Maynard Smith, 1976, 1982; for a review see Hines, 1987), whereas a behaviour maximizing the intrinsic rate of increase of a clone,  $r$ , derived from the Euler–Lotka equation of life history theory (e.g. Roff, 1992; Stearns, 1992), does not usually yield an ESS. It is commonly believed that the  $R_0$  criterion provides an ESS in density-dependent populations. Hastings (1978) specified conditions under which an ESS maximizes the age-structured population size and the density-dependent  $R_0$ . Strict results on the equivalence of the density-independent  $R_0$  criterion and ESS are available for density-dependent populations that are in equilibrium (Mylius and Diekmann, 1995). However, no general results are available for chaotic or stochastic population dynamics (but see Ellner, 1985a,b; Kaitala *et al.*, 1989; Metz *et al.*, 1992; Ferrière and Gatto, 1993; Gatto, 1993).

We next analyse delayed breeding strategies using the concept of evolutionarily stable strategies (ESSs). A particular strategy, the frequency of delayed reproduction in this case, is an

ESS if no other rare strategy can increase in the population when this particular strategy is common. Understanding evolutionary changes in populations involves an analysis of which phenotypes are the most competitive in a population dynamics sense (e.g. Getz and Kaitala, 1993; Kaitala and Getz, 1995). In this approach, two or more different non-interbreeding female phenotypes of the same species, differing only in their strategies, compete under the same environmental conditions. Thus, the strategy is an expression of the phenotype, which in our model is represented by a pair of breeding behaviours ( $f^0, f^1$ ). In other words, two different phenotypes in our model use different values for  $f^0$  and  $f^1$ .

Even though the phenotypes are non-interbreeding, they need to be ecologically linked. A way to link the phenotypes ecologically is to assume that each individual (within the same age class) uses resources and experiences the intra- and interspecific phenomena in the same way, no matter what their phenotype (or strategy) is. Thus, the linking of the phenotypes can be carried out through the frequency- or density-dependent processes of the population dynamics. Here we assume interactions between individuals can be modelled as density dependence in reproduction.

Let  $X$  and  $Z$  denote the population sizes of two different (pheno)types applying breeding strategies ( $f_X^0, f_X^1$ ) and ( $f_Z^0, f_Z^1$ ), respectively. Then, recalling Equations 8 and 9, the competition dynamics between the two types can be modelled as

$$X' = F(X + Z)X \quad (10)$$

$$Z' = G(X + Z)Z \quad (11)$$

where  $F$  and  $G$  are both defined by Equation 9 such that  $F(X + Z) = H(X + Z; f_X^0, f_X^1)$  and  $G(X + Z) = H(X + Z; f_Z^0, f_Z^1)$ . Thus, the dynamics equations for the resident and the mutant types differ in the behavioural strategies that the types apply.

Our treatment of evolutionary stability and invasion resistance follows closely that of Rand *et al.* (1994). In an ESS analysis we investigate the competition between the two types assuming that type  $X$  is common and type  $Z$  is rare. We also refer to these types as the resident and mutant types, respectively. If type  $X$  is able to resist population invasions by a given mutant type  $\hat{Z}$ , then the strategy pair ( $f_X^0, f_X^1$ ) is said to be evolutionary stable to  $\hat{Z}$ . If type  $X$  is able to resist population invasions by any other type, then the strategy pair ( $f_X^0, f_X^1$ ) is an ESS.

At a possible invasion of the population by a mutant type we need to consider the growth rate of the mutant type when the resident type  $X$  is common in the population. Let the population dynamics of the common type alone result in an infinite (stable or fluctuating) sequence of population sizes  $\{X_0, X_1, X_2, \dots\}$  denoted shortly as  $\{X_k\}_{k \geq 0}$ . We say that mutant type  $Z$  invades common type  $X$  if the mean growth rate of mutant type  $Z$  along the population sequence  $\{X_k\}_{k \geq 0}$  is positive. Technically we require that the invasion exponent of the sequence  $\{G(X_k)\}_{k \geq 0}$  is positive (Rand *et al.*, 1994). Let us denote the invasion exponent as

$$\gamma_X(Z) = \lim_{k \rightarrow \infty} \frac{1}{k} \ln \left| \prod_{i=0}^{k-1} G(X_i) \right| \quad (12)$$

Thus, type  $Z$  invades type  $X$  if

$$\gamma_X(Z) > 0 \quad (13)$$

and, alternatively, type  $X$  is resistant to invasion by type  $Z$  if

$$\gamma_X(Z) \leq 0 \quad (14)$$

Note that the invasion exponent has also been referred to in the ecological literature as the Lyapunov exponent (see e.g. Metz *et al.*, 1992).

When the resident population is at equilibrium the invasion exponent  $\gamma_X(Z)$  is equal to the logarithm of the magnitude of the eigenvalue corresponding to  $G(\bar{X})$ . In this case,  $\gamma_X(Z)$  is a continuous function of the parameters of  $G(\bar{X})$ . However, when the resident population size fluctuates, then regularity statements do not easily generalize (R. Ferrière and M. Gatto, submitted).

We begin the analysis by assuming that the population dynamics of the common type is at a population equilibrium. Below, we relax this assumption by considering fluctuating population dynamics. However, although our reference to microtines suggests the importance of analysing ESS strategies in fluctuating populations, there are two main reasons for a thorough analysis of ESS strategies in stable population dynamics. First, the ESS strategies successfully suggest some features that can be observed in dynamic ESS strategies. Second, we expect to encounter delayed maturity and breeding even in animals in which the population fluctuations are not so pronounced as they are in microtines.

### *Stable population dynamics*

Assume that the population dynamics of the common type  $X$  is at a population equilibrium, that is, the population dynamics in Equations 8 and 9 satisfy condition  $X_k = \bar{X}$  for all  $k$ , where  $\bar{X}$  is a steady state defined by the condition  $1 = F(\bar{X})$ . Assume further that the steady state  $\bar{X}$  is locally asymptotically stable such that the population remains at the steady state when no other types are present. In particular, the population dynamics in Equation 8 are locally asymptotically stable if (see e.g. Edelstein-Keshet, 1989)

$$\left| \frac{\partial F(\bar{X})}{\partial X} \bar{X} + 1 \right| \leq 1 \quad (15)$$

which is assumed to hold in all equilibrium analyses of this subsection. No general analytical solution for  $\bar{X}$  is available here for arbitrary but fixed  $f^0$  and  $f^1$ .

To study the local dynamics of the competition between the two strategies when the mutant type is rare, we approximate the dynamics of the non-linear dynamics by linearizing Equations 10 and 11 at  $(X, Z) = (\bar{X}, 0)$ . The eigenvalues of the linearized system are

$$\lambda_1 = \frac{\partial F(\bar{X})}{\partial X} \bar{X} + 1 \quad (16)$$

and

$$\lambda_2 = G(\bar{X}) \quad (17)$$

where

$$F(\bar{X}) = s_{\text{ow}} \{ [f_X^0 + s^J (1 - f_X^0) Y_J(\bar{X}^J)] (1 - f_X^1) s^M Y_M(\bar{X}^M) + s^J [(1 - f_X^1) s^M + f_X^1] Y_J(\bar{X}^J) \} \quad (18)$$

and

$$G(\bar{X}) = s_{\text{ow}} \{ [f_Z^0 + s^J (1 - f_Z^0) Y_J(\bar{X}^J)] (1 - f_Z^1) s^M Y_M(\bar{X}^M) + s^J [(1 - f_Z^1) s^M + f_Z^1] Y_J(\bar{X}^J) \} \quad (19)$$

and  $\bar{X}^M$  and  $\bar{X}^J$  are the steady state solutions corresponding to  $(f_X^0, f_X^1)$ .



