

# Overview: Structure and Evolution of Dormancy

## Introduction

Dormancy responses are both integrated and diverse. Responses are integrated throughout the life cycle to meet multiple constraints, caused by variations in factors such as climate, foodplants and predators that act at all times through development. Therefore life cycle *systems* rather than single dormancies control seasonal timing, as discussed in Chapter 10. Such a holistic view was taken by Sugiki and Masaki (1972, p. 277), in pointing out that the selective advantage of diapause is not determined only by the character of diapause itself. Responses are adaptive as a set so that, for example, a non-diapause strain of the cricket *Gryllus campestris* selected in the laboratory was not viable under certain natural conditions (Fuzeau-Braesch and Ismail 1976).

Dormancy responses are diverse because seasonal problems vary regionally, locally, from year to year, and in so many other ways that different demands are placed on different species and on one species in different places. The wide repertoire of adaptations evolved in response to these demands includes sensitivity in almost any stage, sensitivity to absolute or relative cues provided by photoperiod, temperature, food, moisture, density, and other factors, variations in sensitivity or in the duration of the sensitive stage, and arrested, retarded or accelerated development in almost any life stage including those in following generation(s).

A particular seasonal problem therefore can be solved in a great variety of ways by combining options from this repertoire of responses. Since diapause has evolved independently many times, the combination of options even to solve the same problem — notably to synchronize the time or spread of emergence or reproduction with suitable conditions — may differ widely from one species to another, and even within a species. Clifford (1982) concluded for mayflies that “the more thoroughly a species is studied, the more flexible its life cycle appears”.

Given this diversity, how can useful generalizations about life-cycle systems be arrived at? Two further enquiries help to orientate the answers to this question: What controls, cues, and developmental alternatives are used, and how are they organized; and how did the responses evolve? Those enquiries are the subject of this chapter.

## Structure of dormancy responses

### *Multiplicity of developmental controls*

Far more developmental possibilities are available than are needed to produce any given response. The responses summarized in previous chapters suggest that most

species attain adequate seasonal control with rather few options. Table 40 (Chapter 10) indicates some ways in which responses can be made more complex to meet particular cases, but the majority of species possess relatively simple systems, with respect both to the nature of effective cues, and the number of developmental alternatives. However, very complex responses can be derived by combining only a few options: three successive alternatives provide 8 ( $2^3$ ) different routes of development, as demonstrated for dormancy in eggs of the grasshopper *Chortoicetes terminifera* (see Chapter 10). A similar multiplicity of routes is seen in the eggs of annual fishes from temporary pools (e.g. Wourms 1972). Moreover, the results of each route have a distribution in time, so that either several separate results, or a continuous spread over time, can be achieved (e.g. eggs of the fish *Austrofundulus myersi* may take from 40 to 316 days to hatch (Wourms 1972)).

#### *Cues for the induction and completion of diapause*

As might be expected, diapause in most species is induced by the most reliable and easily perceived cue, absolute photoperiod, often modified by temperature level. In many if not most species investigated in detail photoperiod and temperature interact, or additional, ancillary, responses modify the effect of photoperiod or temperature. Such interaction or modification has often led to argument and confusion (compare, for example, McLeod and Driscoll 1967; Read 1968). Sometimes, alternative cues must be used because habitat filters out the usual cue. However, additional or alternative cues frequently are used in other circumstances, and include change of photoperiod or temperature as well as food, density and other factors. The frequency of use of ancillary cues suggests that relatively minor adjustments of the basic response have significant survival value. A related pattern is for control to depend rather simply on responses of a single stage, but for the effect of cues received earlier, which usually are overridden, to be retained if current cues are ambiguous (e.g. Adkisson and Roach 1971 for *Heliothis zea*). The seasonal signals that induce diapause may readily control also a variety of other developmental processes such as diapause intensity, diapause development, and non-diapause developmental rate (Chapters 7, 8, 10).

To say that the cues used by a given species are those that provide useful seasonal information is perhaps trivial, but such a truism makes clear that the components of sensitivity and response are fully integrated. This integration occurs in the central nervous system (see Chapter 13). Integration has already been recognized by several authors for diapause development (environmental information is integrated through the dormant period), but not clearly stated to apply to diapause induction. Cases of "spontaneous" induction or completion, which are less dependent on external cues, suggest a slightly different perspective, as next outlined, that takes more account of internal programmes.

#### *Developmental alternatives*

A pathway for development may be either active, passive or intermediate, depending on the programme: development continues uninterrupted unless signalled otherwise; development ceases until signalled otherwise; or requirements for either alternative change with time. Failure to recognize that these are simply alternative controls of dormancy has led to some confusion over the existence of "obligate" diapause and

“spontaneous” development, for example. Often such alternatives are combined at the same time (e.g. “fading of internal inhibition” and “external stimulation” end diapause in the bug *Aelia acuminata*: Hodek 1974a, p. 70).

Most authors have assumed that continuous development is “normal” and diapause is “induced”. Certain “obligate” dormancies that require a change in conditions to complete development (e.g. Table 23) are a set of opposite cases, in which *development* has to be induced by an appropriate pattern of external factors. Thanh-Xuan (1967a, b) assumed that diapause was “normal” but could be eliminated by earlier treatments.

Similar partly semantic difficulties have arisen in the discussion of developmental pathways in aphids. For example, conventional wisdom suggests that alatae rather than apterae are produced by given conditions such as crowding of the parents (e.g. Lees 1979, p. 232); but Mittler (1973) believed that alates may be “normal” and certain factors that promote apterization, such as deficient nutrition, should be sought. Active or passive alternatives also prevail in the control of development at the physiological level: some diapauses are maintained by a lack of neurosecretion; others rely on continued neurosecretion (Chapter 13).

Whether a tendency to diapause or not to diapause is more prevalent in a given species presumably depends on the particular seasonal constraints to which it is adapted. In the ichneumonid *Bathyplectes curculionis*, development of the second generation continues only if circumstances of photoperiod and temperature and (to a lesser extent) relative humidity, maternal age, and host, are “ideal”, and any departure increases the incidence of diapause (Parrish and Davis 1978). This pattern reflects a “fail-safe” system or conservative mode of response, which favours diapause. An even more conservative result is produced by a two-stage response requiring a change of conditions before development can continue (see Table 23). More than two stages, usually including more than one successive dormancy, occur in some species from unpredictable habitats. Development of the diapause instar or stage can be arrested at several substages, and the next life stage will not be reached unless a series of particular events is experienced: a supply of moisture or particular patterns of temperature, for example, are required to move development through successive substages (e.g. dormancy of eggs of *Chortoicetes terminifera* discussed in Chapter 10). In contrast to these multiple means of interrupting development, most authors have concluded that in many species development continues unless very specific conditions for diapause are met, such as a narrow range of photoperiod or temperature for induction (compare Chapter 7).

