Maintenance of clonal diversity in *Dipsa bifurcata* (Fallén, 1810) (Diptera: Lonchopteridae). II. Diapause stabilizes clonal coexistence

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We analyze a selection model analogous to a one-locus, two-allele haploid system that can explain recurrent seasonal changes in diversity for communities with diapausing species or populations with diapausing clones. The model demonstrates the potential influence of differential diapause on the stability of species and clonal coexistence and, by extension, on the maintenance of genetic polymorphism in general. Using estimates of clonal fitness values from populations of the parthenogenetic spear-winged fly *Dipsa bifurcata* (Fallén, 1810) (Diptera: Lonchopteridae), the model explains the long-term stable oscillation of clonal frequencies exhibited by these populations. In general, clones or species that share the same spatial habitat can persist in stable coexistence if there are differences not only in their temporarily fluctuating fitness values but also in their dormancy patterns.
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Introduction

A major goal of population biology is to illuminate the factors that generate and maintain genetic variation within and among populations (Lewontin, 2000). Parthenogenetic species with clonal variation provide models for investigating general themes such as the dynamics of speciation, limiting similarity of coexisting species and the maintenance of genetic polymorphism. If clones originate through a polyphyletic origin from a common sexual ancestral population, then ecologically significant variability borrowed from the sexual ancestor may be frozen into clonal microspecies, which may then partition spatial or temporal environmental heterogeneity in a process that mirrors sympatric speciation (Roughgarden, 1972; Parker *et al*, 1977; Parker, 1979; Templeton, 1982; Tomiuk and Loeschcke, 1992, 1994). Alternatively, mutation may create divergence following a monophyletic origin (Suomalainen *et al*, 1987), in which case clonal diversity may be neutral to selection, at least initially. However, with time, a monophyletic lineage will accumulate genetic differences, blurring the distinction between monophyly and polyphyly in the origin of clonal diversity.

We here develop and examine a model of clonal coexistence based on temporally cyclical environmental variation and differential diapause. Our motivation for this investigation is the observation of long-term

seasonal cycles in clone frequencies observed in several populations of the spear-winged fly *Dipsa bifurcata* (Fallén, 1810) (Diptera: Lonchopteridae) (Niklasson, 1995; Niklasson *et al*, 2004). The model is formally analogous to a one-locus, two-allele haploid model and also mimics a situation of two closely related competing species.

In general, single-locus population genetic models have shown limited sets of preconditions for the stable maintenance of polymorphisms due to opposing selection (Prout, 2000). In temporally fluctuating (or, more precisely cylical) environments (reviewed by Hedrick *et al*, 1976; Hedrick, 1986), single-locus stability requires both symmetrical fitnesses and strong selection (Dempster, 1955; Haldane and Jayakar, 1963) or almost complete negative autocorrelation between successive environments (Hedrick, 1974, 1976). Part of the difficulty is that most of these early genetic models assume the same life cycles for all genotypes and only allow for: (1) infinite versus finite population sizes, (2) varying fitnesses and dominance relationships for alleles/genotypes in alternative environments, usually symmetrical for mathematical convenience, and (3) specification of a pattern of changing environments (as a serial autocorrelation, for example). It is perhaps not surprising that polymorphic stability requires either a set of fitnesses or a set of environments that precisely balance each other over the long term, since the different genotypes basically must perform the same way in both environments. Thus, the seemingly improbable stability of polymorphisms in the face of temporal variation may be an artifact of the simplicity of the models. For example, in a classic series of papers, Istock and co-workers (reviewed in Istock, 1978) showed that

facultative summer diapause of some phenotypes of the pitcher plant mosquito *Wyeomyia smithii* (Cocquillett) (Diptera: Culicidae) could explain the maintenance of quantitative genetic variability for development time in natural populations, by providing an 'escape' from selection for slow developing larvae, while the unpredictability of early frosts ensured that the fast developing phenotypes could not fix in the population. Hedrick (1995) added dormancy (or diapause) in his extension of the classic temporal model (Dempster, 1955; Haldane and Jayakar, 1963; Hedrick, 1974, 1976) and showed that stable polymorphism can be maintained for expanded ranges in which parameters can vary.