We next assume that an ESS exists and turn to study the possible characterizations of ESS breeding behaviours. Our main purpose here is to show that delayed maturation or breeding may occur in non-fluctuating populations.

Recall that we have assumed in this subsection that the single-type population dynamics is locally asymptotically stable. It follows from Equation 15 that  $|\lambda_1| < 1$ . It also follows that the evolutionary stability of a fixed strategy pair  $(f_X^0, f_X^1)$ , or the local stability of the equilibrium state  $(\bar{X}, 0)$  of the competition dynamics in Equations 10 and 11, depends on the value of  $\lambda_2 = G(\bar{X})$ . In particular,  $(\bar{X}, 0)$  is locally asymptotically stable if  $|\lambda_2| < 1$ . Furthermore, a mutant type  $Z$  cannot increase in the population if  $|\lambda_2| \leq 1$  at  $\bar{X}$ . Thus, the study of ESS breeding behaviours requires an investigation of the following ESS conditions:

$$F(\bar{X}) = 1 \tag{20}$$

$$G(\bar{X}) \leq 1, \text{ for any } (f_Z^0, f_Z^1) \tag{21}$$

where  $F(\bar{X})$  and  $G(\bar{X})$  are given by Equations 18 and 19 respectively. Recall also the stability condition in Equation 15.

We may have three different types of ESS breeding systems depending on whether, at an ESS, we have  $s^j Y_j(\bar{X}^j) < 1, > 1$  or  $= 1$  (for the proofs, see Appendix 1). In particular, the possible ESS steady state breeding systems are:

$$(f_X^0, f_X^1) = \begin{cases} (1,0) & \text{and } s^j Y_j(\bar{X}^j) < 1 \\ (0, f_X^1) & \text{and } s^j Y_j(\bar{X}^j) > 1, \text{ where } f_X^1 = 1, = 0 \text{ or } 0 \leq f_X^1 \leq 1, \\ & \text{when } s^M(Y_M(\bar{X}^M) + 1) < 1, > 1 \text{ or } = 1, \text{ respectively} \\ (f_X^0, 0) & \text{and } s^j Y_j(\bar{X}^j) = 1, \text{ where } 0 \leq f_X^0 \leq 1 \end{cases} \tag{22}$$

We note immediately that the steady state breeding strategies are density dependent despite the fact that they deal with equilibrium population sizes. This observation is most important as it readily suggests that ESS breeding systems are also density dependent in fluctuating populations (see below).

In the first case,  $(f_X^0, f_X^1) = (1,0)$ , all the spring-born offspring will delay maturity to the next summer and none of the overwintered individuals will postpone breeding to the late summer. Thus, no dimorphic behaviour can be observed in this case. Note that  $s^j Y_j$  is the expected per capita reproductive success (prior to overwintering mortality) both for the spring-born individuals that do not delay maturity over the winter and for the overwintered individuals that pass breeding in spring. However, due to the low reproductive success, neither of these options occurs in this case. As a whole, the expected reproductive success of females that do not pass reproduction in spring compensates for the winter mortality. That is,

$$s^M\{Y_M(\bar{X}^M) + s^j Y_j(\bar{X}^j)\} = \frac{1}{s_{ow}}$$

In the second case,  $(0, f_X^1)$ , none of the spring-born offspring will delay maturity to the next summer because they can multiply before the overwintering period. However, mixed breeding behaviour may be observed in spring, in which case the expected per capita reproductive success of spring-breeding females (that is,  $s^M(Y_M(\bar{X}^M) + 1) s^j Y_j(\bar{X}^j)$ ) is equal to that of females that delay breeding ( $s^j Y_j(\bar{X}^j)$ ). This alternative illustrates clearly that the per capita reproductive success is measured as the number of own daughters and granddaughters entering the wintering period. Thus, the per capita reproductive success includes both the own female offspring produced in summer and the female offspring produced in summer by the own spring-born offspring. Note also that this case also includes the ‘pure’ breeding systems  $(0,0)$  and  $(0,1)$ .

In the third case,  $(f_X^0, 0)$ , no delayed breeding is observed in spring, but a fraction of the spring-born offspring will delay maturity in summer. Thus, the reproductive success in summer is now balanced such that the spring-born individuals are indifferent between early and delayed maturity. We also have  $s^M(Y_M(\bar{X}^M) + 1) = 1/s_{ow} > 1$ .

We conclude the analysis by noting that mixed behaviour (that is,  $(f_X^0, f_X^1)$ ,  $0 < f_X^i < 1$ ,  $i = 0, 1$ ) cannot occur simultaneously both in spring and in summer in steady state populations. This would imply that  $s^J Y_J(\bar{X}^J) = 1$  and  $s^M(Y_M(\bar{X}^M) + 1) = 1$ , in which case the only possible steady state would be  $\bar{X} = 0$ .

### *Fluctuating population dynamics*

We have assumed so far that the population level of the common type remains at a steady state. However, as the population fluctuations are a rule, for example, in microtines, it is of great general interest to study the evolutionary stability of the breeding systems when the populations fluctuate. In particular, we will show that delayed maturity and breeding may be superior as compared to the ‘basic’ breeding systems that lack the options of adjusting reproduction according to the changing circumstances.

The results from the steady state analyses above deal with the evolutionary stability of constant breeding strategies against constant mutant strategies. The strategies specified as constant fractions may be reasonable, for example, when reproductive conditions ahead are unpredictable such that the reproductive decisions are made when the conditions are not known (Kaitala *et al.*, 1989). However, constant strategies are not expected to remain evolutionarily stable when population levels fluctuate and when the individuals have an opportunity to obtain information, e.g. on the population density of conspecifics and on the abundance of predators. On the contrary, motivated by the observation that the steady state strategies (Equation 22) are density dependent, we expect that the evolutionarily stable strategies remain density dependent in fluctuating populations depending on the population levels as well as on other ecological factors, such as predation pressure or environmental uncertainty. Thus, we do not feel it necessary to consider constant breeding strategies in the context of fluctuating population dynamics.

Let  $X$  be an arbitrary but fixed population level. Then, we propose the following pair of strategies, in which the balancing of the reproductive successes between each option is a most important property, to be an ESS.