An important feature of developmental systems is that arresting any step of the process will prevent completion: failure to satisfy the demands of a single subsystem within the sequence of egg development, for example, stops the life cycle; lack of any of the necessary resources, such as moisture and temperature, can prevent development. From this perspective, development is best regarded as a system of gates (along a pathway) and switches (between alternative pathways), some of which are reversible: pre-programmed routes of development are triggered by appropriate successive events or sets of conditions. Exactly the same concept has been used to analyse behaviour, moulting and differentiation, and other characteristics of organisms. The steps in dormancies differ in no qualitative way from these other phenomena, though many of the triggers for diapause and related phenomena (unlike

development regulated in the commonly accepted way) include token stimuli that anticipate a change. Dormancies are thus only a part, albeit sometimes a conspicuous one, of normal schemes of development.

Such a concept may allow "single" stages of development or dormancy to be correctly viewed as a *series* of steps and thus indicate how they can be analyzed experimentally. Between each step, of course, steady development may occur, so that the insect in diapause is not a static object: diapause larvae of the pteromalid *Nasonia* (formerly *Mormoniella*) *vitripennis* undergo the slow but persistent physiological changes of diapause development (cf. Schneiderman and Horwitz 1958, p. 546); eggs of the fly *Delia* (formerly *Leptohylemyia*) *coarctata* must develop at moderate temperatures before cold exposures are effective in producing diapause development (Way 1959).

Switches and barriers to development can take various forms. Hormonal controls have attracted the most attention (Chapter 13). In some insects, the egg chorion is impermeable to water or oxygen until diapause ends, a mechanical system paralleled in some plants by the impermeable seed coat, which prevents water uptake and hence maintains dormancy (e.g. Proceedings: Plant Dormancy 1981).

#### *Linkage between successive controls of development*

In the step-wise view of development just outlined, successive controls are all linked in the sense that developmental requirements for one stage must be met before a subsequent stage is reached and can respond. For example, in the beetle *Henosepilachna vigintioctopunctata*, entry into diapause requires that substantial food reserves are built up, and deficient nutrition as well as appropriate token stimuli therefore prevent diapause (Kono 1979). However, species vary in the degree to which conditions can modify responses (Chapters 4, 7, 8) during a stage or in a subsequent stage (Chapter 5), and in the degree to which the successive components of the response share controlling cues (Chapter 6) or internal systems (Chapters 9, 11, 12, 13).

Apparently, successive steps in development nevertheless are largely controlled independently, just as are most concurrent and related but different aspects of the response to token stimuli, such as seasonal morphs or cold-hardiness in some species and diapause (see Chapter 3). For example, in the mosquito *Aedes triseriatus* the critical photoperiod, and its change with latitude, differs for embryonic development, larval development, and the rate of larval development (Holzapfel and Bradshaw 1981, fig. 6). The critical photoperiods for reproductive diapause and for flight activity in the lacewing *Chrysoperla carnea* are different, and change in opposite directions with latitude (Bowden 1979).

#### *Consequences of alternative pathways for development*

Some characteristics of dormant and diapause-destined individuals were discussed in Chapter 3. These individuals often differ significantly from individuals that develop directly. Some of the features of individuals in diapause, controlled by the same cues as or different cues than the diapause, are merely correlated with the diapause condition, and do not result from it. Other features depend on the particular developmental pathway that is taken; for example, both fecundity and rate of early development often are reduced in individuals that enter diapause.

In a few species, the effects are prolonged from stage to stage. For example, larvae of the grasshopper *Chortoicetes terminifera* that have hatched from non-diapause eggs are more sensitive to the delay in growth caused by short days than are larvae hatched from eggs that have been in diapause (Wardaugh 1979). "Interval timers", which prevent certain responses until after a delay, were discussed in Chapter 9.

An interesting consequence of diapause in some species is the retardation of development that precedes it (Chapter 10). In some species, the more development is delayed, the more variation appears in the subsequent resumption of development. For example, those *Chortoicetes* larvae that grow most slowly also become adult most variably (Wardaugh 1979). In the cricket *Gryllus campestris* (Fuzeau-Braesch 1963; Fuzeau-Braesch and Ismail 1976) delayed development also produces more variation in the duration of development. Some such effects result simply from the fact that there is a somewhat greater range of durations when the mean duration of development is greater, or from additional requirements for food storage for diapause. However, the spreading of risk may be adaptive whenever a response to adversity (diapause) has been programmed, because although conditions will become adverse, they will do so with some degree of unpredictability. Increases in variation among individuals with delayed development may also have a parental component (e.g. Fuzeau-Braesch 1963, p. 794).

### Evolution of dormancy responses

#### *Introduction*

The question "Why did dormancy responses evolve?" supposes that the responses are adaptive. Evidence from geographic variation, which reflects finely tuned reactions to local conditions and favours survival there, most strongly supports this supposition, discounting the statement of Simmonds (1948, p. 413) that the adaptive value of diapause was questionable and its usefulness fortuitous! Evidence from a wide range of organisms shows that responses similar to those discussed for insects in previous chapters are widespread, and accord with the same external (environmental) pressures even in organisms of very different structure and function. This conclusion is illustrated by a few recent examples; a few other examples have already been referred to.

