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Four kinds of extra long diapause in insects: A review of theory and observations

Ilkka Hanski

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In many insect populations some individuals miss one or more breeding opportunities by remaining longer in diapause than others. Extra long diapause (ELD) may be achieved either by entering diapause exceptionally early (premature diapause) or by completing the diapause exceptionally late (prolonged diapause). In both cases diapause induction may be density-independent or density-dependent. This paper reviews models and selected examples illustrating the four kinds of ELD, emphasizing their population dynamic causes and consequences. Many theoretical predictions about ELD have been little tested or not at all, while interesting empirical findings await further theoretical studies. Examples of the latter include different patterns of ELD in species using the same, temporally varying resource, and ELD in coupled host-parasitoid interactions.

Ilkka Hanski, Department of Zoology, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki, Finland.

1. Introduction

The favourable season for breeding is so short in many temperate environments that most insect species can have only one generation per year (are univoltine). The adverse season is often spent in diapause, a "programmed" arrest of development, which saves individual body reserves and reduces the chance of the individual dying, due to unfavourable weather.

Apart from the predictable adverse season, temperate environments pose other problems for annual plants and animals, in particular year-to-year variability in the length and suitability of the breeding season. Diapause is also a possible solution to this type of environmental variability, in the form of extra long diapause (ELD). I shall distinguish two types of ELD, based on individual variation in the timing of the beginning and the end of the diapause. In the next section the two types are further subdivided on the basis of whether diapause induction is density-dependent or not.

The rest of the paper discusses the four kinds of ELD, with theoretical models and examples drawn from the entomological literature. My purpose is not to present an exhaustive review but rather to discuss selected examples to illustrate the variety of situations in which ELD may be expected and has been found to occur. The causes and consequences of ELD are discussed from an evolutionary rather than a mechanistic (physiological) viewpoint, emphasizing the population dynamic context. Two recent and thorough general treatments of insect diapause with ecological and evolutionary considerations are Tauber et al. (1986) and Danks (1987).

2. Four kinds of extra long diapause

Following Danks (1987) I use dormancy to mean "suppressed development", which may be either quiescence, a simple arrest of development that will last while some limiting factor is below the developmental threshold, or diapause, a more profound break of development that is not controlled simply by the prevailing environmental conditions.

Diapause intensity and duration are population-specific characteristics that can be modified by environmental conditions during the prediapause and various diapause stages (Tauber et al. 1986). In extra long diapause (ELD) an individual remains in diapause either for more than twelve months, or for so long that it misses one or more breeding opportunities used by some other individuals, which started or ended their diapause concurrently with the individual in ELD. This definition simplifies a complex phenomenon but it also highlights the point that is of the greatest interest here: individuals in ELD skip a breeding opportunity and opt for survival.

The case of staying in diapause for more than twelve months is included in the above definition for the (rare) situations in which all individuals in a population remain in diapause for two or more winters. It seems preferable to include such cases of multiannual diapause in ELD, whether there is much within-population variation in diapause length or not, because — in the cases that I know of — the only reason for the long diapause is a local adaptation to multiannual fluctuations in resource availability. "Breeding opportunity" refers to discrete episodes of reproduction. Univoltine species have one, but multivoltine species have several breeding opportunities per year.

Most cases and types of ELD are expected to be due to one ultimate cause: temporal variation in fitness, by which I mean variation in the expected fitness of individuals breeding or developing in different times, for example, in different years. If there is no such variation, and if we assume realistically that some mortality occurs during diapause, no benefit can generally be obtained by postponing development and breeding. One possible exception is mentioned in Section 3.2. Temporal variation in fitness can be generated by several processes, both extrinsic and intrinsic to the population, and it is useful to distinguish between several types of ELD.

Density-independent and density-dependent diapause

Let us first make a distinction between density-independent and density-dependent diapause. Diapause is density-dependent when its induction is affected by population size or density. Highly competitive populations provide good examples of density-dependent diapause (Section 4). Density-dependent diapause is also typically frequency-dependent, because what really matters is the number of individuals with which the target individual interacts, which generally depends on the frequency of different diapause behaviours in the population. Game theoretic models (Maynard Smith 1982) are often suitable for an analysis of density-dependent diapause.

Diapause is density-independent if diapause induction is not affected by density; each individual independently faces the same problem, and it does not matter, in principle at least, to any one of them what the others are doing: there is no density- nor frequency-dependence. Note that even when population dynamics are density-dependent, diapause induction may still be density-independent.

An important issue that needs to be addressed here is who controls the diapause, the individual itself (current generation) or its mother (parent generation). Both mechanisms are common, and often both the parent and its offspring contribute to diapause determination (Danks 1987). If the individual itself controls the diapause, and if diapause is density-independent, there are only limited possibilities for ELD due to, for example, different individuals experiencing different environments. In density-independent diapause, the concept of ELD becomes really useful only when the parent generation is in control of diapause, and when the problem is trying to maximize the fitness of a reproducing female (see Westoby 1981 about seed germination in plants). In contrast, in density-dependent diapause, ELD may occur regardless of whether diapause is controlled by the current or the parent generation, and even if all current generation individuals experience the same environment.

There is another significant contrast between density-dependent and density-independent ELD. In density-independent diapause, and assuming that the parent generation is in control of the diapause, all reproducing females should produce the same mixture of ELD and non-ELD offspring, the mixture that gives the highest fitness in the particular environment. A possible complicating factor is that in a real population not all individuals may experience the same environment. In contrast, in density-dependent diapause, regardless of who is in control of the diapause, different females may have different mixtures of ELD and non-ELD offspring. The proportions of ELD and non-ELD offspring in the population are expected to evolve to such values that all the breeding females (if they control diapause) or their offspring (if they control diapause) have equal fitnesses. Between-female differences in the proportion of ELD offspring suggest density-dependent diapause, while if there are no such differences diapause may be density-indepenent or density-dependent.

Premature and prolonged diapause

There is a second dichotomy of ELD which, in principle, is independent of whether diapause induction is density-dependent or not. In premature diapause, an individual enters diapause one or more breeding opportunities earlier than some other individuals in the population. The term "premature" is not ideal, because one could also emphasize the individuals that enter diapause later than the others. However, in the present context it is natural to focus on individuals that commence their diapause early, while conditions are still acceptable for breeding. A more serious difficulty with this definition is that if even a single individual, in an otherwise univoltine population, emerges in late summer to produce a second ("partial") generation, the rest of the population has entered ELD. I cannot see a reasonable way of excluding this case from the definition of ELD.

In contrast, in prolonged diapause individuals stay in diapause one or more breeding opportunities longer than others, typically two or more winters instead of the usual one. Powell (1974) distinguishes between two types of prolonged diapause on the basis of whether all individuals in the population, or only a fraction of them, enter prolonged diapause. The former type may occur if there is temporal variation with a strong multiannual cyclic component in resource availability or in some other essential environmental factor (an example is given in Section 5).

In conclusion, extra long diapause may be achieved either by entering diapause exceptionally early or by staying in diapause for exceptionally long. This is the essential difference between premature and prolonged diapause. The distinction between density-independent and density-dependent ELD is a more fundamental one, as these two kinds of diapause are adaptations to different types of temporal fitness variation. Density-dependent ELD can be advantageous when abundance changes are to some extent predictable, while density-independent ELD is an adaptation to unpredictable temporal variability. All cases of density-dependent diapause are essentially ELD, while simple diapause is typically density-independent, most often induced by a short daylength and low temperatures (Tauber et al. 1986, Danks 1987).

The next section discusses density-independent premature (Section 3.1) and prolonged diapause (Section 3.2). The best known and most studied ELD is density-independent prolonged diapause, which is analogous to a certain type of delayed germination of seeds in plants (Section 7). Density-dependent ELD has been less studied, though especially density-dependent premature diapause is not uncommon in insects (Section 4.1). Density-dependent prolonged diapause is less well documented but may occur in, for example, some forest insects that have occasional outbreaks (Section 4.2). Section 5 extends the previous single-species analyses to multispecies interactions, which have been surprisingly little studied in this context. Section 6 discusses the population dynamic consequences of ELD more explicitly, and Section 7 finally compares ELD to dispersal, and contrasts ELD in insects with seed dormancy in plants.

3. Density-independent ELD

3.1. Density-independent premature diapause: variable length of the breeding season

Seasonality tends to increase temporal variance in fitness, especially in species that may have two or more generations per year. Many such potentially multivoltine species have two options in mid or late summer: they may attempt to complete another generation before winter, or they may diapause until the next breeding season. As the length and suitability of breeding seasons vary from one year to another, it is not clear which alternative is better.