First, assume that  $f_X^1$  is fixed. Let  $\bar{f}_X^0$  denote a strategy that balances, when possible, the reproductive success in summer such that  $s^J Y_J(\bar{X}^J) = 1$ . That is, the spring-born individuals are indifferent between early and delayed maturity or between reproducing in summer or overwintering. We obtain the following behavioural decision rule for the spring-born females:

$$f_X^0 = \begin{cases} 0 & \text{if } s^J Y_J(\bar{X}^J) > 1 \text{ for all } f_X^0 \\ 1 & \text{if } s^J Y_J(\bar{X}^J) < 1 \text{ for all } f_X^0 \\ \bar{f}_X^0 & \text{otherwise} \end{cases} \quad (23)$$

Next, let us assume that Equation 23 is given and let us denote the reproductive success of the overwintered non-delaying type within a reproductive season as:

$$R(X) = s^M[f_X^0 Y_M(\bar{X}^M) + (1 - f_X^0) Y_M(\bar{X}^M) s^J Y_J(\bar{X}^J) + s^J Y_J(\bar{X}^J)] \quad (24)$$

Further, let  $\bar{f}_X^1$  denote a strategy that balances, when possible, the reproductive successes of the delaying and non-delaying types such that  $R(X) = s^J Y_J(\bar{X}^J)$ , where  $f_X^0$  is given by Equation 23. In this case, the overwintered individuals are indifferent between non-delayed and delayed breeding. We obtain the following behavioural decision rule for the overwintered females:

$$f_X^1 = \begin{cases} 0 & \text{if } R(X) > s^J Y_J(X^J) \text{ for all } f_X^1 \\ 1 & \text{if } R(X) < s^J Y_J(X^J) \text{ for all } f_X^1 \\ \bar{f}_X^1 & \text{otherwise} \end{cases} \quad (25)$$

The proposed evolutionary stability of Equations 23–25 is based on the following reasoning. First, under steady state conditions, the dynamic strategy pair (Equations 23–25) yields the same result as the ESS strategies (Equation 22) derived for the steady state populations above. Second, when common, the strategy pair in Equations 23–25 prevents any other mutant strategy from reaching a greater growth rate under any circumstances than that reached by applying Equations 23–25. For example, Equation 25 maximizes the growth rate of the overwintered individuals except when  $R(X) = s^J Y_J(X^J)$ . However, because in this particular case each individual is indifferent between delayed and non-delayed reproduction, no other strategy, when rare, can beat Equation 25. The same reasoning is valid for Equation 23. A strict analytical treatment of this problem is beyond the scope of this paper (see Rand *et al.*, 1994). However, we verify numerically that our ESS candidate (Equations 23–25) can resist population invasion by the most interesting alternative breeding systems (see below).

The breeding strategies or fractions in Equations 23–25 may produce very complicated reproductive patterns under fluctuating conditions. Consider next a deterministic case in which the population dynamics may show periodic or chaotic fluctuations. We assume for simplicity that the survival values in spring and in summer ( $s^M$ ,  $s^J$ ) are both constant. The per capita successes are assumed to be of the Ricker type, which are known to produce complicated population dynamics (e.g. Gatto, 1993). We have

$$Y_M(X^M + Z^M) = e^{\rho_M - \beta_M(X^M + Z^M)} \quad (26)$$

and

$$Y_J(X^J + Z^J) = e^{\rho_J - \beta_J(X^J + Z^J)} \quad (27)$$

where  $\rho^M$ ,  $\beta^M$ ,  $\rho^J$  and  $\beta^J$  are the parameters of the Ricker growth functions.

Figure 2 shows three deterministic density-dependent breeding patterns (Equations 23–25) for different but arbitrary parameter combinations. The predation pressures are identical ( $s^M = s^J = 0.5$ ) but the breeding functions in Equations 26 and 27 differ between the three cases. In Fig. 2a, the breeding functions are identical in spring and summer. No delayed breeding occurs in spring among overwintered females at low population levels, whereas at high population levels the fraction of delayed breeding increases to one-third. The frequency of delayed maturity in young females is higher both at low and high population levels. In Fig. 2b, the density-independent breeding success is lower in spring than in summer. Now, all individuals reproduce at the earliest possible occasion at low population levels. However, at high population levels, all spring-born individuals delay maturity and the fraction of delayed breeding is also high in overwintered females. In Fig. 2c, the density-independent breeding success is much lower in summer than in spring. Delayed maturity is now a rule in young females (except at extremely low population levels), whereas moderate levels of delayed breeding can be observed among the overwintered females only at high population levels.

All three cases studied in Fig. 2 produce chaotic population dynamics. This was verified by calculating numerically the Lyapunov exponents for the population dynamics (e.g. Peitgen *et al.*, 1992), which were 0.7, 0.3 and 0.5, respectively. Positive Lyapunov exponents mean that the population dynamics are sensitive to the initial condition, which is one characteristic of chaotic dynamics. Figure 3a illustrates the chaotic discrete-time population dynamics in the case of Fig.

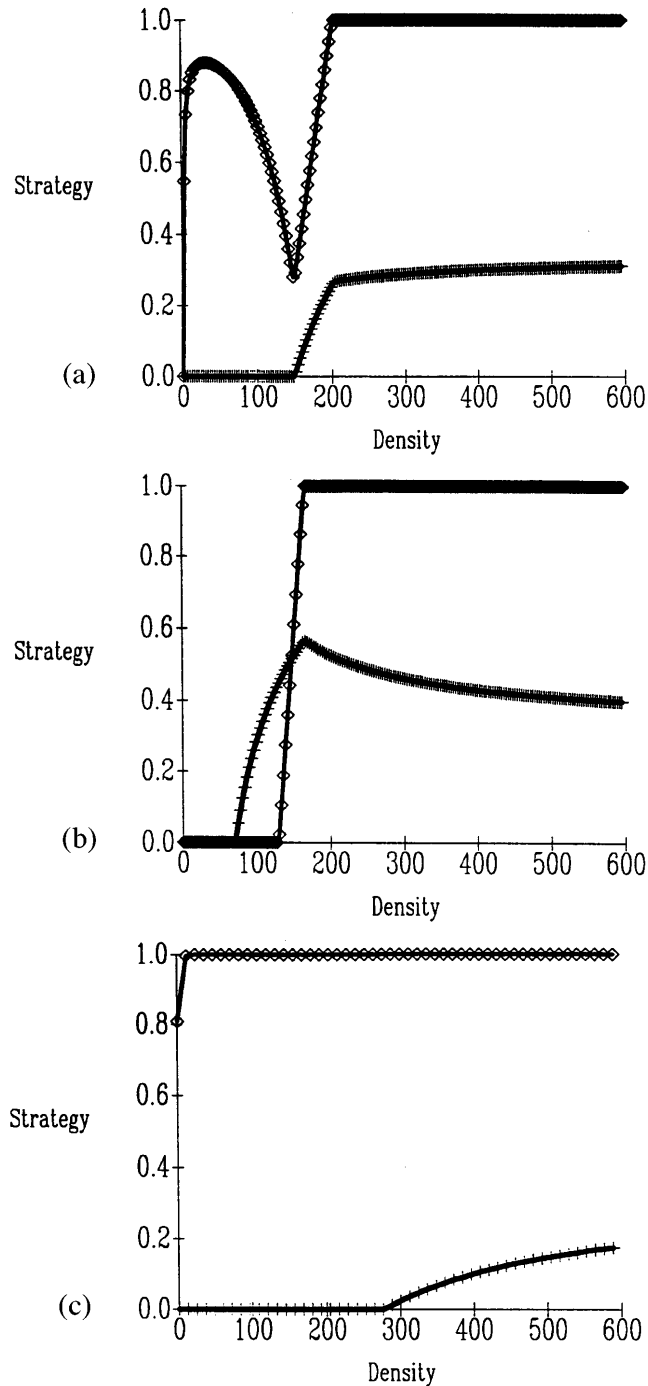


Figure 2. Density-dependent breeding patterns (Equations 23–25) for three different deterministic combinations of breeding functions: (a)  $\rho_M = 5.2$  and  $\rho_J = 5.2$ , (b)  $\rho_M = 2.5$  and  $\rho_J = 5.2$ , (c)  $\rho_M = 5.2$  and  $\rho_J = 1.0$ . The other model parameters are  $s_{\text{ow}} = s^M = s^J = 0.5$  and  $\beta_M = \beta_J = 0.07$  (see Equations 26 and 27). The strategies are given as the functions of the size (density) of the overwintered population: ( $\diamond$ )  $f_X^0$  (spring-born females), (+)  $f_X^1$  (overwintered females).