As in insects, dormancy can be induced by intrinsic rhythms modified by external factors (Marshall and Disney 1957 (birds)), and in a particularly wide variety of organisms by responses to photoperiod (Pourriot *et al.* 1981 (rotifers); De March 1982; Einsle 1967; Madhavan and Shribbs 1981; Marcus 1980, 1982*a, b*; Mocquard *et al.* 1976, 1978, 1980; Nelson *et al.* 1983; Watson and Smallman 1971*a*; Williams 1978; etc. (marine, freshwater and terrestrial crustaceans), Longman 1969 (trees)), including quantitative as well as qualitative responses (Follett 1981 (birds)). Such responses often are cued in detail in a similar way to insects: for example, the photoperiodic threshold includes twilight in many plant species (Greulach 1942); it is usually the absolute value of photoperiod that is important (e.g. Juchault *et al.* 1982 (crustaceans)). Temperature (e.g. Watras 1983 (crustaceans)) — including thermoperiod (Weld and Meier 1983 (fish), Stross 1969*a*, 1971 (suggested for crustaceans)) — food, density and other factors (Carvalho and Hughes 1983 and

references cited there (crustaceans)) can also act as cues for diapause induction. There are also geographic differences among strains in these responses (Ferrari and Hebert 1982; Juchault *et al.* 1980; Marcus 1980, 1984; Stross 1969*b* (crustaceans)). Diapause can be ended (“diapause development”), as in insects, especially by temperature (Gavaud 1983 (reptiles); Marcus 1979 (crustaceans); Young 1974 (turbellarians); Bewley and Black 1982 (many plant seeds)).

These proximate factors that directly control or cue the responses from day to day have been dealt with in detail in previous chapters, and are not considered further here. But their widespread occurrence in insects and in other organisms suggests coincident environmental patterns that have led on many occasions to the evolution of dormancies. This section seeks to define the ultimate selective pressures responsible for this evolution.

Although individual factors must be discussed serially, in fact selective pressures derive from various integrated effects on the life cycle. Discussion of factors that may impose temporal constraints is therefore followed by some consideration of adaptive alternatives among species, of integrated systems that may include different options in single species, and of questions of resource allocation and spreading of risk. A small number of examples has been chosen to illustrate these discussions. The possible origins of diapause, that is *how* rather than *why* it has evolved, are discussed separately.

Two cautions should be kept in mind in this section. Conclusions about adaptation are very difficult and may be spurious (e.g. Shapiro 1980*a*, p. 313, and references cited there). Much speculation about adaptive values and proximate controlling factors has been based only on correlations: for example, cool fall temperatures with rainfall were originally supposed to end adult diapause in the grasshopper *Melanoplus destructor*, because they provide conditions suitable for the growth of foodplants, whereas in fact this diapause is photoperiodically controlled (Middlekauff 1964). The second caution is that no single “selective pressure” is universally responsible for observed adaptations such as dormancy. Even in the same species, several factors act at once, and the same factor may vary in significance in different years, in different generations, or in different places.

### *Selective factors and selection*

#### 1. Physical factors

Factors that vary seasonally and may kill insects directly during the adverse season include unsuitable levels of temperature and moisture. That temperature is the selective force for winter diapause in temperate regions is generally assumed, but this assumption can be refined. Growth and development may have particular requirements that do not simply correspond to temperatures too low for survival. Rather, each life stage — for various reasons — may have particular but different requirements for active development. Egg diapause in the springtail *Lepidocyrtus lignorum* is not related to winter, but rather ensures that hatching will occur at an optimal time for juvenile survival (Leinaas 1983; Leinaas and Bleken 1983). Young larvae of the carabid beetle *Nebria brevicollis* will grow and develop best at low temperatures, but higher temperatures are needed for metamorphosis of the final instar (Thiele 1969). Such sequences have usually been regarded as reflecting the proximate control of

development, but they may indeed reflect particular physiological requirements at different *active* stages not related to temporal control. In certain plankton (marine analogues with respect to dispersal of some aerially-dispersed insects), resting eggs are thought to avoid conditions that are poor for pelagic dispersal, rather than for actual survival (Watras 1980 and references cited there). Adult diapause may delay oviposition so that larvae are not exposed to unsuitable conditions. For example, exposure of overwintering first-instar larvae of the butterfly *Speyeria zerene* to desiccating conditions is decreased by the aestivation of adults (Sims 1984). Physical factors, especially temperature, may also select for diapause by altering the efficiency of active animals (see resource allocation below) rather than their survival as such. These physical factors, of course, change characteristically with latitude and altitude. Other factors besides temperature may vary seasonally and might have selected for diapause, for example salinity (Tones 1977).

High temperature, and its correlate low moisture (and see Geographic correlates of diapause below), has sometimes been assumed to govern aestivation (but see the next subsection).

## 2. Food

Just as low temperature has been supposed to be the key to winter diapause in most species, lack of food has generally been assumed as the key to summer diapause (Masaki 1980). This is best seen in specialized species. For example, diapause of the desert butterfly *Euphydryas chalcedona* allows larvae to avoid the drought period when there are few leaves on the xerophytic shrub that is the foodplant of this species (Mooney *et al.* 1980). Similar conclusions have been drawn for other desert insects such as species of *Diparopsis* (Pearson 1962), larvae of which feed on fruits unavailable in hot dry periods. In the codling moth *Cydia pomonella*, which overwinters in diapause, some larvae of the first generation enter diapause even in the south where winters are not cold, maintaining univoltinism. This early diapause appears to be related to the short fruiting period of the apple hostplant, rather than to winter as such (Sheldeshova 1962, etc.). In Lepidoptera that overwinter in the egg stage and feed on young spring leaves, control of the life cycle and voltinism ultimately depend on synchrony with food of adequate quality (Goldschmidt 1934; Slansky 1974). Shapiro (1974) and others have pointed out that univoltine species of butterflies tend to be monophagous, whereas most of the multivoltine species are polyphagous. Synchrony in phytophagous species can be assured either by variability in the time of hatching or emergence to allow for variability in host phenology, or by the genetic divergence, or at least the distinctness, of populations each specializing (temporally and nutritionally) on a single host. Tauber *et al.* (1986, pp. 276–279) discussed some relevant examples.

The bug *Oncopeltus cingulifer antillensis* can feed on leaves as well as seeds, and so has more generally available supplies of food than its congeners confined to seeds. *O. fasciatus*, for example, which is restricted to seeds, enters reproductive diapause even in southern populations; *O. cingulifer antillensis* does not (Dingle *et al.* 1980).

Food (as well as competition), especially the availability of allochthonous particles of particular size, has been claimed to dictate the seasonality of several stream-dwelling insects such as some caddisflies that aestivate (e.g. Mackay 1972 for *Pycnopsyche scabripennis*). In the same way, a short growth period and a diapause appear to have

been selected by specialized food requirements in some mayflies (e.g. Otto and Svensson 1981 for *Siphonurus aestivalis*). A short season of food availability (dependent on a short growing season) has also been presumed to force multi-year life cycles, with several diapauses in the larval stage and eventual breeding in the spring (e.g. DeZordo 1979a, b, for Carabidae; see also Danks 1981 for arctic insects).