Ecological models have also shown a potentially important role of dormancy and diapause in maintaining coexistence of competing phenotypes or species. Tuljapurkar and Istock (1993) modeled variation in diapause and its effect on population persistence in a stage (or age) structured populations with randomly varying environments. These authors showed that in harsh environments, diapause can maintain population persistence and that an increase in negative serial autocorrelation between benign and harsh environments leads to an increase in the optimal diapause fraction in a population. Hairston *et al* (1996) analyzed mechanisms maintaining biodiversity and focused on the importance of the storage effect (Chesson, 1983), whereby multiple species can be maintained if an environment fluctuates temporally among alternative life history stages and different species have their greatest recruitment under the different environmental conditions (see also Chesson and Warner, 1981).

We here use a similar approach to Tuljapurkar and Istock's (1993) and Hedrick's (1995) models in which different lineages or phenotypes not only have alternating relative fitnesses in two alternating environments but also have differential diapause tendencies. In this paper, we focus on a special case of the general model that can be analyzed in detail, for example, two competing clones and both clones can diapause during the same season. The model is robust against variation in clonal fitnesses and shows that diapause can be important in maintaining clonal diversity in parthenogenetic species.

Using the estimates of the clonal fitness values from the companion paper (Niklasson *et al*, 2004), the model explains the stable oscillation of clonal frequencies over several years in four natural populations of the fly *D. bifurcata*. The model can be applied to various other life cycle strategies and can explain, in general, the coexistence of genotypes (or species), which share the same habitat but that have differences in their temporally fluctuating fitness values.

The model

The model is formally analogous to a one-locus, two-allele deterministic haploid model with two alternating environments. A parthenogenetically reproducing population consists of two clonal lineages A and B with frequencies p_t and q_t in generation t. There are two nonoverlapping generations per year, which each experiences a different environment E_1 and E_2, respectively. The progeny in environment E_1 either diapauses for one season or enters immediately into the next generation in environment E_2 (Figure 1). Each clone has
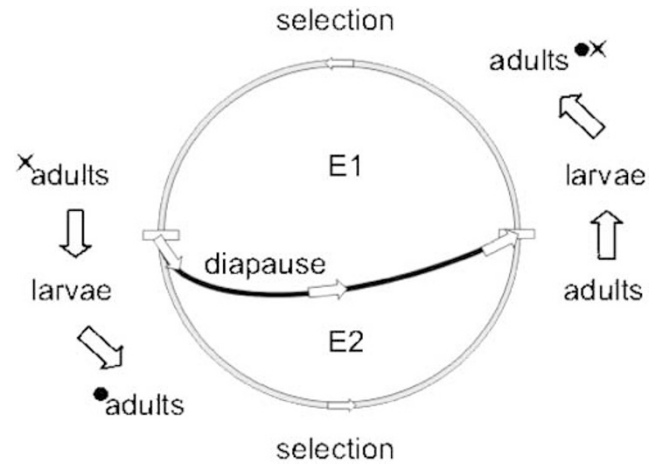

Figure 1 Schematized lifecyclce of an insect passing two environments E_1 and E_2 during two seasons. In each season, selection acts on the population. Individuals can pass environment E_2 through diapausing. Black dots mark the beginning of seasons (ie generations), the crosses indicate the beginning (spring, before selection) and the end of environment E_1 (autumn, after selection and before diapausing).

the potential for diapausing with diapause rates d^A and d^B. The fitness values of clones A and B in generation t are w_t^A and w_t^B, respectively.