2a. As the population level fluctuates with time, then the breeding strategies fluctuate as well (see Fig. 3b) and the breeding strategies differ among the years. This is due to the fact that the breeding strategies in Equations 23–25 depend on the density of the overwintered population. Both the maturation strategy  $f_X^0$  of the spring-born females and the breeding strategy  $f_X^1$  of the overwintered females fluctuate prominently, however, such that the changes in the breeding strategies are more extreme among the spring-born females than among overwintered females.

Figure 4a illustrates a modification of the case shown in Fig. 2a. Now, the predation is assumed to be more intensive in summer ( $s^J = 0.1$ ) than in spring ( $s^M = 0.5$ ). Recall that the reproductive functions in Equations 26 and 27 are identical in this case. At low population levels ( $X < 100$ ), no delayed breeding by overwintered females is observed, whereas the frequency of delayed maturity may be high. For slightly higher population levels ( $100 < X < 150$ ), all the individuals reproduce as early as possible. As the population level increases, then delayed breeding becomes more common among the overwintered females. The increasing fractions of delayed maturity among spring-born females can be observed only at very high population levels ( $X > 400$ ).

Figure 4b illustrates an opposite modification of the case of Fig. 2a. Now the predation is more intensive in spring than in summer ( $s^M = 0.1$  and  $s^J = 0.5$ ). Moderate levels of delayed breeding

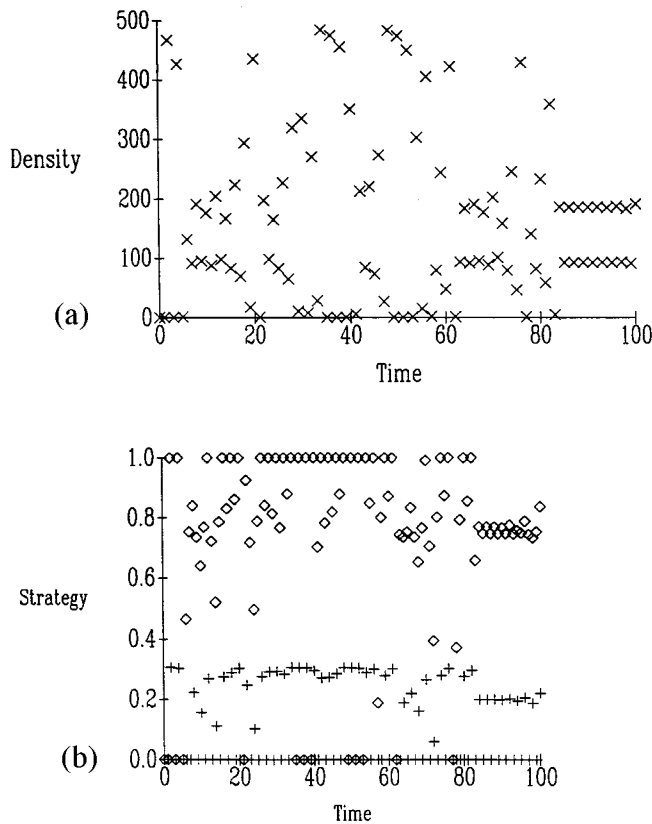


Figure 3. (a) Population density  $X$  fluctuates in time (100 generations) in the case illustrated in Fig. 2a. (b) The fluctuations in the population level  $X$  cause the breeding strategies (Equations 23–25) to fluctuate in time as well. ( $\diamond$ )  $f_X^0$  (spring-born females), (+)  $f_X^1$  (overwintered females).

among the overwintered females are observed at high population levels only, whereas delayed maturity is common among the spring-born females at all but very low population levels.

As a whole, the breeding strategies in Equations 23–25 may produce very complicated patterns that vary from year to year when the individuals adjust their breeding behaviours according to varying population densities and other environmental conditions. The breeding strategies are sensitive with respect to differences between the reproductive periods producing different breeding patterns, e.g. when strong predation occurs mainly in spring or in summer (see Figs 2 and 4). This can be the case, e.g. in our microtus example, where the predation pressure by specialized small mustelids varies between spring and summer depending on the phase of the cycle (Korpimäki *et al.*, 1991; Ylönen, 1994). The simulation results also suggest that younger

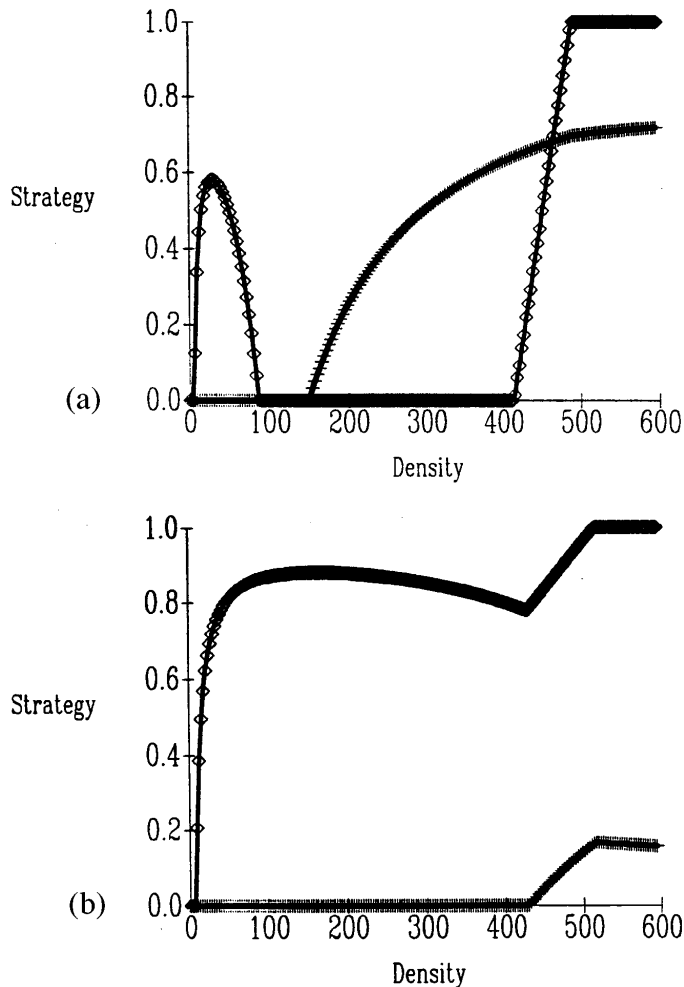


Figure 4. The breeding patterns (Equations 23–25) change as the predation parameters of Fig. 2a are changed. (a) High predation mortality in summer ( $s^M = 0.5$  and  $s^J = 0.1$ ). (b) High predation mortality in spring ( $s^M = 0.1$  and  $s^J = 0.5$ ). Other parameters are as in Fig. 2a. ( $\diamond$ )  $f_X^0$  (spring-born females), ( $+$ )  $f_X^1$  (overwintered females).

age classes are more flexible in adjusting the timing of reproduction and that the fraction of spring-born females delaying maturity tends to be higher than that of overwintered individuals delaying breeding. It is also interesting to note that, unlike in the steady state populations, temporal co-existence of partially delayed maturity and suppressed breeding can be observed from time to time. (This is observed, for example, in Fig. 2a when the population level is slightly below 200.) Finally, the results show that intraspecific factors (e.g. density and social regulation mechanisms) as well as ecological factors (predation and interspecific competition) may strongly affect the breeding and maturation patterns in the population.