Adaptation to seasonal supplies of animal food has been shown most clearly for several parasitic insects, especially species confined to a narrow range of hosts. Many of these species are in diapause with their hosts, ensuring that parasites will not emerge until hosts are again available (see Chapters 7, 8). The responses on different hosts differ in some species in a way supposed to be adaptive. Saunders *et al.* (1970) suggested that the greater number of larvae in diapause produced by the pteromalid *Nasonia vitripennis* on *Sarcophaga* blow flies than on other hosts was related to the seasonal pattern of host availability. Other smaller blow flies that overwinter as larvae or adults become less common in fall, but *Sarcophaga* spp. overwinter as pupae and may therefore provide the major overwintering reservoir for parasitoids in diapause.

Seasonal selective pressures on parasites have been discussed especially for true parasites such as nematodes (e.g. Schad 1977), in which dormant stages have been suggested to balance the host-parasite load by delaying the impact of some individuals on the host, as well as to time development and transmission appropriately in relation to the seasonality of the host or of the environment. Discussions of population dynamics and selective pressures on insect parasitoids, as opposed to the control of seasonal activity (reviewed by Tauber *et al.* 1983, 1986), have seldom been given a clear seasonal emphasis.

Food may be constrained seasonally for some predators, although its temporal restriction tends to be less marked than in parasitoids and phytophages because most predators are general feeders. However, Penney (1969) showed that the summer diapause period of the predaceous carabid beetle *Nebria brevicollis* is correlated with a much reduced abundance of micro-arthropod prey such as collembolans and mites.

### 3. Predation and parasitism

It is very difficult to document the supposition that biological adversity from natural enemies ultimately controls seasonal activity. Natural enemies are thought to be responsible for the very prolonged 13- and 17-year life cycles of periodical cicadas, *Magicicada* spp. The enemies profiting from the periodical feast in years of adult emergence are limited by the many intervening years of famine while the cicada larvae live underground (Lloyd and Dybas 1966 and later papers). A similar argument has been made for the alternate-year emergence of some northern moths (Douwes 1980; Mikkola 1976), and for some cases of prolonged diapause (e.g. Trofimov 1975; Maeda *et al.* 1982).

Eulophid egg parasitoids have been suggested as a possible agent selecting for late oviposition and early egg hatch (and hence a later larval diapause) in *Neodiprion* sawflies (Knerer 1983). Masaki (1980) and others (e.g. Wiklund *et al.* 1983) have suggested from limited evidence that aestivation of larvae may be a response to predation, but it is more likely that seasonal timing or voltinism is involved. Bradshaw and Holzapfel (1983b, 1984) argued that predation affects the seasonal "strategy" of tree-hole mosquitoes and chaoborids, except for *Aedes triseriatus*, which has a

refuge from predation (in transient habitats) and is geared to winter harshness and unpredictable spring weather (cf. Risk spreading below). In the other tree-hole species, overwintering stages and variability of development in spring appear to be adapted to predation by *Toxorhynchites rutilus*. For example, predation may be avoided by diapause at a young stage, so that only small individuals coincide with predators that prefer larger prey (Bradshaw and Holzapfel 1984).

Hairston *et al.* (1983) have recently reviewed the possibility that the diapause eggs of copepods are an adaptation to predation by fish. Strickler and Twombly (1975) claimed that diapause of the copepodite stage of *Cyclops* copepods allows them to escape predation by then-adult larger *Epischura* copepods.

#### 4. Interspecific competition

The general literature of ecology is full of work which suggests that seasonal timing (as well as other ecological features such as food range and microhabitat) are selected or modified by competition with other species (but see Lewin 1983 for an interesting review of recent arguments about the existence of competition and the measurement of its effects). Müller (1980), for example, supposed that ecosystem partitioning by seasonal factors, especially overwintering and dormancy, as well as microclimate and food, took place in leafhoppers. Sota (1985) discussed the role of interspecific interactions, as well as climatic factors, in governing the life cycles of some carabid beetles.

Unfortunately, as with the belief that ecologically equal species cannot coexist (competitive exclusion principle), such hypotheses cannot usually be falsified: certainly interspecific differences exist, and even if none has been discovered, differences can be supposed to have been overlooked since every conceivable factor cannot be measured. But it is often impossible to decide, except provisionally through correlation and the apparent reasonableness of the supposed adaptation, whether differences have resulted from competition, or merely from divergences in physiology or other features evolved in other circumstances, and not actually adaptive (i.e. favouring survival) at present by reducing competition.

#### 5. Intraspecific interactions

Some seasonal adaptations appear to favour survival by controlling the synchrony of development. Adult emergence can be synchronized most easily by dormancy at a fixed stage late in pre-reproductive life (Corbet 1964). Growth responses and other features may help to synchronize entry to the dormant state (e.g. Sharov and Safonkin 1980 for cocoon formation by *Neodiprion pini*; Fuzeau-Braesch 1963, p. 794, for larval growth of *Gryllus campestris*). Such synchrony favours mate-finding by adults as well as coincidence with temporary food supplies, and these elements of timing might be more relevant than winter survival in some cases.

Asynchrony may also have advantages. For example, staggered hatching of eggs may avoid overcrowding of larvae in an area of limited food resources (Resh and Solem 1978, p. 39). Diapause cued by crowding presumably serves to limit intraspecific competition (cf. Barak and Burkholder 1977). Istock *et al.* (1975) believed that summer diapause of the pitcher-plant mosquito *Wyeomyia smithii* was adaptive in avoiding competition because it deferred development and so prevented overcrowding. (Fish and Hall (1978, p. 180), on the other hand, believed that this arrest in development

was merely quiescence induced by starvation, and was not an adaptation to density.) Polis (1980) reported that adult scorpions eat smaller ones, a pursuit that would select for the observed differences in seasonal and nightly times of activity. Asynchrony also helps to spread the risk of extinction by unpredictable catastrophes (see below).

#### 6. Adaptive alternatives

Different species may have evolved different life cycles because their requirements are different, but also because the same requirements can be met in more than one way.