The optimal solution also depends upon who is in control of diapause: the parent generation, the current generation, or both. Taylor (1980, 1986) has analysed the optimal switching time for diapause induction when the target individual itself is in control of the decision (for another approach see Roff 1983). Variability in the length of the season tends to result in an earlier median switching time being selected, than the optimal switching time in a constant environment with the same mean length (Taylor 1986), but this effect depends on the mode of inheritance and the effect was not great in Taylor's (1986) simulations. In a population of similar individuals living in the same environment, and under the assumption that diapause induction is controlled by the current generation, there is no possibility of polymorphism occurring with respect to diapause.

Cohen (1970) has analysed the same problem with a density-independent population model and implicitly assuming parental control of diapause (see also León 1985). Cohen (1970) assumed that there is always one generation in early summer with W_1 adults produced per emerging adult. He analysed conditional diapause decisions based on the time of development, which may vary between individuals. For the cases in which all individuals complete their larval development at the same time, the following difference equation model describes population growth from one year to another:

$$N_{t+1} = N_t W_1 S_2 (DS_1 + QW_2). \qquad (1)$$

Here W_2 is the production of adults per adult in the second generation, D is the fraction of first generation individuals entering premature diapause, $Q = 1-D$, S_1 is the probability of diapausing individuals surviving during summer, and S_2 is the probability of surviving during winter. W_i and S_i are random variables and independent of population density.

Cohen (1970) suggests that the optimal value of D is found by maximizing the geometric mean growth rate with respect to D. This gives the following conditions:

$$\begin{array}{lll} D = 1 & \text{when } \mathrm{E}(W_2) \le \mathrm{H}(S_1) & \text{(2a)} \\ D = 0 & \text{when } \mathrm{H}(W_2) \ge \mathrm{E}(S_1) & \text{(2b)} \\ 0 < D < 1 & \text{when } \mathrm{E}(W_2) > \mathrm{H}(S_1) & \\ & \text{and } \mathrm{H}(W_2) < \mathrm{E}(S_1). & \text{(2c)} \end{array}$$

Here E is the expectation, and H denotes the harmonic mean of the variable. (Harmonic mean equals the expectation when the variance of a non-negative random variable is zero; H decreases with increasing variance, and is particularly affected by small values.)

Cohen's (1970) model makes the not so surprising predictions that when the breeding season is sufficiently long (assumed to lead to large W_2 with small variance) all individuals should be bivoltine, while when the breeding season is short (W_2 small and/or variance large) all individuals should be univoltine. These predictions are in agreement with a commonly observed geographical pattern: the number of generations per year decreases with increasing latitude. To take an example, Wiklund et al. (1983) reported on Swedish populations of the butterfly *Pararge aegeria*, with a mixture of univoltine and bivoltine individuals. As expected, the frequency of bivoltinism decreases with increasing latitude. Wiklund et al. (1983) also found that the second generation pupae are lighter than the first generation ones, indicating another cost of bivoltinism.

Cohen's (1970) model (see condition [2c]) also makes the more interesting prediction that when the variances of W_2, S_1, or both are large (leading to small harmonic means), the population is likely to be a mixture of univoltine and bivoltine individuals. When the variances are small, the population is expected to consist of either univoltine or bivoltine individuals. Fig. 1 gives a hypothetical example. As far as I know, nobody has attempted to test this prediction.

3.2. Density-independent prolonged diapause

Theory

Cohen's (1966, 1968) pioneering work on delayed germination of annual plants also applies to insects with prolonged diapause. In this section I shall first sketch the basic idea using Cohen's (1966) model. I then review the more recent theoretical work, based on density-dependent population models. The next subsection summarizes the observations on prolonged diapause in insects, and lastly insects breeding in conifer seeds and cones, a paradigmatic example of prolonged diapause, will be discussed in some detail.

Cohen (1966) assumed that the environment is always in either of two states, good or bad, and that the two states occur in a random sequence with probabilities p and $1-p$, respectively. In good years, the breeding individuals multiply by a factor W, whereas in a bad year they leave no progeny at all. Proportion S of individuals in prolonged diapause survives from one year to another. Cohen (1966) asked what the optimal fraction Q of individuals (read: offspring of a particular female) that should emerge in any one year is, given that no other information than the value of p is available about the environment. With these assumptions Cohen (1966) constructed a density-independent population model and solved for the optimal Q by maximizing the geometric mean growth rate, obtaining

$$Q = (pW - S)/(W - S). \qquad (3)$$

Q is predicted to increase with increasing frequency of good years p, and for large values of W the frequency of emerging individuals is approximately equal to p.

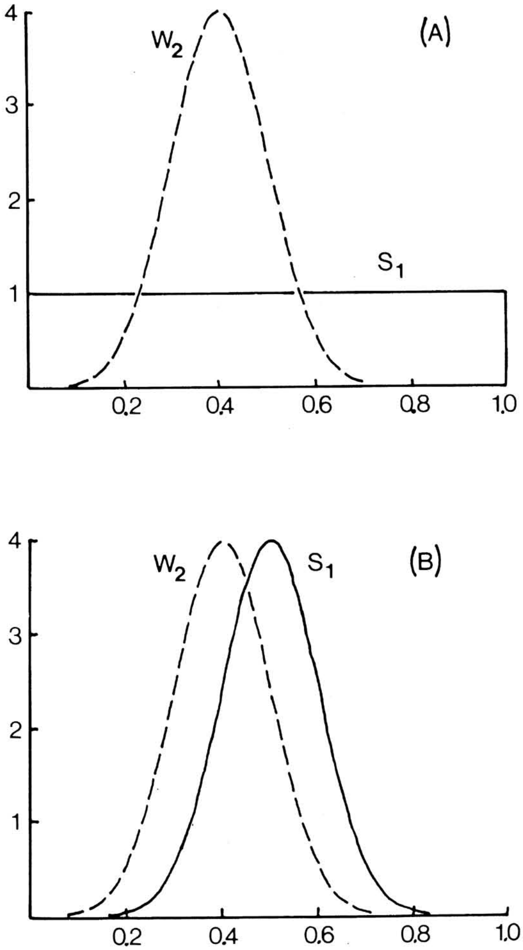

Fig. 1. Two hypothetical distributions of W_2 and S_1, with the same mean but different variance. In (a) condition (2c) in the text is fulfilled, and Cohen's model predicts a mixture of univoltine and bivoltine individuals. W_2 is normally distributed with mean 0.4 and S.D.=0.1, S_1 is uniformly distributed between 0 and 1. In (b) condition (2a) is fulfilled, and the model predicts a univoltine population. W_2 as in (a), S_1 is normally distributed with mean 0.5 and S.D.=0.1.

Cohen's (1966) work was particularly inspired by dormancy in desert annuals; their main problem is how to exploit the rare periods, following rains, when development is possible. Rainfall is highly variable and unpredictable, hence a "risk-spreading" prolonged diapause is often a better solution than simple dormancy (quiescence).

Cohen's (1966) solution implicitly assumes a single population in which all individuals experience the same conditions, or a set of localities where the temporal changes are spatially highly correlated on the scale of dispersal. Several authors have generalized this model to allow for dispersal between local populations with more or less independently varying environments (MacArthur 1972, Venable & Lawlor 1980, Metz et al. 1983, Bulmer 1984, León 1985, Klinkhamer et al. 1987). Such dispersal provides an alternative risk-spreading mechanism to ELD, and tends to decrease the frequency of prolonged diapause. These models thus predict that the frequency of prolonged diapause is negatively correlated with dispersal rate, a prediction in agreement with the common notion in the ecological literature (e.g. Southwood 1977) that diapause and dispersal are alternative ways of escaping unfavourable conditions "here and now". It is also clear that if fluctuations are well synchronized across local populations, selection tends to favour ELD instead of dispersal (Gadgil 1971, Ellner & Shmida 1981, Klinkhamer et al. 1987).

The prediction that prolonged diapause and dispersal rate are negatively correlated does not appear to have been properly tested with insects (for botanical examples see e.g. Cook 1980, Venable & Lawlor 1980, Klinkhamer et al. 1987). An anecdotal example is *Zygaena* moths, which are known to be poor dispersers (C. Naumann pers. comm.) and which often have complicated patterns of prolonged diapause (Wipking & Neumann 1986). The same prediction can be applied to premature diapause: for example, populations with partial second generation (risky behaviour) are expected to have a greater dispersal rate than univoltine populations, other things being equal. In water striders *Gerris*, univoltine populations tend to be short-winged (allowing no dispersal) while multivoltine populations are polymorphic or entirely long-winged (giving potential for dispersal), in agreement with the prediction. But as emphasized by Vepsäläinen (1978), habitat heterogeneity and stability are important determinants of winglength in water striders and complicate any test on dispersal and voltinism. Some moth and butterfly species that sporadically immigrate to northern Europe, indicating much dispersal, lack diapause altogether (K. Mikkola pers. comm.), but in this case dispersal occurs between climatically different regions and the relevance of this example in this context is questionable.