No general principles or analytical results are available at the moment for proving the evolutionary stability of Equations 23–25 when the population levels fluctuate. Consequently, we need to rely on numerical simulations in checking the evolutionary stability of the strategies. It should be noted, however, that it is impossible to test the evolutionary stability against all possible density-dependent strategies. (A complete analysis of this problem is beyond the scope of this paper.) Instead, our aim is to show that delayed maturity or breeding may be evolutionarily superior as compared to the breeding systems that lack the option of adjusting the breeding behaviour according to changing conditions. Thus, the candidates of interest are the following mutant ‘pure’ breeding systems:

(1)  $(f_Z^0, f_Z^1) = (0, 0)$  – no reproductive delay at any time, the overwintered females breed in spring and their young mature early and breed during the summer of their birth.

(2)  $(f_Z^0, f_Z^1) = (1, 0)$  – no delayed breeding in spring and spring-born offspring delay maturity to the next spring.

(3)  $(f_Z^0, f_Z^1) = (f_Z^0, 1)$  – all the overwintered individuals pass breeding in spring (the reproductive behaviour of spring-born offspring is here immaterial since the mutants do not breed in spring).

The invasion exponents of these three candidate breeding systems are all strictly  $< 0$  when computed along the population trajectories of the cases studied in Fig. 2a–c:  $-0.17$ ,  $-0.25$  and  $-0.45$  for  $(f_Z^0, f_Z^1) = (0, 0)$ ,  $-0.25$ ,  $-0.85$  and  $-0.016$  for  $(f_Z^0, f_Z^1) = (1, 0)$  and  $-1.5$ ,  $-0.66$  and  $-2.8$  for  $(f_Z^0, f_Z^1) = (f_Z^0, 1)$  ( $f_Z^0$  arbitrary), respectively. An analysis of the invasion exponents in Fig. 4 further illustrates the evolutionary stability of the strategies in Equations 23–25 to the three ‘pure’ breeding systems. In both cases the attractor of the population dynamics under the behavioural decision rules (Equations 23–25) is a cycle. When  $s^M = 0.5$  and  $s^J = 0.1$  (see Fig. 4a), then the population dynamics ultimately become cyclical, oscillating between the levels 432 and 216. The corresponding invasion exponents are 0.00,  $-0.24$  and 0.00 for the mutant strategy pairs  $(0, 0)$ ,  $(1, 0)$  and  $(f_Z^0, 1)$ , respectively. When  $s^M = 0.1$  and  $s^J = 0.5$  (see Fig. 4b), then the population dynamics become cyclical, oscillating between the levels 439 and 220. The corresponding invasion exponents are 0.00, 0.00 and  $-0.69$  for the mutant strategy pairs as above. These results show that the density-dependent strategy (Equations 23–25) is evolutionary stable to these three ‘pure’ breeding systems, at least under the population dynamics studied in Figs 2 and 4.

It is worth noting that the invasion exponents for mutant strategies may be exactly zero. This occurs when both components Equations 23 and 25 of an ESS are mixed strategies along the population trajectory such that the reproductive successes between the two available options are balanced each year, or when either Equation 23 or Equation 25 is a non-mixed strategy (0 or 1) and the other component of the ESS is a mixed strategy along the population trajectory. An obvious example of the latter case is a breeding system in which an ESS, characterized by  $(f_Z^0, f_Z^1) = (f_Z^0, 0)$ ,  $0 < f_Z^0 < 1$ , results in an equilibrium population size (see Equation 22). Then the invasion exponent of the mutant strategy  $(f_Z^0, f_Z^1) = (0, 0)$  would be zero. However, the inverse result that the invasion exponent of the same ESS attempting to invade other strategies

would also be zero does not hold. To see this, consider the previous example and assume that  $(f_Z^0, f_Z^1) = (0, 0)$  is common in the population resulting in an equilibrium population dynamics. Assume further that the reproductive successes between the delayed and undelayed breeding in summer are different. Then, the ESS, being dimorphic in summer breeding but unable to balance the reproductive successes, would either be better off or worse off than the resident strategy  $(f_Z^0, f_Z^1) = (0, 0)$ . Thus, the invasion exponent of the ESS would either be positive or negative. Note also that a strictly negative invasion exponent of the ESS would mean that either the ESS is non-unique or there exists some other strategy that can invade the population occupied by the  $(0, 0)$  type. These results generalize to more complicated population dynamics.

## Conclusions

In this paper, we have studied the evolutionary question of delayed maturation and reproduction in age-structured animal populations reproducing in seasonal environments. We have traded in our study realism to generality by using the simplest population dynamics model that can show both delayed maturation and delayed breeding as behavioural options in an age-structured population. We considered a population of short-lived (maximum two breeding seasons) animals which can breed twice within a breeding season. Spring-born females can either mature early and breed in the summer of their birth or postpone breeding to the next season. The overwintered females can breed in spring and again later in summer or they can pass breeding in spring and breed only once in summer. Our aim was to develop a theoretical model to understand the evolutionary mechanisms that are capable of maintaining mixtures of these behaviours in a population.

### *Populations at equilibrium*

Our results show that three breeding patterns can be evolutionarily stable in our model under non-fluctuating conditions. First, when the expected per capita reproductive success in summer is 'poor' (the first option in Equation 22), no matter what the maturation strategy of the spring-born females is, then all of the spring-born individuals will delay maturity over next winter. Furthermore, none of the overwintered individuals will pass breeding in spring. Thus, the main breeding in this population is carried out by the overwintered females and the summer breeding is only due to the females that are carrying out their 'terminal' breeding. In this case no mixed strategies can be observed within any age class. Second, when the expected per capita reproductive success in summer is 'good' (the second option in Equation 22), no matter what the maturation strategy of the spring-born females is, then none of the spring-born individuals will delay maturity over winter. The reproductive behaviour of the overwintered individuals can range from undelayed spring breeding to a complete passing of spring breeding. In the latter case we observe a population in which breeding occurs in summer only. Note that this case also includes the alternative that a small fraction of overwintered females breed in spring prior to the main breeding season (see Fairbairn, 1977). Finally, a mixed strategy can be observed among the overwintered individuals, in which case summer breeding includes females from both age classes. Third, when the expected per capita reproductive success in summer depends of the frequencies of behaviours and stabilizes to 1 (the third option in Equation 22), a mixed maturation behaviour can be observed among the spring-born individuals. This is due to the fact that the final reproducers will reproduce in any case and the group of females that is able to balance their reproductive success is the spring-born one. This case occurs only when delayed breeding in spring is never an advantageous option for overwintered individuals. In this case all overwintered individuals breed in spring and the summer breeding is carried out by old females and by a fraction of spring-born individuals maturing early.