The basic needs of different species vary greatly, and fatal conditions for one species are preferred conditions for another. For example, egg diapause in several species of tree-feeding moths (some lasiocampids, lymantriids, etc.) allows them to survive the winter, and the earliest possible hatch in spring permits larvae to feed on the buds and new leaves of the host trees. On the other hand, egg diapause in the cricket *Teleogryllus* (formerly *Acheta*) *commodus* prevents hatch in the relatively cool, wet early spring, delaying the appearance of the larvae until the warmer, drier summer which is favourable for their growth (Hogan 1960a).

Diapauses serve to avoid the adverse season. Avoidance can also be achieved by movement: either as an alternative to dormancy (long-distance migration) or in conjunction with diapause (see Johnson 1969 for examples); on a smaller scale by movement between habitats (e.g. certain colonists of temporary pools: Wiggins *et al.* 1980); and more generally by seeking out sheltered sites during the adverse season (most insects in north temperate regions, see Danks 1978b; Chapter 3).

Finally, a dormant period may not be necessary if environmental conditions are relatively uniform and hence never sufficiently adverse to prevent activity. A fixed dormant period may also be absent if conditions are so unpredictable that they do not have a clear seasonal component (e.g. Towns 1981).

#### 7. Integration of responses

There is far more than one adaptive element in life histories, for a given species is adapted to many factors simultaneously. Habitat choice, viability from egg to adult, rate of development, timing of diapause and activity, length of breeding season, energy allocation, and other features must all be coadapted if they are to be of value to the organism as a whole (e.g. Vepsäläinen and Jarvinen 1979). Each of these features depends in turn on several sets of more detailed characters, for example, the pattern in which eggs are deposited, and changes in the sex, size, or diapause characteristics of the progeny with time. Such sets of responses have usually been referred to as "strategies". Wilbur *et al.* (1974, p. 805), stated that this term "implies a suite of adaptive responses accumulated over evolutionary time, without any teleological implications". Root (1975), however, prefers the term "adaptive syndrome" to "strategy", because it does not imply any direction to the response; the term emphasizes the multipartite nature of the adaptation.

"Single" responses may thus have many facets. For example, slower growth may help to synchronize individuals in the population; it may lower mortality of diapause individuals by delaying entry into the diapause stage, so reducing exposure to high temperature in summer (e.g. Goettel and Philogène 1978); it may permit additional monitoring of ambiguous inductive signals (see Chapter 7); it may favour survival

on reduced food supplies; and so on. And more than one of these benefits may accrue simultaneously. Indeed, Wilbur *et al.* (1974) concluded that attempts to explain life histories in terms of *single* selective pressures have tended to obscure life-history evolution.

Integrated responses also operate in series (see especially Chapter 10). For example, embryonic dormancy normally governs overwintering of the mosquito *Aedes triseriatus*; but there is also a larval diapause, not normally present but available as a fail-safe device, as it were, if an unduly warm spring triggers an unusually, and thus potentially damaging, early hatch (Holzapfel and Bradshaw 1981). Many species have a similar “back up” control, which comes into play if the main life-cycle control (response or cue) does not operate; but many other species do not, and these species would probably be the easiest to rear continuously under constant laboratory conditions.

The requirement for simultaneous adaptations forces compromises among the various aspects of the response. For example, the need to ensure survival during winter and therefore anticipate it may conflict with the need to use as much of the season as possible for growth and reproduction. In larvae of the corn borer, *Ostrinia nubilalis*, the need for water to be taken up before development resumes after diapause may derive from the fact that water has been lost as part of the requirements for cold-hardiness (Monchadsky 1935). Selection may operate more or less independently in larval and adult stages, but these stages are serially dependent on one another (see Istock 1978 for discussion). In other words, single life-history characters cannot be precisely optimized. Rose and Charlesworth (1981) discuss the existence of “antagonistic pleiotropism” in *Drosophila*, showing how there may be a trade off between the *opposite* effects on fitness of a particular genotype at different times during the life cycle (see also Chapter 9; Rose 1983).

#### 8. Intraspecific options

Although the basic physiology of a given species limits its possible cold-hardiness, growing season, temperature thresholds for diapause development, and other characteristics — and thus restricts its range — various developmental options allow the species to master wide fluctuations of conditions across extensive segments of space and time. Some of these options are quite striking, including, in the present context, the presence or absence of diapause. Other options are less conspicuous and are not usually emphasized in the context of geographic variation; for example, the longer emergence period of some strains of sawflies, which may allow a longer oviposition season in regions of maritime climate (Knerer and Atwood 1972). In some species the same response (diapause) is used differently across space, as in aestivation in southern populations and overwintering in northern ones (e.g. Rivnay 1958 for *Delia* (formerly *Hylemya*) *antiqua*; Masaki 1956b, 1961, Masaki and Sakai 1965 for *Mamestra brassicae*) or even diapause in northern ones and quiescence in southern (e.g. Eertmoed 1978 for *Peripsocus quadrifasciatus*); or across time, as in aestivation in summer and overwintering in winter (usually in different life stages, see Chapter 10).

In other cases, local subpopulations may be sharply delimited in response to very local effects, such as the density of aphid prey controlling ovarian development in the beetle *Coccinella septempunctata* (Honěk 1978). Examples of sharp boundaries

in response (e.g. in number of generations and consequently size and other features) along a steady geographic gradient were discussed in Chapter 9 (e.g. Masaki 1978*a*; see also Blau 1981*a*, p. 122).

#### 9. Resource allocation

Survival depends on resources, and the possible adaptive value of diapause therefore can be analyzed by budgeting the acquisition and consumption of energy with time. Analysis of this sort may explain, for example, why there is a male diapause in so few of the species in which females have a diapause: eggs require far more energy to produce and maintain than sperm (cf. Sláma 1964*b*).

An energetics analysis of the life cycle is just as complex and difficult as a general analysis based on survival. Body size, metabolic rate, amount of energy reserves, availability of food energy, flight energy required for dispersal, energy expenditure during diapause, energy budgets during reproduction, and other items factor in such an analysis, which seeks to show where there may be a temporary shortfall of available energy that might be offset by a period of dormancy, provided the energetic cost of the dormancy is not disproportionate. Although complete analyses of this sort are not available, some features of individual life histories appear to respond to the need to conserve energy, as supposed, for example, by Goldson (1981*a*), for adults of the weevil *Listronotus bonariensis* that emerge in the fall. Most of these weevils enter diapause immediately, so conserving resources, whereas earlier-emerging individuals reproduce for a time before entering diapause.