In environment E_1 and generation t, clones A and B (comprising diapausing and nondiapausing individuals) have been selected with w_t^A and w_t^B, respectively. In generation $t+1$, the frequency of nondiapausing individuals of clone A is proportional to

$$\tilde{p}_{t+1} = w_t^A(1-d^A)p_t \tag{1}$$

and correspondingly for nondiapausing individuals of clone B

$$\tilde{q}_{t+1} = w_t^B(1-d^B)q_t \tag{2}$$

The normalization gives the new frequencies p_{t+1} and q_{t+1} of clones A and B, respectively, in generation $t+1$

$$p_{t+1} = \tilde{p}_{t+1}/(\tilde{p}_{t+1} + \tilde{q}_{t+1})$$

and

$$\tag{3}$$

$$q_{t+1} = 1 - p_{t+1}$$

In environment E_2 and generation $t+1$, nondiapausing individuals of clones A and B experience selection with w_{t+1}^A and w_{t+1}^B, respectively. Now $d^A p_t$ and $d^B q_t$ are the proportions of diapausing individuals of clones A and B, respectively, which add to the fractions of nondiapausing individuals $w_{t+1}^A p_{t+1}$ and $w_{t+1}^B q_{t+1}$ in generation $t+2$. For clone A in generation $t+2$, we have

$$\tilde{p}_{t+2} = w_{t+1}^A p_{t+1} + d^A p_t \tag{4}$$

and correspondingly for clone B

$$\tilde{q}_{t+2} = w_{t+1}^B q_{t+1} + d^B q_{t+1} \tag{5}$$

Again normalization gives the frequencies p_{t+2} and q_{t+2} of clones A and B, respectively, in generation $t+2$

$$p_{t+2} = \tilde{p}_{t+2}/(\tilde{p}_{t+2} + \tilde{q}_{t+2}) \text{ and } q_{t+2} = 1 - p_{t+2} \tag{6}$$

For a given set of initial values, that is, the fitness values, the diapause rates and the clone frequencies, the discrete

solutions of the model are calculated by a C-program. The stability of solutions is examined by using random variation of initial values. The diapause rates and the fitness values can vary uniformly within a given range around their mean values. For some special cases analytical solutions are given.

Results

Analytical conclusions

Clones A and B are assumed to experience different selection regimes with the alternating sequence of *121212...* We consider the properties of the model for the special case where each clone has a selective advantage in one of the two environments, that is, clone A has a relative selective disadvantage $0 \leqslant w^A \leqslant 1$ in environment E_1 but an advantage in environment E_2, and *vice versa* for clone B. The initial frequencies of clone A are p_0 and p_1, respectively, and for generation $t > 1$ we have

$$\tilde{p}_{t+1} = (1 - d^A)w^A p_t, \quad \tilde{q}_{t+1} = (1 - d^B)q_t$$

and

$$\tilde{p}_{t+2} = p_{t+1} + d^A p_t, \quad \tilde{q}_{t+2} = w^B q_{t+1} + d^B q_t \qquad (7)$$

If the two clones coexist permanently, there will be equilibrium frequencies at the beginning of seasons E_1 and E_2, which can be represented by p_{E_1} and p_{E_2}, respectively. Setting $p_t = p_{t+2}$, we obtain the equilibrium frequencies

$$p_{E_1} = \frac{(1 - d^B)(d^B - d^A) - w^A(1 - d^A) + w^B(1 - d^B)}{(d^B - d^A)[1 - d^B - w^A(1 - d^A)]}$$

$$q_{E_1} = 1 - p_{E_1}$$

and $\qquad (8)$

$$p_{E_2} = \frac{w^B p_{E_1} - (d^A - d^B)p_{E_1} q_{E_1}}{1 - (1 - w^B)p_{E_1}}$$

$$q_{E_2} = 1 - p_{E_2}$$

Rearranging the inequalities $0 < p_{E_1} < 1$ and $0 < p_{E_2} < 1$, we obtain a combination of fitness values, w^A and w^B, and diapause rates, d^A and d^B, which results in clonal coexistence. The parameter set defines an area with boundaries $w^B(1 - d^B)/(1 - d^A)(1 - d^B + d^A)$ and $(w^B + d^B - d^A)(1 - d^B)/1 - d^A$ (see Figure 2).