Cohen's (1966) original model does not include density-dependent population regulation. Bulmer (1984), Levin et al. (1984), Ellner (1985a,b) and

León (1985) have studied analogous density-dependent models. It is important to note that in all these models diapause is still density-independent. The simplest of Bulmer's (1984) models assumes that fecundity is held constant at such a level that the geometric mean fitness is unity. In this case one does not get an explicit solution for the optimal (ESS) Q, but Bulmer (1984) gives approximations for two special cases. When the survival of individuals in prolonged diapause (S) is very low, the ESS value of Q approaches p, the frequency of good years (as in Cohen's model; see also Ellner 1985b). In the opposite extreme, when survival in prolonged diapause is high, the ESS value of Q may be substantially lower than p. For a very high survival, an approximate solution is (Bulmer 1984)

$$Q = [2p\,(1-S)\,/\,(1-p)]^{1/2}. \tag{4}$$

Note that in this case Q is an increasing function of p and a decreasing function of S. When $S = 1$, the optimal $Q = 0$!

Assuming continuous temporal variability and the lottery model of competition (Chesson & Warner 1981), $Q = 1$ (no prolonged diapause) is an ESS if the following condition is met:

$$\mathrm{E}(X_{t-1}/X_t) < 1/S, \tag{5}$$

where X_t is a random variable with mean M and variance V, representing the average number of offspring produced by a surviving adult in year t (Bulmer 1984). The expectation in Eq. (5) increases with increasing V and hence, as expected, prolonged diapause becomes increasingly probable with increasing variability in the suitability of breeding seasons. It is worth reiterating that although population dynamics in this model are density-dependent, diapause is density-independent, and individuals are independently "hedging their bet".

The selection pressure for prolonged diapause is not due to environmental variability as such but to temporal variability in population size and ultimately in fitness, regardless of the source of variability. Bulmer's (1984) analysis of the exponential model of competition makes this point clear. With no environmental variability ($V = 0$) the exponential model exhibits cyclic or chaotic dynamics with large values of M, and prolonged diapause will be selected because of temporal variation in fitness, even though this variation is solely due to unstable population dynamics.

Ellner (1987) has pointed out that competition may promote ELD (dormancy) even without density fluctuations if competition tends to occur between siblings and if the parent generation is in control of diapause. By spreading the emergence of offspring in time a parent reduces competition among her own offspring and thereby increases her fitness. This argument seems to assume some but not too much dispersal, and may apply widely to plants which Ellner (1987) discussed. In insects, dispersal is likely to be more effective in reducing sib-competition than ELD (cf. Hamilton & May 1977).

Prolonged diapause: summary of observations

Danks (1987) has recently compiled a long list of cases of prolonged diapause in insects, and the following analysis is based on data in his table 27. It should be realized that the documented cases of prolonged diapause cannot be considered an unbiased selection: prolonged diapause will rarely be detected where it is not looked for, and it is generally only looked for where it is expected to occur. The following set of examples must therefore be interpreted cautiously (for additional examples see e.g. Powell 1974). Unfortunately, there is no sensible way of comparing this set of species with species without prolonged diapause.

In terms of micro- and macrohabitat occurrence, three categories can be discerned in species with prolonged diapause (Table 1). A number of cases are known from the tundra, arctic, and arid regions. It may be assumed that year-to-year temporal variability is greater in these regions than in, for example, temperate regions, and that this results in a higher than average frequency of prolonged diapause. The *Pegomya* flies (Anthomyiidae) breeding in *Leccinum* (Boletaceae) mushrooms are a case in point (Hanski 1988). In southern Finland prolonged diapause has been recorded rarely in only one species (Hackman 1976), but in Finnish Lapland prolonged diapause occurs in all the seven common species (Ståhls 1987). The probable reason for this difference is the greater year-to-year variation of mushroom production in the north than that in the south. In one study lasting six years, the maximum and minimum figures for mushroom production were 363 and 0.3 kg/ha in Lapland (Ohenoja & Metsänheimo 1982), while no such extremely low figures have been published for southern Finland (Ohenoja & Koistinen 1984).

Table 1. Micro- and macrohabitats of insects with prolonged diapause. Data from Danks (1987).

Habitat	Number of Species	Genera	Families
Tundra, arctic	6	5	4
Arid environments	9	6	4
Cones, fruits, nuts	27	16	9
Host individuals, galls	25	22	11
Mushrooms	2*	1	1
Leaves, flowers	60	41	22
Vegetation	13	8	4
Mixed	13	10	7

* A rearing experiment by Ståhls (1987) revealed prolonged diapause in 2 genera and 8 species of Anthomyiidae (Diptera) breeding in *Leccinum* in Finnish Lapland (see Section 6 and Table 2).

Another group of species with prolonged diapause breeds in cones, fruits, nuts, galls, mushrooms, and host individuals — in other words, in patchy and ephemeral microhabitats, which often have a great temporal variation in availability. Prolonged diapause is especially frequent in cone insects (below).

The largest group of species in Table 1 consists of herbivorous insects and is more difficult to fit into the theory reviewed above. Two taxa with many known cases of prolonged diapause are sawflies (especially Diprionidae) and butterflies (e.g. Pieridae). The former includes many well-known outbreak species, in which prolonged diapause is common (Section 4.2). The large number of known cases of prolonged diapause in butterflies may simply reflect the fact that their ecology is relatively well known.

Fig. 2 gives the distribution of the maximum lengths of prolonged diapause in the species in Danks' (1987) sample. The majority of species remains in prolonged diapause for at most two or three years, but some species have been reported to stay in diapause for up to ten years or more. Insects enter prolonged diapause in all developmental stages, but there are clear taxonomic biases (Danks 1987), presumably related to similar differences in the stage of ordinary diapause in these taxa. For instance, prolonged egg diapause is especially common in Orthoptera and Cheleutoptera, prolonged prepupal diapause is frequent in sawflies, and prolonged pupal diapause has been reported in many butterflies and moths (Danks 1987).

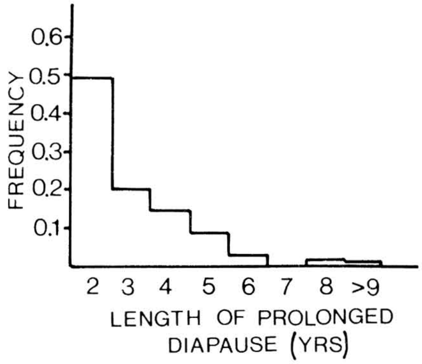

Fig. 2. Frequency distribution of the maximum length of prolonged diapause in 149 species of insects. Data from Danks (1987).

Insects breeding in conifer seeds and cones

Prolonged diapause is conspicuously common in insects breeding in conifer seeds and cones (Danks 1987), undoubtedly because the cone production of many coniferous trees shows dramatic temporal variation. Bulmer's (1984) model predicts that species using more variable resources should have a higher incidence of prolonged diapause than species using more constant resources. Annila (1982) compared two species of *Megastigmus* (Hymenoptera: Torymidae) breeding in the seeds of the Siberian fir *Abies sibirica* (*M. specularis*) and the Douglas fir *Pseudotsuga menziesii* (*M. spermotrophus*). The Siberian fir has abundant or moderate cone crops frequently, and no total failures; its seed predator *M. specularis* mostly emerged after one winter without prolonged diapause. In contrast, in the Douglas fir *Pseudotsuga menziesii* the number of cones per tree varies from zero to thousands per year, and cone production is often well synchronized between trees (Bakke 1963, Winjum & Johnson 1964, Smith & Balda 1979). The seed predator *M. spermotrophus* mostly emerged after three to five years.

Janzen (1971) suggested that fluctuations in the seed production of many trees have evolved in response to seed predation: the predator satiation hypothesis. Prolonged diapause is clearly a counteradaptation in the insects. There is also a strong selection pressure in the insects to learn to "predict" the size of the cone crop in the following year, and many species are in fact quite successful in doing this (Bakke 1963, Stadnitskii et al. 1978, Annila 1981, Hedlin et al. 1982). Possible environmental cues that the insects may use include temperature at critical periods for cone production (Miller and Hedlin 1984). Emergence may be timed to coincide with favourable breeding conditions also in other species than cone insects, for example, in the Nearctic moth *Ethmia semilugens* inhabiting desert margins and other arid places. Powell (1974) reports on individuals that emerged, after spending thirty-three months in diapause, only forty days following artificial watering, suggesting that sporadic rainfalls may terminate their diapause. Unfortunately, little work has been done so far on models in which species are able to adjust the length of prolonged diapause in response to cues that are indicative of future environmental conditions (but see Cohen 1967, Venable & Lawlor 1980, León 1985).