The need to enter diapause may depend, from the point of view of energy, not only on the availability of food, but also on the ability of the organism to use it. MacLean (1975) noted that arctic insects, even those characteristic of the region, were not always active at low temperatures. He stated that activity would be profitable only if assimilation of energy from food exceeded energy consumed by respiration, and he suggested that an inability to assimilate rather than to respire at low temperatures forced activity to cease.

#### 10. Risk spreading

Adaptations are also compromised by the fact that universal precise adaptation to an event leads to extinction if ever the event does not occur. Constancy of response is related to the stability of climates or habitats; variability responds to lability, and also allows new environments to be invaded.

Some responses contain considerable variations, apparently themselves adaptive to unpredictable conditions — they influence parameters of the photoperiodic and other responses (by which the presence or timing of entry into diapause, the timing of completion, and hence the number of generations are varied), prolonged diapause, and other features discussed in Chapter 9 (see also Dingle 1984). In several species, responses are graded (non-diapause, short diapause, long diapause), or continuous, or complex (e.g. diapause, non-diapause; and migratory, non-migratory), not simply alternative (cf. Solbreck 1978). A number of less striking cases suggest that such “spreading of risk”, “bet hedging” or “mixed strategies” (see Den Boer 1968, Stearns 1976, for an introduction to these ideas; Istock 1981 for a specific insect example) are more or less universal in diapause as in other aspects of adaptation. For example, some adult boll weevils are in diapause in their hibernation quarters all year, where

hostplant (crop) developments do not influence them. (These adults periodically emerge, potentially creating pest problems.) Females of the cricket *Gryllus firmus* deposit mixed diapause and non-diapause egg batches, governed by the environment (Walker 1980), and this behaviour leads to complex mixtures of generations, which collectively buffer the population against unpredictable conditions across time. In certain species of *Gerris*, notably those found in unpredictable habitats, the risks are spread by long life and oviposition in small dispersed batches, in addition to the delay of reproduction achieved through diapause (Vepsäläinen 1978).

### *The origins of diapause*

There are two main approaches to the question "How did diapause evolve?". One approach seeks to define taxonomic and physiological, habitat-related, or geographic correlates of diapause, with a view to explaining what sorts of organisms were vulnerable to selection for diapause and hence how and where the basic machinery evolved. The second approach asks mainly genetic questions about the mode of selection and retention of diapause responses. A related body of speculation concerns the possible role of diapause responses in speciation, and this too is discussed briefly in this section.

#### 1. Taxonomic and physiological correlates of diapause

The detailed adaptations of diapause are similar in related organisms only in a very general way. The stage of diapause often is similar among species within a given taxon (see Chapter 5, Table 9, for example). However, the differences in diapause stages among related species, and especially the many differences in response to environmental cues, are perhaps the more striking. Indeed, Thiele (1979a) concluded that physiological race formation was faster than morphological, and Ushatinskaya (1976, pp. 90–91) stated that the evolution of diapause depended on exogenous controls, not on phylogeny. Group-by-group summaries (e.g. Krause 1982 for chrysomelids; Hayes 1983 for butterflies) do not contradict this point of view: even closely related species in a group may show different diapause responses (e.g. Begon 1976, Ichijo *et al.* 1980 for *Drosophila*). In the carabid beetle genus *Pterostichus*, comprising relatively large ground-dwelling species, the many different types of annual rhythmicity and dormancy suggest a polyphyletic development of these adaptations (Thiele 1971, p. 367).

Selection of diapause in diverse lineages is most strongly confirmed by evidence for the independent origins in different species of many similar responses to particular seasonal constraints. For example, univoltinism evolved independently in a number of *Drosophila* lineages, so that species showing it are not related (Lakovaara *et al.* 1972, p. 94). Pinger and Eldridge (1977, p. 440) concluded that the type of photoperiodic induction of egg diapause in mosquitoes was correlated with neither geographic range nor phylogenetic affinities. Authors of several more general reviews also have concluded that diapause evolved independently in various groups (e.g. Masaki 1980, p. 5; Way 1962, p. 596). Polyphenism (as controlled by photoperiod or temperature or both) has arisen by different selective routes, and responses converge in unrelated lineages (Shapiro 1980b). Nor do the supposed "evolutionary sequences" of systems controlling diapause, such as the photoperiodic

response, correspond with phyletic evolution (Tyshchenko 1973, 1983), and Pittendrigh (1972, p. 2734) cautioned that convergence might produce responses to the same signals through different underlying mechanisms, creating the likelihood of confusion in interpretation.

Nevertheless, some authors have sought to explain at the physiological level how the control of diapause responses by photoperiodic token stimuli — allowing environmental change to be anticipated — has evolved (Tyshchenko 1977). Most recently, Tauber *et al.* (1986) supposed that three steps were involved, the measurement of seasonal time by the biological clock, its coordination with neuroendocrine systems, and the linkage of these functions, by means of a “memory”, to seasonal cues.

The many independent origins of similar diapauses suggest, as Way (1962) believed, that diapause is a relatively simple adaptation to develop. This may be so because, at the physiological level, ordinary development proceeds under the control of rather few powerful hormones, and these major factors of development might readily be “captured” to institute pathways that include a period of diapause (see Chapter 13). Even so, differences in the nature of the hormonal control, even in related species (e.g. Bradfield and Denlinger 1980, p. 105; Chippendale 1977), confirm the diverse evolutionary origins of diapause.

## 2. Habitat correlates of diapause

The occurrence of diapause is correlated with both spatial and temporal aspects of habitat (microhabitat and stability). The very necessity of diapause, indeed, nearly always relates to seasonal change. Therefore, many denizens of habitats with very stable temperatures, such as the soil beneath insulating dead plant material or snow, deep lakes and rapid streams, do not require any period of dormancy, or are well adapted to seasonal change merely by quiescence as temperatures gradually decrease. In contrast, many caddisflies inhabiting unstable temporary waters have an adult diapause in late summer when habitats are dry (e.g. Gower 1967; Lelannic 1975; Novak and Sehnal 1963, 1965; Svensson 1972). However, larvae of some of the same species in Iceland occupy more stable permanent waters instead, and there is no adult diapause in the short summer season (Gíslason 1978).