*Fluctuating populations*

The steady state analysis dealt with constant breeding strategies only. Because population fluctuations are common in microtines, we also raised the question of evolutionarily stable breeding and maturation under fluctuating conditions. We showed that, in fluctuating populations, breeding strategies may become dynamic depending on the population level and on other ecological factors, such as predation or environmental uncertainty. Such strategies may produce complicated reproductive patterns. For example, the reproductive patterns can vary from year to year and follow the changes in the population levels, predation and other environmental conditions in a way that is difficult, if not impossible, to derive, for example, from the estimates of population sizes and mean breeding successes. Furthermore, the reproductive patterns are sensitive with respect to differences among the breeding conditions in spring and in summer. Our results also suggest that younger age classes more commonly delay maturity than the older individuals postpone breeding.

Since the reproductive patterns strongly depend on intraspecific factors (density and social regulation mechanisms) and ecological factors (predation and interspecific competition), all empirical work on testing the predictions related to breeding behaviours need to be carefully controlled. This problem could possibly be approached by analysing the long-term data on fennoscandian microtine population fluctuations. In particular, it should be recognized that the reproductive behaviours may differ among females experiencing high conspecific population densities and females expecting or experiencing a population crash. Furthermore, the conclusion is valid with respect to predator densities as well, that is, the reproductive behaviours of females may differ at high predator densities and at post-crash low predator densities (Ylönen, 1994).

There are two key factors in our model that explain the breeding patterns observed. First, the expected per capita reproductive success in summer tells the spring-born individuals whether or not it is worth reproducing before the onset of the overwintering period. If, for example, an individual can expect to make at least one offspring of her own sex overwinter despite her own death due to reproduction, then it is worth not delaying maturity. In the opposite case it may be better to delay maturity and overwinter herself instead of 'suicidal breeding and zero survival of the young'. The second key factor is the 'final reproduction' of the overwintered individuals. Knowing the expected per capita reproductive success of the final reproduction in summer, the overwintered individuals are able to compare the relative advantages of breeding and postpone breeding in spring. For example, if the breeding conditions in spring are poor due to high predation pressure but the final reproduction can be expected to succeed, then delayed breeding can be observed. As shown above, the frequencies of different breeding behaviours can regulate the relative advantages of these behaviours.

It is interesting to note that none of the steady state ESS breeding patterns includes the case in which a mixed breeding behaviour would have been observed within each age class at the same time. Such a co-existence of partial maturation and partially delayed breeding seems to occur in microtines (Ylönen and Ronkainen, 1994; Koskela and Ylönen, 1995) and, indeed, this possibility is observed in the case of fluctuating population levels (Korpimäki *et al.*, 1994). Thus, the analysis of non-equilibrium behaviour of populations may add to the theory features that cannot be observed otherwise.

Because the breeding behaviours are density dependent, there exists a mutual interaction between the population dynamics and the breeding system: the population dynamics affect the breeding strategies and the breeding decisions affect the population dynamics. Thus, one may raise the question of whether more simple strategies, such as constant fractions of cohorts delaying breeding, would produce more simple or complicated population dynamics. The same question can be posed in a more general and meaningful evolutionary context as follows: is it possible that destabilization

of the population dynamics could be an essential part of evolutionary stability? Indeed, Gatto (1993) has shown that iteroparity (reproducing many times) may evolve as an ESS in some species only in the context of complex population dynamics. Ferrière and Gatto (1993) have also shown that individual selection may favour oscillatory or chaotic population dynamics.

It is illuminating to compare the present study with the papers by Felsenstein (1979) and Orzak and Tuljapurkar (1989). Felsenstein (1979) studied the evolution of growth rates and carrying capacities (that is,  $r$ - $K$  selection) in chaotic populations in non-fluctuating environments. The population dynamics model was characterized by two constant growth rates, one below and another above a threshold population level. It was shown that natural selection will favour cycles with more time spent above the threshold population level and will also favour an increase in the threshold. However, no behavioural or life history interpretation was given to the growth rates or carrying capacity. Orzak and Tuljapurkar (1989) studied the evolution of iteroparity in age-structured density-independent populations living in fluctuating environments. They concluded that no general reason for the evolution of iteroparity in a fluctuating environment can be specified and that the direction of evolution of reproductive schedules depends on the environmental variation and the correlation structure of the vital rates between age classes. However, the evolutionary criterion used was a stochastic density-independent growth rate and, hence, their analysis does not cover the evolution of reproductive schedules in populations where the age-specific reproductive successes are sensitive to population density, as is the case in the present study. (For broader reviews of the theories of iteroparity, see Roff (1992) and Stearns (1992).)

We have defined the breeding behaviours of the females as a mixed strategy in which a fraction of females in each age class can delay breeding. We have proposed, by using the paradigm of evolutionarily stable strategies applied in the context of population dynamics models, that the selection for this kind of breeding behaviour can be frequency dependent such that relative expected per capita reproductive successes will be balanced when co-existence of different behaviours (within an age class) can be observed. We have proposed that density dependence in ecological processes could be one mechanism through which frequency-dependent selection will be realized. Furthermore, other ecological factors, such as predation, can have an intensive effect on frequency-dependent selection. The mechanisms through which the animals can realize the balancing between the behaviours are expected to vary among the animal species. It has been suggested, for example, that social breeding or pregnancy suppression can be related to several factors in microtine populations: (1) restricted availability of exclusive home ranges or breeding territories and population density (Boonstra and Rodd, 1983; Bujalska, 1985; Kawata, 1987), (2) balance between population density and environmental capacity (Bujalska, 1985), (3) intensive social interaction among young females due to crowding (Saitoh, 1981), (4) individual quality (Teferi and Millar, 1993) or (5) recruitment of the young produced (Fairbairn, 1977). The direct effects of specialized predators on breeding suppression or delayed maturity are controversial (Ylönen, 1989; Korpimäki *et al.*, 1994; Ylönen and Ronkainen, 1994; Koskela and Ylönen, 1995). Nevertheless, our model predicts that the specialized predation pressure (see Cushing, 1985) can have an equally important effect on the breeding behaviour of small rodents and that the role of predation becomes more clear when studied in the context of the social regulation of breeding.

We finally note that neither the timing of the mortalities prior to breedings nor their assumed connection to specialized predation are crucial for the general results obtained in this paper. Mortality could have been assumed to occur, for example, during or after breedings due to physiological reasons or it could have been introduced in the form of juvenile mortality. Specialized predation was identified as the mortality factor for the sake of easy argumentation in the context of microtine population dynamics.

Any change in the assumptions will change the details and the interpretation of the population dynamics model. However, our general result, stating that partially or totally delayed breeding and maturity (within an age class) may occur in fluctuating populations due to ecological (e.g. predation) or intraspecific reasons (e.g. density or social control), will remain valid. Deterministic and stochastic modifications introducing different behavioural options, life history trade-offs or ecological relationships (e.g. fluctuating predation) will be most interesting extensions of our study.

## Acknowledgements

We appreciate the detailed comments by R. Ferrière, M. Mangel and two anonymous referees on earlier drafts. We thank O. Diekmann and S.D. Mylius for providing their manuscript prior to publication.