4. Density-dependent ELD

4.1. Density-dependent premature diapause

Theory and its application to blowflies

In seasonal environments, population size decreases during the non-breeding season because of mortality, and it generally increases during the breeding season. In food-limited, multivoltine species, such as blowflies, intraspecific competition will often increase in successive generations during the summer. Under such conditions, it may be advantageous for some individuals to enter premature diapause after the first generation to avoid the most competitive season, mid and late summer. In other cases, the density-dependent rate of predation or parasitism may increase with advancing season (Spence 1986, Janzen 1987), and it may be advantageous for some prey individuals to enter premature diapause.

This section outlines a model of density-dependent premature diapause that has been developed with one particular example in mind, but which is also applicable more widely. The example is flies breeding on carrion, which typically comprise a very competitive guild of several similar, yet coexisting species (Hanski 1987a,b). In southern Finland blowflies may have up to three or four generations per year, but some first generation prepupae of two numerically dominant species, *Lucilia illustris* and *L. silvarum* (Calliphoridae), enter premature diapause at the end of June (Hanski 1987a, unpubl.).

Ives & Hanski (unpubl.) have modelled this system in the following manner for one species that may have one or two generations per year. Let P_{1t} and P_{2t} denote the spring and summer generation numbers of prepupae in year t, respectively. Proportion D of P_{2t} enters premature diapause while proportion Q emerges to produce the summer generation ($D+Q=1$). Changes in population size are given by

$$P_{2t} = W_1 P_{1t} f_1 (W_1 P_{1t}) \tag{6a}$$

$$P_{1t+1} = S_2 [DS_1 P_{2t} + QW_2 P_{2t} f_2 (QW_2 P_{2t})], \tag{6b}$$

where W_1 and W_2 are the maximal fecundities, realized at a low population density, and f_1 and f_2 are the density-dependent survivorship functions in the two generations, respectively. S_1 is the survival probability in premature diapause during summer, while S_2 is the survivorship over winter, assumed to be the same for all individuals. Whether it is advantageous for an individual to enter premature diapause, or not, clearly depends on what the other individuals in the population do, and how many of them there are.

The problem is to find the ESS value of Q, Q^*, if it exists. At this value, all individuals have equal fitness regardless of their diapause behaviour, hence

$$S_1 = W_2 f_2 [Q^* W_2 P_2^*(Q^*)]. \tag{7}$$

Provided that the population size reaches a stable two-point cycle (P_1^*, P_2^*) and that $d(QP_2^*(Q))/dQ > 0$, Q^* is given by (Ives & Hanski unpubl.)

$$Q^* = [S_2 W_1 f_1^{-1}(1/S_2 W_1)] \,/\, [W_2 f_2^{-1}(S_1/W_2)]. \tag{8}$$

Fig. 3 illustrates this condition for the negative exponential survivorship function, $f = \exp(-an)$. When winter mortality is very low, no premature diapause should occur, because without winter mortality there is effectively no seasonality, and no temporal variation in fitness that would result in ELD. In the other extreme, when winter mortality is very high, premature diapause is again selected against, now because the population decreases to such a low density in spring that competition is not severe even in late summer. At intermediate values of winter mortality, and especially when fecundity is high and hence competition is strong, it is predicted that some indi-

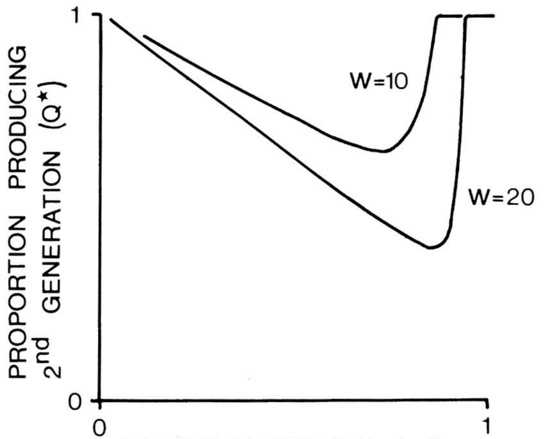

Fig. 3. Frequency of premature diapause in the model of Eq. (8) as a function of winter mortality $1-S_2$. $W = W_1 = W_2$ and $a = 1$.

viduals will enter premature diapause. A constant number of individuals should not enter premature diapause; at this density competition in the second generation is just severe enough to decrease the fitness of non-diapausing individuals to the level of the early-diapausing ones.

Observations and preliminary experiments on *Lucilia* show that, as predicted, populations are polymorphic with respect to diapause behaviour (Hanski 1987a, unpubl.). Whether premature diapause is induced by high larval density and/or food scarcity in *Lucilia* is not yet known. Vinogradova (1986) has reported on intrapopulation variation in the diapause behaviour of *Calliphora vicina*, another carrion-breeding species. Her experiments showed that both the incidence and intensity of diapause could be changed by selection.

Other examples

Istock et al. (1975) have reported on premature diapause in the pitcher-plant mosquito *Wyeomyia smithii*. They demonstrated experimentally that crowding increases the frequency of premature diapause, and that this response is adaptive because of severe competition in late summer. Istock et al. (1975) found that mass selection for rapid development practically eliminated premature diapause from the population, suggesting that fast development is genetically associated with a reduced tendency for diapause in this species.

Livdahl & Edgerly (1987) found that the hatching rate of the eggs of the treehole mosquito *Aedes triseriatus* decreased with increasing larval density, and that the eggs which did not hatch entered (premature) diapause. Livdahl & Edgerly (1987) discussed the physiological mechanisms by which a high density of larvae weakens the hatching stimulus for eggs, and they pointed out that the premature egg diapause is probably adaptive because of cannibalism and resource competition, in which large larvae have an adverse influence on newly-hatched, small larvae.

In some populations, competition is so severe that it alone leads to temporal variation in population size, regardless of seasonality, and various types of developmental delays may be expected to occur. In the drosophilid *Chymomyza costata* crowding induces either quiescence in larval development or larval diapause in a constant laboratory environment (Botella & Mensua 1987). In the former case development is renewed immediately following improvement of the rearing conditions, while the diapausing larvae require diapause-terminating stimuli to resume their development (Botella & Mensua 1987).

Premature, crowding-induced diapause is well documented for stored-product insects (Tauber et al. 1986, Danks 1987, and references therein), many of which live in a rather constant environment. In some cases frequent contacts between individuals seem to be a necessary stimulus for diapause (Tsuji 1959, Barak & Burkholder 1977), while in other species diapause is induced by some residue produced during larval feeding (Burges 1963, Hagstrum & Silhacek 1980; but see Nair & Desai 1972).

In some populations of *Ephestia cautella*, density-dependent larval diapause leads to a seasonal population cycle that is synchronized with the changing availability of food in warehouses. When the warehouse is empty, only diapausing individuals survive. In March the warehouse is refilled, and the adults emerge. With the progressing season and increasing population density the incidence of diapause increases, and is again high in December, at the end of the storage period (Hagstrum & Silhacek 1980).

Selection experiments with stored-product insects have been successful in modifying the incidence and intensity of prolonged diapause (Tsuji 1960, Barak & Burkholder 1977, Hagstrum & Silhacek 1980). Nair & Desai (1973) working on *Trogoderma granarium* (Dermestidae) demonstrated density-dependent diapause in strains in which density-independent diapause had been eliminated by selection, suggesting that more than one set of genes are involved in diapause determination in this species.

To prevent giving the impression that competition necessarily increases the incidence of diapause, I shall conclude this section with a counter-example, the ichneumonid *Exenterus abruptorius* parasitizing *Neodiprion sertifer* larvae (Martinek 1985 and references therein). If the parasitoid larva remains alone in the host eonymph, it enters summer diapause in the first instar. In late summer the parasitoid continues its development, kills its host and finally enters winter diapause. However, if another parasitoid (*Lophyroplectus*) is present in the same host individual, the *Exenterus* larva develops without summer diapause at an increased rate, thereby outcompeting the *Lophyroplectus* larva that has a slower rate of development.

4.2. Density-dependent prolonged diapause

In contrast to the numerous examples of density-dependent premature diapause, density-dependent prolonged diapause appears to be a rare phenomenon. The reason is probably that this type of ELD is not an adaptive response to most kinds of temporal variability that are present in nature. Some forest insects, such as pine-feeding sawflies, provide possible examples.