Simulations

In the following, we analyzed the behavior of the solutions with computer simulations. The combinations of the fitness values, w^A and w^B, and the diapause rate, d^A and d^B, which resulted in clonal coexistence were given in Figure 2. Stable clonal coexistence was found for a parameter set that gave the dotted area. The bound functions also determined the black area where unstable clonal coexistence occurred. Using parameter sets allowing for clonal coexistence, clonal frequencies rapidly converged to an oscillating equilibrium state (Figure 2) that did not depend on initial clonal frequencies p_0 and p_1. Varying the initial values, p_0 and p_1, in the simulations, clonal frequencies converged to the same cyclic patterns (Figure 3).

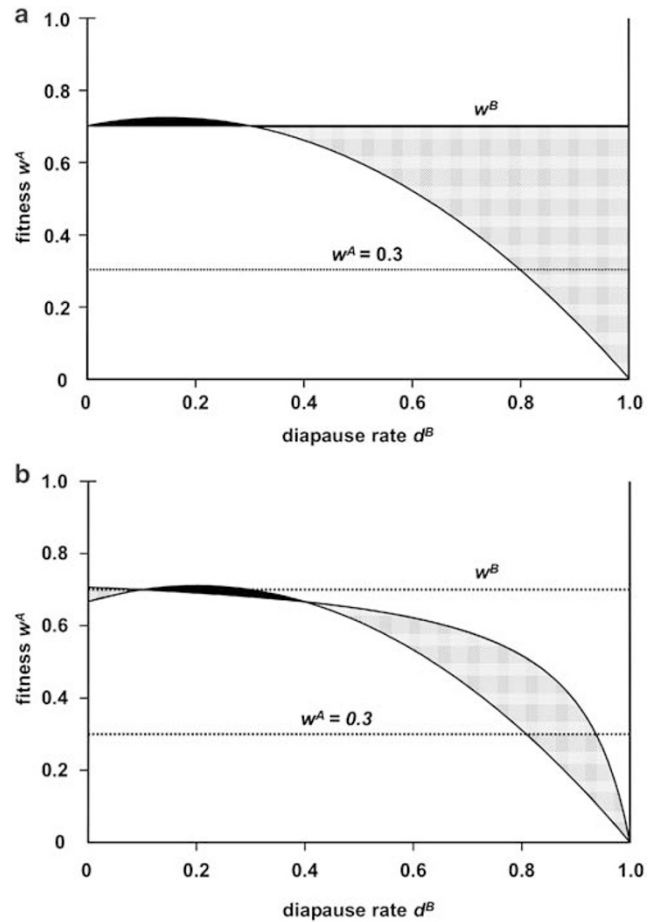Figure 4 shows the strong effect of diapause on clonal coexistence. Increasing the diapause rate of

Figure 2 Stable coexistence is found for parameter sets in the dotted area and unstable equilibria exist for parameter sets defined by the black area. Fitness values w^A and w^B and diapause rate d^B for which clones can coexist where (**a**) $d^A = 0$ and (**b**) $d^A = 0.1$.
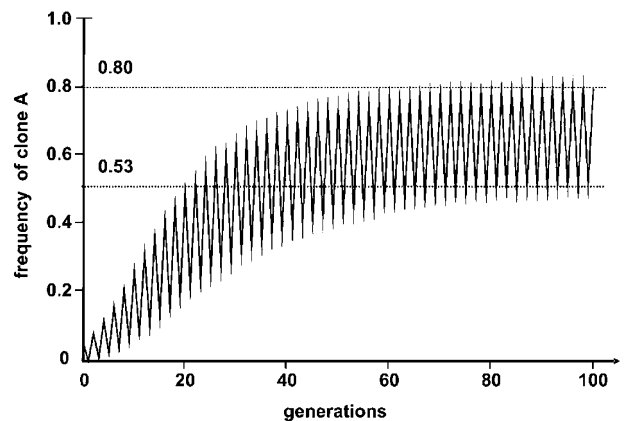