## References

- Boonstra, R. and Rodd, F.H. (1983) Regulation of breeding density in *Microtus pennsylvanicus*. *J. Animal Ecol.* **52**, 757–80.
- Bujalska, G. (1973) The role of spacing behaviour among females in the regulation of reproduction in the bank vole. *J. Reproduct. Fertil. Suppl.* **19**, 461–72.
- Bujalska, G. (1985) Regulation of female maturation in *Clethrionomys* species, with special reference to an island population of *C. glareolus*. *Ann. Zool. Fenn.* **22**, 331–42.
- Bujalska, G. (1990) Social system of the bank vole, *Clethrionomys glareolus*. In *Social Systems and Population Cycles in Voles* (R.H. Tamarin, R.J. Ostfeld, S.R. Push and G. Bujalska, eds), pp. 155–67. Birkhauser Verlag, Berlin.
- Charlesworth, B. (1980) *Evolution in Age-structured Populations*. Cambridge University Press, Cambridge.
- Cushing, B. (1985) Estrous mice and vulnerability to weasel predation. *Ecology* **66**, 1976–8.
- Edelstein-Keshet, L. (1989) *Mathematical Models in Biology*. Random House, New York.
- Ellner, S. (1985a) ESS germination strategies in randomly varying environments. I. Logistic-type models. *Theor. Pop. Biol.* **28**, 50–79.
- Ellner, S. (1985b) ESS germination strategies in randomly varying environments. II. Reciprocal yield-law models. *Theor. Pop. Biol.* **28**, 80–116.
- Fairbairn, D.J. (1977) Why breed early? A study of reproductive tactics in *Peromyscus*. *Can. J. Zool.* **55**, 862–71.
- Felsenstein, J. (1979) *r*- and *K*-selection in a completely chaotic population model. *Am. Nat.* **113**, 499–510.
- Ferrière, R. and Clobert, J. (1992) Evolutionary stable age at first reproduction in a density-dependent model. *J. Theor. Biol.* **157**, 253–67.
- Ferrière, R. and Gatto, M. (1993) Chaotic population dynamics can result from natural selection. *Proc. R. Soc. Lond. B* **251**, 33–8.
- Gatto, M. (1993) The evolutionary optimality of oscillatory and chaotic dynamics in simple population models. *Theor. Pop. Biol.* **43**, 310–36.
- Getz, W.M. and Kaitala, V. (1993) Ecogenetic analysis and evolutionary stable strategies in harvested populations. In *The Exploitation of Evolving Resources*. Lecture Notes in Biomathematics, Vol. 99 (T.K. Stokes, J.M. McGlade and R. Law, eds), pp. 187–203. Springer-Verlag, Berlin.
- Hansson, L. and Henttonen, H. (1988) Rodent dynamics as community process. *Trends Ecol. Evol.* **3**, 195–200.
- Hastings, A. (1978) Evolutionary stable strategies and the evolution of life history strategies: I. Density dependent models. *J. Theor. Biol.* **75**, 527–36.
- Henttonen, H. (1987) The impact of spacing behaviour in microtine rodents on the dynamics of least weasels *Mustela nivalis* – a hypothesis. *Oikos* **50**, 366–70.

- Hines, W.G.S. (1987) Evolutionary stable strategies: a review of basic theory. *Theor. Pop. Biol.* **31**, 195–272.
- Kaitala, V. (1990) Evolutionary stable migration in salmon – a simulation study of homing and straying. *Ann. Zool. Fenn.* **27**, 131–38.
- Kaitala, V. and Getz, W.M. (1995) Population dynamics and harvesting of semelparous species with phenotypic and genotypic variability in reproductive age. *J. Math. Biol.* **33**, 521–56.
- Kaitala, V., Kaitala, A. and Getz, W.M. (1989) Evolutionary stable dispersal of a waterstrider in a temporally and spatially heterogeneous environment. *Evol. Ecol.* **3**, 283–98.
- Kaitala, A., Kaitala, V. and Lundberg, P. (1993) A theory of partial migration. *Am. Nat.* **142**, 59–81.
- Kawata, M. (1987) Pregnancy failure and suppression by female–female interaction in enclosed populations of the red-backed vole, *Clethrionomys rufocanus bedfordiae*. *Behav. Ecol. Sociobiol.* **20**, 89–97.
- Korpimäki, E., Norrdahl, K. and Rinta–Jaskari, T. (1991) Response of stoats and least weasels to fluctuating food abundances: is the low phase of the vole cycle due to mustelid predation? *Oecologia* **88**, 552–61.
- Korpimäki, E., Norrdahl, K. and Valkama, J. (1994) Reproductive investment under fluctuating predation risk: microtine rodents and small mustelids. *Evol. Ecol.* **8**, 357–68.
- Koskela, E. and Ylönen, H. (1995) Suppressed breeding in the field vole (*Microtus asrestis*): an adaptation to cyclically fluctuating predation risk. *Behav. Ecol.* **6**, 311–15.
- Maynard Smith, J. (1976) Evolution and the theory of games. *Am. Sci.* **64**, 41–5.
- Maynard Smith, J. (1982) *Evolution and the Theory of Games*. Cambridge University Press, New York.
- Metz, J.A.J., Nisbet, R.M. and Geritz, S.A.H. (1992) How should we define ‘fitness’ for general ecological scenarios? *Trends Ecol. Evol.* **7**, 198–202.
- Mylius, S.D. and Diekmann, O. (1995) On evolutionary stable life histories, optimization and the need to be specific about density dependence. *Oikos* **74**, 218–24.
- Nordahl, K. (1993) Regulation of cyclic small mammal populations by avian and mammalian predation. PhD dissertation, University of Helsinki, Helsinki.
- Orzak, S.H. and Tuljapurkar, S. (1989) Population dynamics in variable environments. VII. The demography and evolution of iteroparity. *Am. Nat.* **133**, 901–23.
- Peitgen, H.-O., Jürgens, H. and Saupe, D. (1992) *Chaos and Fractals*. Springer-Verlag, New York.
- Rand, D.A., Wilson, H.B. and McGlade, J.M. (1994) Dynamics and evolution: evolutionary stable attractors, invasion exponents and phenotypic dynamics. *Phil. Trans. R. Soc. Lond. B* **343**, 261–83.
- Reznick, D. (1992) Measuring the costs of reproduction. *Trends Ecol. Evol.* **7**, 42–5.
- Roff, D.A. (1992) *The Evolution of Life Histories. Theory and Analysis*. Chapman & Hall, New York.
- Saitoh, T. (1981) Control of female maturation in high density populations of the red-backed vole, *Clethrionomys rufocanus bedfordiae*. *J. Animal Ecol.* **50**, 79–87.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Teferi, T. and Millar, J.S. (1993) Early maturation by northern *Peromyscus maniculatus*. *Can. J. Zool.* **71**, 1743–7.
- Wasser, S.K. and Barash, D.P. (1983) Reproduction suppression among female mammals: implications for biomedicine and sexual selection theory. *Q. Rev. Biol.* **58**, 513–38.
- Ylönen, H. (1989) Weasels *Mustela nivalis* suppress reproduction in cyclic bank voles *Clethrionomys glareolus*. *Oikos* **55**, 138–48.
- Ylönen, H. (1994) Vole cycles and antipredatory behavior. *Trends Ecol. Evol.* **9**, 426–30.
- Ylönen, H. and Ronkainen, H. (1994) Breeding suppression in the bank vole as antipredatory adaptation in a predictable environment. *Evol. Ecol.* **8**, 658–66.