The food resources of folivorous sawflies are abundant and vary little between years. Instead, the size of many sawfly populations varies enormously as a result of occasional population outbreaks (see Schwenke 1982 for a comprehensive review and Hanski 1987c for a discussion). Following the peak of an outbreak, the population decreases to 1% or less of the maximum density (Hanski 1987c). *Diprion pini*, currently the most serious outbreak pine sawfly in central Europe, is a good example. Outbreaks usually involve a normally bivoltine "lowland type" (Eichhorn 1982), which becomes univoltine during an outbreak and switches largely to prolonged cocoon diapause at the end of an outbreak (Eichhorn 1982). If the switch from bivoltinism to univoltinism is considered as a case of premature diapause, *D. pini* exemplifies a species in which diapause is extended at both ends.

Eichhorn (1982) suggests that the decline in population growth rate, due to increasing frequency of prolonged diapause, is instrumental in ending an outbreak. Alternatively the population decrease, whatever its cause, could be the cause of prolonged diapause. Survival, not reproduction, is at its premium in a declining population, and survival may be best achieved by prolonged diapause, in which state individuals are not affected by many of the factors often playing a major role at the end of an outbreak (food shortage, disease, and egg and larval predation and parasitism; Schwenke 1982 and references therein). There is some evidence indicating that the declining quality of foliage and changing microclimate in defoliated trees may induce prolonged diapause in sawflies (Kolomiets et al. 1979). ELD in pine sawflies appears to be a good example of density-dependent prolonged diapause.

Prolonged diapause in the parasitoids of pine sawflies could also be explained in these terms: the decreasing host population necessarily causes a decrease in the parasitoid population, and the best an individual parasitoid may be able to do is to stay in prolonged diapause during the marked decrease. In this case, the crucial element however is a varying resource level rather than parasitoid density-dependence.

Like density-dependent premature diapause in some stored-product insects, ELD in sawflies is attributable to unstable internal dynamics, though in the latter case some other species (natural enemies) are probably involved (Hanski 1987c). When ELD is due to unstable population dynamics and not to environmental variability, one could generally expect evolution towards density-dependent ELD, which would allow an individual to better exploit the favourable breeding opportunities than density-independent ELD does. On the other hand, density-dependent ELD may significantly reduce population fluctuations (Section 6) and, thereby, tends to eliminate the dynamics that led to the evolution of ELD in the first place.

5. Extra long diapause in multispecies interactions

Extra long diapause is an important ingredient in many multispecies interactions, but there is practically no theoretical work done in this field and the empirical results are scattered in the literature. The best I can do is to present some examples of interspecific competition and host-parasitoid interaction in which ELD is involved.

5.1. Interspecific competition

The single species model of density-dependent premature diapause in Section 4.1 may be extended to two competing species (Ives & Hanski in prep.). Hanski (1987a) found evidence for a higher frequency of premature diapause in an inferior (*L. silvarum*) than a superior competitor (*L. illustris*) in blowflies. This result is predicted, because the same amount of competition has a stronger negative effect on an inferior than a superior competitor.

Cambefort (1984) has studied seasonality in the dung beetle community of the savannas in the Ivory Coast. Amongst the near-twenty ball-rolling species, which are typically engaged in exceptionally severe competition, several species of *Sisyphys* (*biarmatus, seminulum, goryi* and *costatus*) develop continuously during the eight-month rainy season and may have up to five generations per year (Paschalidis 1974). In contrast, several other similar species, for example, *Scarabaeus palemo, Gymnopleurus coerulescens*, and *G. puncticollis*, have only one generation per year, in the very beginning of the rainy season. There is no reason to assume that these species have a substantially lower potential rate of development (if at all) than the *Sisyphys* species, and it is difficult to understand their seasonality without interspecific competition. Not enough is known about these species to draw definite conclusions, but I predict that the *Sisyphys* species are, in one way or another, superior competitors, and that some *Sisyphys* have premature diapause.

Let us now turn from premature to prolonged diapause. Annila's (1981) study of the seed and cone insects of the Norway spruce *Picea abies* gives a good example of prolonged diapause in a set of four competing species (there are more than four species in this community but the rest are rare; Annila pers. comm.). All four species have prolonged diapause, but with important quantitative differences (Fig. 4). Most individuals of the spruce cone moth *Laspeyresia strobilella* and the spruce cone fly *Hylemyia anthracina* emerged after one winter, without entering prolonged diapause, while the two seed predators, the spruce seed gall midge *Plemeliella abietina* and the spruce seed chalcid *Megastigmus strobilobius*, stayed two to four years in diapause (Fig. 4).

The cone production of the Norway spruce varies greatly from one year to another, but there is also a clear indication of 3-year cyclicity in Fennoscandia (Fig. 5). It is tempting to suggest that the relative magnitudes of the two components of temporal variation in cone production determine which type of prolonged diapause is selected: when the regular, cyclic component is weak in comparison with the random one, the diapause type represented by the two cone insects should be favoured (low incidence of short prolonged diapause), while when the cyclic component is strong, one expects individuals to delay emergence by the length of the cycle, as the two seed insects appear to do (cf. Figs. 4 and 5).

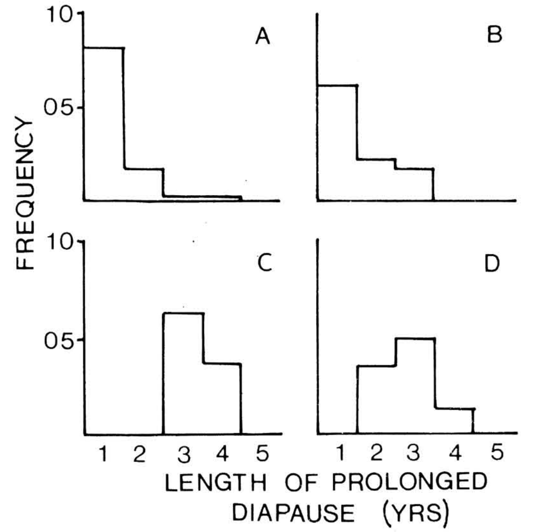

Fig. 4. Distribution of diapause length in four species of insects breeding in the cones (A and B) and seeds (C and D) of the Norway spruce. The species are (number of individuals reared in brackets) A *Laspeyresia strobilella* (2780), B *Hylemyia anthracina* (443), C *Plemeliella abietina* (610), and D *Megastigmus strobilobius* (1441). Data from Annila (1981).

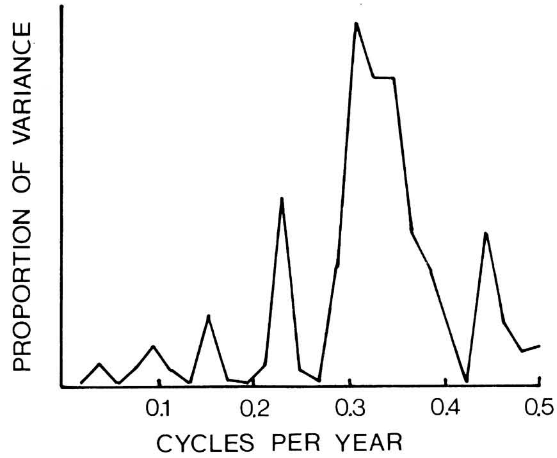

Fig. 5. Spectral analysis of cone crop fluctuations in the Norway spruce during 53 years in southern Sweden. Note the peak indicating 3-year cyclicity. Data from Hagner (1965).

But why should there be any difference between the four species, which after all experience the same variation in cone production? The explanation appears to be twofold. First, competition is often severe in seed and cone insects, and it may restrict the number of coexisting species (e.g. Mattson 1986). When the emerging insect population is large in comparison with the number of cones, all or nearly all cones and cone-breeding insects die (Stadnitskii & Grebenschchikova 1971, Mattson 1980, Miller & Hedlin 1984). Second, if populations are constrained to adopt one of the two types of prolonged diapause illustrated in Fig. 4, the optimal diapause behaviour depends on what the other species are doing, and coexistence should be easier if two species have different diapause behaviours. The species with short diapause has a refuge from interspecific competition in the years of low cone production, while the species with long diapause has a relative abundance of resources in the years of peak cone production. Admittedly, one polymorphic species could use all of the resource regardless of temporal variation. Why the four species in Fig. 4 show two distinct types of ELD is not clear.

The above idea can be demonstrated using a model of two species with different diapause behaviours. Since the seed insects are competitively inferior to cone insects (Annila 1981), I have assumed an asymmetric competitive interaction, with the cone species having the shorter diapause (as in Fig. 4). The following model has been modified from Bulmer (1984):

$$N_1(t+1) = N_1(t)\{DS + Q\exp[r(1-QN_1(t)/K(t))]\} \quad (9a)$$

$$N_2(t+n) = N_2(t)\, S^{n-1} \exp\{r\,[1-(N_2(t) + QN_1(t))\,/\,K(t)]\} \quad (9b)$$

In the competitively superior species, fraction Q of individuals in prolonged diapause emerges in any one year, while the rest (fraction D) remains in diapause; in the inferior species, ELD is always n years long. Individuals in prolonged diapause survive with probability S from one year to another. The carrying capacity $K(t)$ is a sum of two components, $K(t) = R(t) + C(t)$, where $R(t)$ is a random variable and represents random year-to-year variation in the cone crop size, while $C(t)$ is a cyclic component attaining a constant positive value C every nth year and being zero in other years.