Figure 3 Seasonal changes of frequencies of clone A using initial frequencies $p_0 = p_1 = 0.1$. Parameters are $w^A = 0.3$, $w^B = 0.7$, $d^A = 0.1$ and $d^B = 0.88$. The dashed lines give the upper and lower bounds of equilibrium values.

clone A from zero to 0.1 reduced considerably the range of coexistence (Figure 4a and b). Furthermore, temporal variation of diapause rates decreased clonal
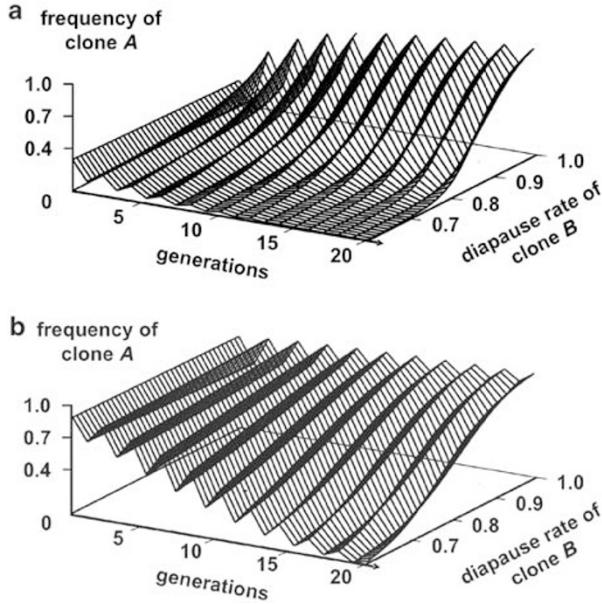
Figure 4 Frequency of clone A where $w^A = 0.3$, $w^B = 0.7$, $d^A = 0.1$ and $0.6 \leqslant d^B \leqslant 1.0$. Initial frequencies are: (**a**) $p_0 = p_1 = 0.1$ and (**b**) $p_0 = p_1 = 0.9$.
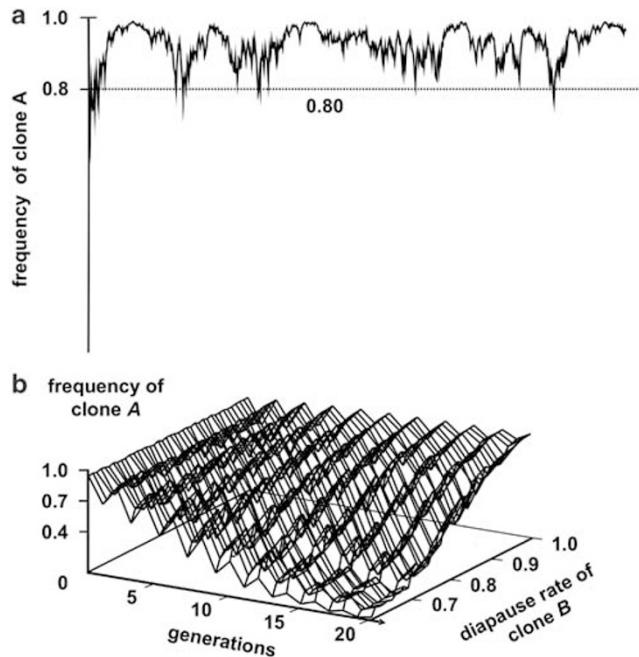

Figure 5 (**a**) Frequency of clone A where $w^A = 0.3$, $w^B = 0.7$, $p_0 = p_1 = 0.1$ (cross) and diapause rates are randomly varied within $d^A(1 \pm 0.3)$ and $d^B(1 \pm 0.3)$. The dashed line gives the equilibrium frequency in environment E_1. (**b**) Frequency of clone A where $d^A = 0.3$, $d^B = 0.7$, $p_0 = p_1 = 0.9$ and the fitness values w^A and w^B are varied within $w^A(1 \pm 0.4)$ and $w^B(1 \pm 0.4)$.

diversity in the long term (Figure 5a), whereas random variation of fitness values showed minor effects for clonal coexistence (Figure 5b). Even if fitness values varied widely, clonal diversity could be maintained and clonal frequencies oscillated temporarily.