Despite such diversity among species, seasonal pressures on species from different habitats tend to be equalized, because climatic patterns are pervasive and influence a wide range of habitats, and because the habitats of many species change during the life cycle. For example, larvae of aquatic insects live in habitats that may be less variable than many of the habitats on land. However, most of these species have terrestrial adults, which are just as susceptible to adverse terrestrial conditions during the critical reproductive period as are fully terrestrial species. Diapause in some chironomids of temporary pools is terminated by chilling, rather than simply by moisture (Grodhaus 1980). This requirement for chilling avoids the premature resumption of development during wet spells in fall, and parallels the chilling requirement for diapause development in species from more stable habitats that prevents premature development when there is a warm spell in fall (Chapter 8).

## 3. Geographic correlates of diapause

Geographic variations in diapause accord with latitudinal patterns in photoperiod, growing season, and so on (Chapter 9). The very existence of diapause, indeed, accords

with the apparent need for it in different regions, and diapause is less common in New Zealand's relatively temperate (and less severe Pleistocene) climate, for example (Roberts 1978; Watt 1973). Species with a diapause in Hawaii, where the climate is even more equable, are all invaders from other regions according to Nishida (1955).

But where did diapause originate? Although the most conspicuous examples were first recorded and studied in detail in cool temperate regions characterized by long cold winters, several authors have concluded that diapause originally evolved in tropical regions. Diapause ability often increases as species extend from (sub)tropical to temperate regions (e.g. Readshaw and Bedford 1971 for *Didymuria violescens*), but the basic ability to enter diapause was already present. Many tropical insects, in fact, are strongly seasonal in response to seasonal variations in rainfall and foodplants (e.g. Denlinger 1980, 1986; Wolda 1980; other references cited in Chapter 7). In the seasonal dry tropics, most adults enter reproductive diapause during the dry season according to Janzen (1973). Many other tropical species and tropical strains of widespread species have a diapause, though often only for short periods, or only in part of the population (Tauber and Tauber 1981a), or only in especially adverse years (e.g. Denlinger 1974). Ushatinskaya (1959) proposed that diapause was originally an adaptation to drought, and more recently evidence for the tropical origin of diapause in response to dry conditions has been adduced and argued for by Denlinger (1979) for sarcophagids, by Krysan *et al.* (1977) for species of *Diabrotica* beetles, and especially in the review by Tauber and Tauber (1981a, pp. 292-294). The clear-cut diapause responses of many insects from temperate regions are supposed to have resulted from further selection of a reaction to token stimuli, coupled with the endocrine control of development, already evolved in tropical source populations.

#### 4. Modes of selection of diapause

From the viewpoint of an insect, the ability to survive depends on many genetic traits: some of these traits are compromises with other aspects of local survival; some are not expressed or not fully expressed phenotypically in a given generation. From the viewpoint of the environment, selective parameters even in one place vary from one season to the next, because there is different weather, a different combination of natural enemies, and so on. Basic features of both the insect and the environment therefore derive from long-term averages. Selection, however, acts on individuals: either an individual present at a given time survives and reproduces, or it does not. Therefore, populations survive according to the prevailing balance of optimization, variability, and flexibility of response among their individuals with environmental trends and variation. This makes it very difficult to analyze "selection" or "strategies", because the particular genetic makeup of the population may very well reflect the integrated effect of the past ten or fifty years of local selection, quite apart from still longer-term effects. Moreover, from a genetic point of view, selection acts upon integrated phenotypes more than single loci (e.g. Johnson 1974).

Factors influencing survival during the adverse season may also be modified independent of selection for diapause. For example, Baust and Edwards (1979) and Baust and Lee (1981) have suggested that the year-to-year differences in cryoprotectant substances observed in the antarctic midge *Belgica antarctica* might be a result of differences in nutrient status, which would influence the composition of the precursors that were sequestered. Such interactions, if substantiated, would have unexpected

effects on survival from year to year, and long-term selection might therefore depend on some sort of average composition of cryoprotectants.

Selection by conditions that vary, together with a gene pool that is partly protected from selection by various genetic mechanisms, including phenotypic plasticity (see Shapiro 1984), explains part of the general variation in dormancy responses. Northern populations of the butterfly *Pieris occidentalis* retain (though normally suppressed) the adaptations for diphenism and multivoltinism that are advantageous farther south (Shapiro 1975). Part of the retained variation results too from an intermittent but sometimes not obvious exposure to direct selection, as in the case of tropical populations of the cynipid *Leptopiliana boulandi*, which enter diapause in response to cold temperatures at higher elevations in the region of collection (Claret and Carton 1980), and which evidently exchange genetic material among different elevations.

Masaki (1961, p. 69) supposed that “obligate” or deeper diapause evolves through intermediate stages from non-diapause. With the same assumption, a few authors have even tried to organize diapause responses into a series presumed to reflect successive steps in evolution. For example, Müller (1970, p. 19) believed that eudiapause must have followed parapause phylogenetically (for definitions see Chapter 2), but such a simple conception for complex and multiple evolutionary processes is untenable, as the review of Tauber and Tauber (1981a) shows.

Most specific genetic ideas developed by general students of genetics can be applied to the evolution of diapause, although their actual application has been haphazard, and there are few rigorous analyses despite some preliminary discussions. These consider, for example: gene flow (e.g. Iwao *et al.* 1980: local adaptations in some northern populations of *Drosophila* species are hindered by gene flow from larger populations to the south); geographic restriction (e.g. Showers 1979: further spread of the introduced species *Ostrinia nubilalis* has been held up at latitudinal barriers until suitable responses to alter the number of generations can evolve); canalization (Shapiro 1981: developmental buffering has evolved in northern *Nymphalis antiopa*, so that it does not respond to cold shock by changing the phenotype like other populations); genetic assimilation (Matsuda 1982 discussed ways in which environmentally induced responses might be converted into fixed genetic responses; but see Duncan 1985, Pearson 1985).

Recent theoretical discussions of reproductive and behavioural “Evolutionarily Stable Strategies” (ESS) might also be applied to diapause. As recently re-defined by Lloyd (1983) “a phenotype is an ESS if, from any initial frequency, it is protected from loss by its fitness advantage.” In the terminology of Maynard Smith (1982), Evolutionarily Stable Strategies may comprise pure strategies (one response), stable polymorphisms (genetically programmed fractions with different responses), mixed strategies (genetically programmed decisions are made according to conditions, either reversibly or irrevocably). Each of these types of response appears to exist among dormancies, but the problem of supporting the hypothesized adaptive value of such ESS remains, since most of the observations can be explained in other ways (e.g. Maynard Smith 1981, 1982).