Fig. 6 shows one result of numerical simulations of this model. Coexistence between the two species is possible if C exceeds a critical value, and for a given value of C, coexistence becomes easier with increasing S. This model gives a transparent example of coexistence mediated by temporal variation in resource availability (for a general model see Levins 1979). The different types of ELD may significantly contribute to the coexistence of the four competing species on the same resource. More generally, even without different patterns of diapause, ELD may facilitate coexistence of competitors due to the "storage effect" (Chesson 1983).

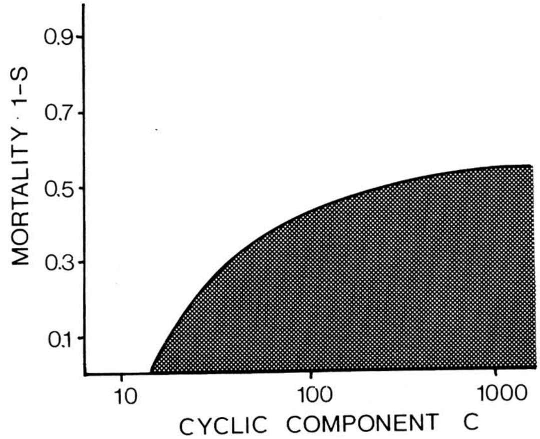

Fig. 6. Results of numerical simulations of the model of Eq. (9). The two species coexist in the shaded region, while species 2 is excluded elsewhere in the parameter space. The following parameter values were used: $r = 1.5$, $n = 3$, R uniformly distributed between 10 and 110, and $Q = 0.52$, which is the ESS value for species 1 (solved numerically).

5.2. Host-parasitoid interaction

A complex situation of prolonged diapause occurs in an unknown number of host-parasitoid systems, with a fraction of both host and parasitoid individuals entering prolonged diapause. The best documented examples include the seed and cone insects and their parasitoids (e.g. Annila 1981), and pine sawflies (Diprionidae) and their parasitoids (e.g. Kolomiets et al. 1979).

Annila (1981) studied the seed and cone insects of the Norway spruce and their parasitoids in Finland (see Section 3.2). Prolonged diapause is very common in these insects, apparently because of the greatly varying resource availability from one year to another. Prolonged diapause is equally characteristic for the respective parasitoids; their emergence is furthermore well synchronized with host emergence. The parasitoids of *Plemeliella abietina* tended to emerge synchronously with the host individuals even if they had developed in different years, suggesting that emergence of both the host and the parasitoid were at least partly timed by the same external cues (Annila 1981). In other cases, when the parasitoid has not killed the host individual during its early development, it may simply follow the diapause behaviour of the host, whether it is simple or prolonged. Two examples are the ichneumonid *Lamachus eques* and the tachinid *Drino gilva* parasitizing *Neodiprion sertifer* (Martinek 1985 and references therein).

An interesting detail is that the parasitoids (*Atractodes, Melanips*) of *Hylemyia anthracina* stayed in prolonged diapause consistently longer, on average, than the host individuals (7 comparisons; Annila 1981). The results of Kolomiets et al. (1979) on the sawfly *Neodiprion sertifer* and its parasitoid *Pheolophus basizonus*, also indicate that the parasitoid stayed in prolonged diapause longer on average than its host. Whether the longer diapause in the parasitoid than in the host is a general phenomenon, and whether it is adaptive, remain open questions.

Another interesting question is whether host-parasitoid or predator-prey dynamics alone can lead to prolonged diapause in the host and/or the parasitoid population. If the parasitoid regulates the host population to a stable equilibrium density, there is little scope for evolution of prolonged diapause, because there is little temporal variation in fitness. If the dynamics are cyclic or chaotic the situation is different, and some form of prolonged diapause may evolve, as in Bulmer's (1984) single species competition model (Section 3.2). As far as I know, there are no studies on this topic.

6. Extra long diapause and population dynamics

Extra long diapause tends to decrease variation in population size when emergence is independent of immediate environmental conditions as seems to be the case in most insects. Takahashi (1977) calls such increased stability a "carry-over" effect: prolonged diapause buffers population size against drastic declines in poor breeding seasons. Takahashi's (1977) carry-over effect is analogous to Chesson's (1983) "storage effect" in iteroparous species. Note that this is a population level consequence of prolonged diapause, not an argument as to why prolonged diapause has evolved in the first place.

Table 2. Prolonged diapause in *Pegomya* (Diptera: Anthomyiidae) breeding in *Leccinum* (Boletaceae) fruiting bodies in Finnish Lapland. The frequency of prolonged diapause and species' abundance are correlated at 5% level (Olmstead-Tukey's corner test; Sokal & Rohlf 1981). A total of 6941 flies were reared from more than 100 sporophores in 2 years. Data from Ståhls (1987).

Species	Frequency of prolonged diapause (% of individuals)	Relative abundance in 2 years
P. scapularis	16	0.50
P. transgressa	21	0.21
P. flavoscutellata	68	0.11
P. zonata	20	0.10
P. notabilis	7	0.04
P. incisiva	13	0.02
P. circumpolaris	4	0.02

Fungivorous *Pegomya* flies breeding in *Leccinum* mushrooms in Lapland provide an example. The frequency of prolonged diapause varies highly significantly between species, from 4 to 68% in one large set of material (Table 2). The interesting point is that the species with a high frequency of prolonged diapause tended to be more abundant than species with a low frequency of prolonged diapause — as one would expect if prolonged diapause significantly buffers the population against bad summers. A few flies emerged after three winters (Ståhls, pers. comm.), and all these individuals were *P. transgressa*, the only *Pegomya* in Table 2 which is restricted to Lapland in Finland.

Most *Pegomya* in Lapland occur at the northern limit of their geographical range. Wipking & Neumann (1986) have shown that prolonged diapause is common in the German populations of the Burnet moth *Zygaena trifolii*, but not in the Spanish populations of the same species. The German populations occur at the northern limit of the species, in small and isolated habitat patches. Prolonged diapause may generally be important for the survival of marginal populations, which presumably experience a high level of "temporal variability" in the environment to which they are poorly adapted (for other examples see Waldbauer 1978).

Prolonged diapause can also increase population stability when fluctuations are due entirely to population dynamic causes. MacDonald (1976) has analysed the following discrete time single species model:

$$N_{t+2} = (1-D)\,N_{t+1}\exp(r - aN_{t+1}) + DN_t\exp(r - aN_t), \qquad (10)$$

where a fraction D of individuals enters a 2-year diapause. With D=0 the model has a stable equilibrium point for $r < 2$, and a 2-point cycle for $2 \leq r \leq 2.53$ (May 1974). For D in the range 0.02–0.2 the range of r values over which the 2-point cycle is stable is dramatically increased, for example, for D=0.1 the critical value of r is approximately 4.4 (MacDonald 1976). This simple model suggests that 2-year cycles should be relatively common in species with a moderately large values of D.

Moths in the genus *Xestia* show a striking 2-year abundance cycle in northern Europe (Mikkola 1976) and northern North America (Lafontaine et al. 1987). These species are said to have two obligatory diapauses at larval and prepupal stages (Lafontaine et al. 1987). The problem that needs to be explained is the scarcity (typical in most parts of northern Europe; Mikkola 1976) or apparent absence (e.g. the Kilpisjärvi region in Finnish Lapland and the whole of North America; Lafontaine et al. 1987) of the alternate-year population. Kettlewell (in Ford 1955) and Mikkola (1976) have suggested that the 2-year development time is an adaptation against parasitism and/or predation. However, such a mechanism would not be effective against generalist parasitoids and predators with alternative host species, and specialist parasitoids could presumably adopt the same 2-year development time as their host species (see previous Section) — or they would become extinct, in which case there would be selection back to the 1-year development time.

The model of Eq. (10) suggests an alternative or complementary explanation to the observed alternate year flight in *Xestia* moths. The small size of the population in every second year, and the observed mosaic distribution of the odd- and even-year populations in northern Europe (Mikkola 1976) could be explained by a 2-year abundance cycle. Interspecific synchrony (Mikkola 1976, Lafontaine et al. 1987), which is another characteristic feature of *Xestia* abundance dynamics, may have been brought about by exceptionally bad or good years (Valle 1933). Unfortunately, there are no good data on the development time of *Xestia* under different conditions (Mikkola pers. comm.). Perhaps some populations are polymorphic, as assumed in the model. If, as seems to be the case for other populations, the development time is fixed to two years, this may have happened because individuals emerging in the low year of a large-amplitude 2-year cycle had difficulty in finding a mate.