Fit with the empirical data

To explain the coexistence of several clones, we must assume either a more complex selection scenario or a neutral coexistence of different clonal lineages with the same life cycle strategy. Both cases may be realized in the parthenogenetic fly *D. bifurcata*. This species has at least eight different clones present in some populations, but only four clones are frequent enough to be present in all populations sampled during all of the years over which this study was based (1981–1983, 1986–1988). Based on enzyme genotypes (Niklasson, 1995), the most abundant clone A is more distantly related to all of the other clones than those are to each other. In addition, clone A shows the opposite trend in seasonal frequency changes than the other common clones (B, C and D, see Figure 4 in Niklasson *et al*, 2004). For these 'non-A' clones, we may be dealing with a group of clones that have a common ancestral origin, and therefore, are similarly adapted to environmental changes. Therefore, we consider here the special case of competition between two clones and calculate the absolute and relative fitness of clone A versus the average fitnesses for the three 'non-A' clones from Appendix 2 in Niklasson *et al* (2004) as our best estimates of the spring and autumn fitnesses for a two-clone case. As the four localities were sampled at approximate 1 month intervals and because sampling dates are not the same over all localities, we arbitrarily pooled data for each population and season into 'spring' (= all collections before June 22) in a given year and 'autumn' (= all collections after this date). Fitnesses over the winter and summer for each locality and year were then estimated as the ratios of clone frequencies in two successive seasons (see Niklasson *et al* (2004) for further details).

Applying the model to the experimental data, the population living in enviroment E_1 was considered to be the summer season where p_{E_1} is the frequency of clone A in spring before selection. Correspondingly, p_{E_2} gives the frequency of clone A at the beginning of the winter season (Figure 1, black dots). Frequency estimates of clonal diversity were available for spring and autumn populations (crosses in Figure 1 and Niklasson *et al*, 2004), where the frequency of clone A in the latter populations was given by

$$p_{\text{autumn}} = \frac{w^A p_{E_1}}{w^A p_{E_1} + q_{E_1}}$$

and

$$q_{\text{autumn}} = 1 - p_{\text{autumn}}$$

(9)

We estimated the relative mean fitnesses of clones A and B (= B + C + D) over all localities and years as $w^A \approx 0.3$ (summer) and $w^B \approx 0.7$ (winter), respectively, in their 'bad' environments, otherwise the relative fitnesses are 1. Observations of natural populations also indicate low diapause rates of clone A but high diapausing of B clones (see companion paper, Niklasson *et al*, 2004). If we assume that 10% of the individuals of clone A diapause, stable coexistence occurs if clone B has a diapause rate, $0.81 < d^B < 0.94$ (cf. Figure 2). In Figure 6, the experimental data of the natural population of *D. bifurcata* (Niklasson *et al*, 2004) are compared with the equilibrium frequencies given by the model, where clone B has diapause rate $d^B = 0.88$. The observed frequencies of the clone A, averaged over the four populations, are close to the expected extreme values 0.80 and 0.53.
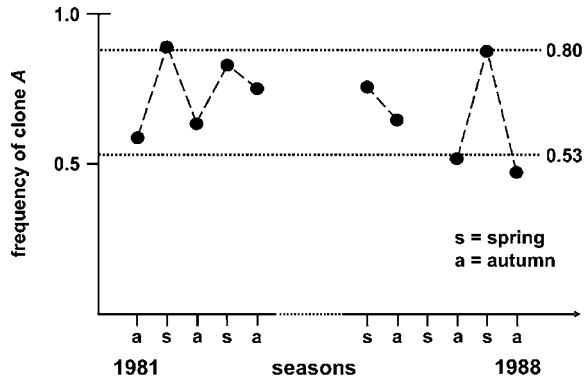
Figure 6 Observed frequencies of one clone of *D. bifurcata* (●---●) during a study of 8 years (Niklasson *et al*, 2004). The dashed lines give the upper and lower bounds of equilibrium values where $w^A = 0.3$, $w^B = 0.7$, $d^A = 0.1$ and $d^B = 0.88$.