## Appendix 1: ESSs under equilibrium population dynamics

The equilibrium ESS analyses are based on studying the necessary conditions in Equations 20 and 21.

- (1) Assume that, at an ESS, we have

$$s^j Y_j(\bar{X}^j) < 1 \quad (\text{A1})$$

We show that  $(f_X^0, f_X^1) = (1, 0)$  is an ESS.

We begin the proof by noting that  $f_X^1 = 1$  cannot be an ESS, since the population would become extinct.

We next show that  $f_X^0 = 1$  is an ESS. Let us make a counter-assumption that  $f_X^0 < 1$  is an ESS and consider a mutant strategy pair  $(f_Z^0, f_Z^1) = (1, f_X^1)$ ,  $f_X^1 < 1$ . Then Equation 21 reads

$$G(\bar{X}) = s_{ow}\{(1 - f_Z^1)s^M Y_M(\bar{X}^M)\} + s_{ow}\{s^J[(1 - f_Z^1)s^M + f_Z^1] Y_J(\bar{X}^J)\} \leq 1$$

Since  $f_Z^1 = f_X^1$ , expression  $F(\bar{X})$  (see Equation 18) differs from  $G(\bar{X})$  in that the first term of the sum above is multiplied by the factor  $f_X^0 + (1 - f_X^0)s^J Y_J(\bar{X}^J)$ . It follows that for Equation 20 to be satisfied we must have  $f_X^0 + (1 - f_X^0)s^J Y_J(\bar{X}^J) \geq 1$ . Recalling Equation A1, this is achieved only if we take  $f_X^0 = 1$ , meaning that  $f_X^0 < 1$  cannot satisfy the necessary conditions for an ESS. Thus,  $f_X^0 = 1$  must be included in an ESS.

We next show that  $f_X^1 = 0$  is an ESS. Again, let us consider a counter-assumption that  $f_X^1 > 0$  is an ESS. Now,  $f_X^0 = 1$  yields

$$F(\bar{X}) = (1 - f_X^1)s_{ow}s^M[Y_M(\bar{X}^M) + s^J Y_J(\bar{X}^J)] + f_X^1 s_{ow} s^J Y_J(\bar{X}^J) = 1 \quad (\text{A2})$$

Assume next that a mutant strategy  $(f_Z^0, f_Z^1) = (1, 0)$  attempts to invade the population where  $(1, f_X^1)$ ,  $f_X^1 > 0$ , is common. Then Equation 21 becomes

$$G(\bar{X}) = s_{ow}s^M[Y_M(\bar{X}^M) + s^J Y_J(\bar{X}^J)] \leq 1$$

Since  $s_{ow}s^J Y_J(\bar{X}^J) < 1$ , Equation A2 is a linear combination of two terms, one of which is  $\leq 1$  and the other is strictly  $< 1$ . Thus, it is necessary for Equation A2 to hold that  $f_X^1 = 0$ , which contradicts the counter-assumption. Thus, if an ESS exists such that Equation A1 holds, then  $(1, 0)$  is an ESS. Furthermore,  $s_{ow}s^M[Y_M(\bar{X}^M) + s^J Y_J(\bar{X}^J)] = 1$ .

(2) Assume that, at an ESS, we have

$$s^J Y_J(\bar{X}^J) < 1$$

Then,  $(f_X^0, f_X^1) = (0, f_X^1)$ ,  $0 \leq f_X^1 \leq 1$ , is an ESS.

Consider the counter-assumption that  $f_X^0 > 0$  is an ESS. Taking  $(f_Z^0, f_Z^1) = (0, f_X^1)$  yields ESS condition

$$G(\bar{X}) = s_{ow}\{s^J Y_J(\bar{X}^J)(1 - f_Z^1)s^M Y_M(\bar{X}^M) + s^J[(1 - f_Z^1)s^M + f_Z^1] Y_J(\bar{X}^J)\} \leq 1$$

Since  $f_Z^1 = f_X^1$ , Equation 20 can only be satisfied by choosing  $f_X^0$  such that  $f_X^0 + (1 - f_X^0)s^J Y_J(\bar{X}^J) \geq s^J Y_J(\bar{X}^J)$ . Thus,  $f_X^0 = 0$  is an ESS.

Next, assuming that  $f_X^0 = f_Z^0 = 0$  and using the same type of reasoning as above, it is possible to show that an ESS  $f_X^1 = 0$ ,  $= 1$  or  $0 \geq f_X^1 \geq 1$  if  $s^M(Y_M(\bar{X}^M) + 1) > 1$ ,  $< 1$  or  $= 1$ , respectively.

(3) Assume that, at an ESS, we have

$$s^J Y_J(\bar{X}^J) = 1$$

It follows that  $f_X^0$  does not occur explicitly in the ESS conditions. Thus we have  $0 \leq f_X^0 \leq 1$ .

The ESS condition becomes

$$F(\bar{X}) = s_{ow}\{(1 - f_X^1)s^M[Y_M(\bar{X}^M) + 1] + f_X^1\} = 1 \quad (\text{A3})$$

$$G(\bar{X}) = s_{ow}\{(1 - f_Z^1)s^M[Y_M(\bar{X}^M) + 1] + f_Z^1\} \leq 1 \quad (\text{A4})$$

From Equation A3, we have  $s^M(Y_M(\bar{X}^M) + 1) > 1$ . It follows that  $f_X^1 = 0$  is an ESS, since any  $f_Z^1 < f_X^1$  will violate Equation A4 if  $f_X^1 > 0$ .

## Appendix 2: list of symbols

### *Basic population dynamics*

Symbols are listed in the order of their appearance in the text or in equations.

$M, J$ : upper indexes denoting spring ( $M$  = March–May) and summer ( $J$  = June–July) breedings, respectively

$X$ : overwintered population size of a common type

$X'$ : overwintered population size ‘next year’ (Equation 7)

$\bar{X}$ : equilibrium population size (Equation 15)

$X^M, X^J$ : population sizes breeding in spring and summer, respectively (Equations 2 and 5)

$x^M, x^J$ : offspring population sizes born in spring and summer, respectively (Equations 3 and 6)

$f^1, f^0$ : fractions that delay breeding in spring and summer, respectively (Equations 1 and 4)

$Y_M, Y_J$ : density-dependent per capita reproductive rates in spring and summer, respectively (Equations 3 and 6)

$s^M, s^J$ : survival rates of females reproducing in spring and in summer, respectively (Equations 2 and 5)

$s_{ow}$ : overwintering survival rate (Equation 7)

$H$ : population dynamics function (Equations 8 and 9)

### *Evolutionary dynamics*

$Z$ : overwintered population size of a mutant type

$F$ : population dynamics function for common type  $X$  (Equation 10)

$G$ : population dynamics function for mutant type  $Z$  (Equation 11)

$\gamma$ : invasion exponent (Equation 12)

$k$ : time index updating the reproductive seasons or years (Equation 12)

$\lambda$ : eigenvalue variable (Equations 16 and 17)

$\bar{f}^1, \bar{f}^0$ : breeding strategies balancing reproductive successes (Equations 23 and 25)

$R$ : reproductive success within the whole reproductive season of the overwintered non-delaying type (Equations 24 and 25)

$\rho_M, \beta_M, \rho_J, \beta_J$ : parameters of the Ricker reproductive functions in spring and summer, respectively (Equations 26 and 27)