7. Discussion

This final section is limited to two comparisons that are of wider ecological interest: the contrast between diapause and dispersal, and the comparison of dormancy in insects with that in plants (seeds). The latter comparison is appropriate also because nearly all of the theoretical studies reviewed in this paper were originally inspired by botanical examples, dormancy and delayed germination of seeds.

Dispersal and diapause (dormancy) are often contrasted as two alternative responses to unfavourable environmental conditions (e.g. Southwood 1977). The models reviewed in Section 3.2 support this notion. A more detailed classification would distinguish between simple diapause and ELD on the one hand, and movements within and between populations on the other. Simple diapause is analogous to within-population movements, in particular to movements in search of a suitable breeding microhabitat. Between-population movements have an analogous function to prolonged diapause: in both cases individuals move, in time or space, to a population dynamic and environmental situation that is only partly or not at all predictable from the current one. Some seasonal movements between habitats may be comparable to those cases of density-dependent premature diapause in which an individual times its breeding so that it occurs during predictable periods of low density (e.g. *Lucilia* in Section 4.1).

The above distinctions may clarify comparisons between annual plants and insects. Multiannual dormancy is common in plants, while apparently much less common in insects. There may be several reasons for this difference, for example, dormancy is probably metabolically cheaper for seeds than for insects, making very long seed dormancies feasible. But note that unlike insects, plants cannot use "within-population dispersal" to locate a suitable germination site: seeds, once dispersed from the parent plant, cannot move voluntarily (notwithstanding Harper 1977: 51). If a seed is buried at a depth or at a site where germination would fail, it is obviously better for it to stay dormant and wait for a chance event (e.g. soil disturbance) that would bring it to a suitable germination microhabitat. Such a situation is uncommon in insects, though perhaps not nonexistent. Price & Tripp (1972) suggest that the depth of the soil at which the cocoons of the Swaine jack pine sawfly *Neodiprion swainei* are located may play a role in the induction of prolonged diapause in this species.

In conclusion, an important general difference in the long dormancies of plants and insects appears to exist. Dormant seeds in the soil may be in "innate", "enforced" or "induced" dormancy, but in most cases their dormancy is supposed to be broken by the appropriate deterministic stimuli (Harper 1977). There are exceptions, however, as discussed by Grubb in this volume. In contrast, the length of ELD in insects appears to be more independent of the prevailing environmental conditions, though again there are exceptions (above and Section 5). One reason why seed-type ELD may be uncommon in insects is their ability to move, and thereby locate suitable microhabitats for breeding. If a comparison is made in the frequency of risk-spreading multiannual dormancies, plants and insects may not be as different as at first appears.

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References

Annila, E. 1981: Fluctuations in cone and seed insect populations in Norway spruce. (In Finnish with English summary.) — Commun. Inst. Forest Fennica 101:1–32.

—"— 1982: Diapause and population fluctuations in Megastigmus specularis Walley and Megastigmus spermotrophus Wachtl. (Hymenoptera, Torymidae). — Ann. Entomol. Fennici 48:33–36.

Bakke, A. 1963: Studies on the spruce-cone insects Laspeyresia strobilella (L.) (Lepidoptera: Tortricidae), Kaltenbachiola strobi (Winn.) (Diptera: Itonidae) and the parasites (Hymenoptera) in Norway. — Meddel. Norske Skogf. 19:1–151.

Barak, A. V. & Burkholder, W. E. 1977: Studies on the biology of Attagenus elongatulus Casey (Coleoptera: Dermestidae) and the effects of larval crowding on pupation and life cycle. — J. Stored Prod. Res. 13:169–175.

Botella, L. & Mensua, J. L. 1987: Larval diapause induced by crowding in Chymomyza costata (Diptera: Drosophilidae). — Ann. Entomol. Fennici 53:41–47.

Bulmer, M. G. 1984: Delayed germination of seeds: Cohen's model revisited. — Theor. Pop. Biol. 26:367–377.

Burges, H. D. 1963: Studies of the dermestid beetle Trogoderma granarium Everts. VI. Factors inducing diapause. — Bull. Entomol. Res. 54:571–587.

Cambefort, Y. 1984: Étude écologique des Coléoptères Scarabaeidae de Côte d'Ivoire. — Travaux des Chercheurs de la station de Lamto, Université d'Abidjan (unpublished Ph.D. thesis).

Chesson, P. L. 1983: Coexistence of competitors in a stochastic environment: the storage effect. — In: Freedman, H. I. & Strobeck, C. (eds.), Population biology. Lecture Notes in Biomath. 52:188–198.

Chesson, P. L. & Warner, R. R. 1981: Environmental variability promotes coexistence in lottery competitive systems. — Amer. Nat. 117:923–943.

Cohen, D. 1966: Optimizing reproduction in a randomly varying environment. — J. Theor. Biol. 12:119–129.

—"— 1967: Optimizing reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. — J. Theor. Biol. 16:1–14.

—"— 1968: A general model of optimal reproduction in a randomly varying environment. — J. Ecol. 56:219–228.

—"— 1970: A theoretical model for the optimal timing of diapause. — Amer. Nat. 104:389–400.

Cook, R. 1980: The biology of seeds in the soil. — In: Sollbrig, F. (ed.), Demography and evolution in plant populations. Botanical Monographs 15:107–131.

Danks, H. V. 1987: Insect dormancy: An ecological perspective. — Biological Survey of Canada No. 1, Ottawa.

Eichhorn, O. 1982: Untersuchungen zur Ökologie der gemeinen Kiefern-Buschhornblattwespe, Diprion pini (L.) (Hym., Diprionidae). VII. Populationsdynamische Faktoren. — Zeitschr. Angew. Entomol. 94:271–300.

Ellner, S. 1985a: ESS germination strategies in randomly varying environments. I. Logistic-type models. — Theor. Pop. Biol. 28:50–79.

—"— 1985b: ESS germination strategies in randomly varying environments. II. Reciprocal-yield laws. — Theor. Pop. Biol. 28:80–116.

—"— 1987: Competition and dormancy: a reanalysis and review. — Amer. Nat. 130:798–803.

Ellner, S. & Shmida, A. 1981: Why are adaptations for long-range seed dispersal rare in desert plants? — Oecologia 51:133–144.

Ford, E. B. 1955: Moths. — London.

Gadgil, M. 1971: Dispersal: population consequences and evolution. — Ecology 52:253–261.

Hackman, W. 1976: The biology of Anthomyiid flies feeding as larvae in fungi (Diptera). — Notulae Entomol. 56: 129–134.

Hagner, S. 1965: Cone crop fluctuations in Scots Pine and Norway Spruce. — Studia Forest. Suecica 33:1–21.

Hagstrum, D. W. & Silhacek, D. L. 1980: Diapause induction in Ephestia cautella: an interaction between genotype and environment. — Entomol. Exp. & Appl. 28:29–37.

Hamilton, W. D. & May, R. M. 1977: Dispersal in stable habitats. — Nature 269:578–581.

Hanski, I. 1987a: Carrion fly community dynamics: patchiness, seasonality and coexistence. — Ecol. Entomol. 12:257–266.

—"— 1987b: Nutritional ecology of dung- and carrion-feeding insects. — In: Slansky, F. Jr. & Rodriguez, J. G. (eds), Nutritional ecology of insects, mites, spiders, and related invertebrates: 837–884. John Wiley and Sons, New York.

—"— 1987c: Pine sawfly population dynamics: patterns, processes, problems. — Oikos 50:327–335.

—"— 1988: Fungivory: fungi, insects and ecology. — Symp. R. Entomol. Soc. London (in press).

Harper, J. L. 1977: Population biology of plants. — Academic Press, London.

Hedlin, A. F., Miller, G. E. & Ruth, D. S. 1982: Induction of prolonged diapause in Barbara colfaxiana (Lepidoptera: Olethreutidae): correlations with cone crops and weather. — Can. Entomol. 114:465–471.

Istock, C. A., Wasserman, S. S. & Zimmer, H. 1975: Ecology and evolution of the pitcher plant mosquito. 1. Population dynamics and laboratory responses to food and population density. — Evolution 29:296–312.

Janzen, D. H. 1971: Seed predation by animals. — Ann. Rev. Ecol. Syst. 2:465–492.

—"— 1987: When, and when not to leave. — Oikos 49:241–243.