Discussion

For sexual species, diapause can greatly broaden the possibility of the maintenance of polymorphism in a temporally varying environment (Hedrick, 1995). As one empirical example which had long anticipated the theoretical development, Istock and co-workers (review in Istock, 1978) demonstrated that quantitative genetic variation in development rate was probably maintained by correlated genetic variance for facultative midsummer diapause in pitcher plant mosquitoes, *W. smithi*, subject to unpredictable onset of winter in a north temperate population. Later demographic modeling of this scenario (Tuljapurkar and Istock 1993) showed that conditions of harsh stochastic environmental variability as well as high negative serial autocorrelation of environmental state tended to stabilize polymorphism for facultative diapause.

For clonally diverse parthenogenetic species, which can be directly compared to guilds of competing species, we have shown that diapause may also be a very important trait for maintaining stable coexistence. The study of natural populations of *D. bifurcata* revealed cyclic changes of clone frequencies between the seasons over 8 years (Niklasson *et al*, 2004) in four different populations. This can be explained by a balancing effect of biotic and abiotic factors, which maintain clonal diversity within these populations. Indeed, our model shows that differences in the clonal fitness values and in diapause rates can explain such dynamic, yet apparently stable population structures. If different clones, however, have similar life cycle strategies, for example, if some lineages of two *D. bifurcata* clones both diapause, competition becomes stronger (Figure 2) and the range of stable coexistence becomes considerably narrowed. Furthermore, increased clonal variation of fitness and diapause rates due to large random environmental fluctuation highly endangers clones with lifecycle strategies at the border of stability ranges. In total, this suggests that the number of clones with different lifecycle strategies is limited and most variation observed at the molecular level should be neutral.

In natural populations of obligate parthenogenetic species, we often observe a relatively large number of genetically different clones (eg Lokki *et al*, 1975; Saura

et al, 1976; Parker 1979, Suomalainen *et al*, 1987; Niklasson, 1995). To explain the coexistence of several clones, we have to assume either a more complex selection scenario or a random coexistence of different clonal lineages with the same life cycle strategy. Both cases may be realized in the parthenogenetic fly *D. bifurcata*. Based on enzyme genotypes (Niklasson, 1995), the most abundant clone A is more distantly related to all of the other clones than those to each other. In addition, clone A shows the opposite trend in seasonal frequency changes than the other clones. In early spring collections, dark and worn specimens of clone A, most probably overwintering adults, dominate, while the first individuals collected of the other clones are newly emerged, perhaps from diapause eggs and or larvae. Except for clone A, we may be dealing with a large group of clones that have a common ancestral origin and, therewith, they are similarly adapted to environmental changes. However, first observations indicate differences also among the *non*-A clones. They may be favored in different temporal niches related to seasonal conditions, for example, temperature and humidity.

In nature, climatic conditions often regulate the size of the diapause rate within species, for example, daphnia (review in Hebert, 1987) or in aphids (review in Hales *et al*, 1997). For example, the induction of diapause can be reduced in a mild climate. Therewith, selection becomes more effective and clonal diversity decreases if the diapause rate decreases. However, climatic conditions can drastically influence clonal frequencies. The cyclic fluctuation observed in natural populations of *D. bifurcata* can obviously be explained with our model.

The model can be easily generalized for insect–plant interactions where clones or species show differences in their temporally fluctuating fitness values. Assuming different host preferences and migration rates, even the special case considered in this paper can easily be applied. For the general model, various parameter combinations may explain niche separation of species and therewith the beginning of speciation processes.

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