Klinkhamer, P. G. L., De Jong, T. J., Jong, T. J., Metz, J. A. J. & Val, J. 1987: Life history tactics of annual organisms: the joint effects of dispersal and delayed germination. — Theor. Pop. Biol. 32:127–156.

Kolomiets, N. G., Stadnitskii, G. V. & Vorontzov, A. I. 1979: The European pine sawfly. — Amer. Publ. Co., Pvt. Ltd., New Delhi.

Lafontaine, J. D., Mikkola, K. & Kononenko, V. S. 1988: A revision of the genus Xestia Hbn. subg. Pachnobia Gn. (Lepidoptera: Noctuidae), with descriptions of two new subspecies. — Entomol. Scand. (in press).

León, J. A. 1985: Germination strategies. — In: Greenwood, P. J., Harvey, P. H. & Slatkin, M. (eds.), Evolution. Essays in honour of John Maynard Smith: 129–142. Cambridge University Press, Cambridge.

Levin, S. A., Cohen, D. & Hastings, A. 1984: Dispersal strategies in patchy environments. — Theor. Pop. Biol. 26:165–191.

Levins, R. 1979: Coexistence in a variable environment. — Amer. Nat. 114:765–783.

Livdahl, T. P. & Edgerly, J. S. 1987: Egg hatching inhibition: field evidence for population regulation in a treehole mosquito. — Ecol. Entomol. 12:395–399.

MacArthur, R. H. 1972: Geographical Ecology. — Harper & Row, New York.

MacDonald, N. 1976: Extended diapause in a discrete generation population model. — Math. Biosc. 31:255–257.

Martinek, V. 1985: Egg- and larval parasites of the European pine sawfly Neodiprion sertifer (GEOFF.) in Bohemia. — 123 pp. Ceskoslovenska Akademie Ved, Praha.

Mattson, W. J. 1980: Cone resources and the ecology of the red pine cone beetle, Conophthorus resinosae (Coleoptera: Scolytidae). — Ann. Entom. Soc. Amer. 73: 390–396.

—"— 1986: Competition for food between two principal cone insects of red pine, Pinus resinosa. — Envir. Entom. 15:88–92.

May, R. M. 1974: Biological populations with non-overlapping generations: stable points, stable cycles and chaos. — Science 186:645–647.

Metz, J. A. J., De Jong, T. J., Jong, T. J. & Klinkhamer, P. G. L. 1983: What are the advantages of dispersing; a paper by Kuno explained and extended. — Oecologia 57:166–169.

Mikkola, K. 1976: Alternate-year flight of northern Xestia species (Lep., Noctuidae) and its adaptive significance. — Ann. Entomol. Fennici 42:191–199.

Miller, G. E. & Hedlin, A. F. 1984: Douglas-fir cone moth and cone gall midge: relation of damage and prolonged diapause to seed cone abundance in British Columbia, Canada. — In: Yates, H. O. (ed.), Proc. cone and seed insect working party conference: 91–100. Athens, Ga., Usa, Working party S2.07.01.

Nair, K. S. S. & Desai, A. K. 1972: Some new findings on factors inducing diapause in Trogoderma granarium Everts (Coleoptera, Dermestidae). — J. Stored Prod. Res. 8:27–54.

—"— 1973: Studies on the isolation of diapause and non-diapause strains of Trogoderma granarium Everts (Coleoptera, Dermestidae). — J. Stored Prod. Res. 9: 181–188.

Ohenoja, E. & Koistinen, R. 1984: Fruit body production of larger fungi in Finland. 2. Edible fungi in northern Finland 1976–1978. — Ann. Bot. Fennici 21:357–366.

Ohenoja, E. & Metsänheimo, K. 1982: Phenology and fruiting body production of macrofungi in subarctic Finnish Lapland. — In: Arctic and alpine mycology (eds. Laursem, G. A. & Ammirati, J. F.): 390–409. University of Washington Press, Seattle.

Paschalidis, K. M. 1974: The genus Sisyphys Latr. (Coleoptera: Scarabaeidae) in southern Africa. — Thèse de M.Sc., Univ. of Rhodes, Grahamstown (unpublished).

Powell, J. A. 1974: Occurrence of prolonged diapause in ethmiid moths. — Pan-Pac. Entomol. 50:220–225.

Price, P. W. & Tripp, H. A. 1972: Activity patterns of parasitoids on thé Swaine Jack Pine sawfly Neodioprion swainei (Hymenoptera: Diprionidae) and parasitoid impact on the host. — Can. Entomol. 104:1003–1016.

Roff, D. 1983: Phenological adaptation in a seasonal environment: a theoretical perspective. — In: Brown, V.K. & Hodek, I. (eds.), Diapause and life cycle strategies in insects: 253–270. Dr. W. Junk Publ., The Hague.

Schwenke, W. 1982: Die Forstschädlinge Europas. Haultflügler und Zweiflügler. — Paul Parey, Hamburg.

Smith, C. C. & Balda, R. P. 1979: Competition among insects, birds and mammals for conifer seeds. — Amer. Zool. 19:1065–1083.

Sokal, R. R. & Rolf, F. J. 1981: Biometry. — Freeman and Company, San Francisco.

Southwood, T. R. E. 1977: Habitat, the templet for ecological strategies. — J. Anim. Ecol. 46:337–365.

Spence, J. R. 1986: Interactions between the scelionid egg parasitoid Tiphodytes gerriphagus (Hymenoptera) and its gerrid hosts (Heteroptera). — Can. J. Zool. 64:2728–2738.

Stadnitskii, G. V., Iurchenko, G. I., Smetanin, A. N. & al. 1978: Vrediteli shishek i semian svoinykh porod. — Lesnaia promyshlennost Publ. House, Moscow.

Ståhls, G. 1987: Diptera levande i svamp i Kilpisjärvi-trakten. — M.Sc. Thesis, Univ. Helsinki (unpubl.).

Takahashi, F. 1977: Generation carryover of a fraction of population members as an animal adaptation to unstable environmental conditions. — Res. Popul. Ecol. 18: 235–242.

Tauber, M. J., Tauber, C. A. & Masaki, S. 1986: Seasonal adaptations of insects. — Oxford University Press, Oxford.

Taylor, F. 1980: Optimal switching to diapause in relation to the onset of winter. — Theor. Pop. Biol. 18:125–133.

—"— 1986: Toward a theory for the evolution of the timing of hibernal diapause. — In: Taylor, F. & Karban, R. (eds.), The evolution of insect life cycles: 236–257. Springer-Verlag, New York.

Tsuji, H. 1959: Studies on the diapause of the Indian-Meal Moth, Plodia interpunctella Hübner. II. The effect of population density on the induction of diapause. — Jap. J. Appl. Entomol. Zool. 3:34–40.

—"— 1960: Studies on the ecological life history of the Indian-Meal Moth, Plodia interpunctella Hübner. I. Comparative studies of the three stocks with special reference to the onset of diapause. — Jap. J. Appl. Entomol. Zool. 4:173–180.

Valle, K. J. 1933: Die Lepidopterenfauna des Petsamogebietes. — Ann. Zool. Soc. Vanamo 1:1–262.

Venable, D. L. & Lawlor, L. 1980: Delayed germination and dispersal in desert annuals: escape in space and time. — Oecologia 46:272–282.

Vepsäläinen, K. 1978: Wing dimorphism and diapause in Gerris: determination and adaptive significance. — In: Dingle, H. (ed.), Evolution of insect migration and diapause: 218–253. Springer-Verlag, New York.

Vinogradova, E. B. 1986: Geographical variation and ecological control of diapause in flies. — In: Taylor, F. & Karban, R. (eds.), The evolution of insect life cycles: 35–47. Springer-Verlag, New York.

Waldbauer, G. P. 1978: Phenological adaptation and the polymodal emergence patterns of insects. — In: Dingle, H. (ed.), Evolution of insect migration and diapause: 127–144. Springer-Verlag, New York.

Westoby, M. 1981: How diversified seed germination behavior is selected. — Amer. Nat. 118:882–885.

Wiklund, C., Persson, A. & Wickman, P. O. 1983: Larval aestivation and direct development as alternative strategies in the speckled wood butterfly, Pararge aegeria, in Sweden. — Ecol. Entomol. 8:233–238.

Winjum, J. K. & Johnson, N. E. 1964: Differences in cone numbers, lengths, and cut-counts in the crowns of young open-grown Douglas-fir. — J. For. 62:389–391.

Wipking, W. & Neumann, D. 1986: Polymorphism in the larval hibernation strategy of the burnet moth, Zygaena trifolii. — In: Taylor, F. & Karban, R. (eds.), The evolution of insect life cycles: 123–134. Springer-Verlag, New York.

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