Finally, insight into the evolutionary consequences of diapause has been sought by modelling diapause phenomena (see Reporting of diapause responses in Chapter 14).

### 5. Possible roles of diapause in speciation

The processes of speciation cause properties characteristic of particular taxa to diverge, and thus may operate on many traits including diapause and other seasonal characteristics.

Mayr (1963) believed that most speciation takes place as a result of the divergence of geographically separated populations in response to local conditions (allopatric speciation). The divergence will tend to create some potential reproductive isolation between the populations, so that even subsequent mixing of the two isolates may precipitate various forms of selection that reinforce the differences among them. Divergence in diapause characteristics is one such possibility (e.g. Tauber *et al.* 1986, p. 280).

Other authors reviewing speciation (Bush 1975; White 1978) have placed greater emphasis on other possible types of speciation, of which parapatric and sympatric speciation result from natural selection. Both have been examined briefly in the context of diapause (Tauber and Tauber 1981a; Tauber *et al.* 1986).

Populations that vary clinally along a geographic gradient may evolve reproductive barriers between adjacent populations (parapatric speciation). This process may include both selection of mating barriers as such, and selection of climatically controlled differences that adapt each subpopulation to local conditions. Masaki (1978a, 1983) used the term "climatic speciation" for such a situation, in which different types of life cycle may be selected for by different seasonal conditions along the climatic gradient. Endler (1977), Tauber and Tauber (1981a), and others have recently suggested that parapatric speciation may be more prevalent than previously thought.

Alexander and Bigelow (1960) and Alexander (1968) argued that sympatric speciation could occur in crickets, the specific divergence being enforced by allochrony (separation in time) based on seasonal responses (see also Bigelow 1958, 1960, 1962; Lloyd and Pace 1975). More recently, Walker (1974) has suggested that seasonal isolation may have initiated speciation in two other species of *Gryllus* crickets. However, the allochronic pairs of crickets are not (as theory would require) the nearest relatives in the genus (Harrison 1979).

Studies by Wallace and Sullivan (1972, p. 1060) on sawflies showed that Maxwell's (1958) conclusion that diapause and life-history patterns are not stable isolating factors was unwarranted. Obvious or subtle differences in diapause, foodplants, and other adaptations have led to a complex of "races" in many "species" of related diprionid sawflies (Knerer and Atwood 1972, 1973; Knerer and Marchant 1973): some of the divergences appear to have allochronic elements. Knerer and Marchant (1973, p. 108) stated, for example, that "new genetic units can emerge in the same locality by a mutation that switches egg diapause to prepupal diapause or vice-versa", allowing the spontaneous separation of races.

Tauber and Tauber (1977a, b, 1978b, 1981b, 1982a, b; Tauber *et al.* 1977) have argued most extensively for the sympatric evolution of species, basing their argument on similarities or differences in the seasonal characteristics of lacewings. They believed that *Chrysoperla plorabunda* (as *Chrysopa carnea*) and *C. downesi* speciated sympatrically in North America. According to Tauber and Tauber, the differences resulted from habitat divergence and the subsequent evolution of temporal and spatial reproductive isolation. The dark green *C. downesi* inhabits coniferous forests; its

long diapause lasts from summer through winter. The lighter green *C. plorabunda* inhabits fields, and its diapause supervenes only in the fall. The difference is under relatively simple genetic control, resulting from allelic differences at only two autosomal loci (Tauber *et al.* 1977).

Tauber and Tauber's conclusions were soon challenged by Hendrickson (1978), Henry (1979, 1980) and Futuyma and Mayer (1980). Tauber and Tauber (1982*a, b*) in turn rebutted some of the detailed arguments presented, but the basic conclusion of Henry (1982) remains: that the data of Tauber and Tauber (1977*a, b*; 1982*a*) can be interpreted in more than one way, and therefore (whether or not sympatric or allopatric speciation has in fact occurred) they are still insufficient to demonstrate conclusively that speciation was sympatric. However, Henry (1985*a, b*) has indicated that substrate-borne sounds produced during courtship, which can readily be changed on the basis of a few alleles, might themselves have been the focus of sympatric evolution. Cryptic species, some of them sympatric (including *C. plorabunda* and *C. downesi*, and other "song morphs" in the western mountains of North America, as well as *C. carnea* and related species in Europe), can be distinguished.

### General conclusions

This review shows that diapause and related characteristics form a substantial part of the adaptive responses of insects in nature, and in most species are geared to conditions likely to be encountered, anticipating predictable seasonal trends in habitat quality. For these reasons, responses usually are very complex; a wide range of features has been integrated into every system of seasonal control of the life cycle. Moreover, these features may vary greatly among species, even when the species are closely related. Conversely, environmental pressures can select for convergent adaptations in unrelated species. In other words, syndromes of dormancy are diverse and related to the total life-cycle strategy (see Chapter 10). This diversity makes both critical studies and conclusions very difficult; each detailed hypothesis with some generality is soon found to lack universal validity. But this is not necessarily a bad thing; as R. Mitchell (1981) pointed out: "Indeed reductionist models are discarded as we continually rediscover the complexity of nature, but each discarded model broadens our vision and strengthens the armory of tools with which nature can be explored." Boulding (1980) confirmed that "knowledge increases...not by the direct perception of truth but by...the perception of error." Therefore, the first general conclusion of this review should not be surprising: that dormancy and related responses are so complex that great caution must be exercised in drawing general conclusions! Some comments on the nature of dormancies can nevertheless be given. No attempt is made here, however, to summarize the detailed information presented in previous chapters.

The structure of dormancy responses in a given species can be understood only by taking "fixes" on various parameters of the life cycle. This review shows that some or all of the parameters listed here in Table 45 (some of which often are overlooked) may be important to understanding the response. In addition, the total response needs to be summarized in terms of the properties of the local environment: under given circumstances it is more important for organisms to identify and respond to some factors than to others.

The most rewarding way to summarize much of this sort of information for a given species is not in a static tabular form, but as a series of alternative pathways for development (see for example Chapter 10, Fig. 34). Grouping and classifying sets of convergent responses (e.g. "eudiapause") is valuable only insofar as it helps to organize information and is not a useful means of interpreting their evolution, since seasonal responses have arisen and are controlled in different ways.

The study of the evolution and genetic control of diapause is in its infancy, but one general conclusion emerges: responses that are very different (e.g. voltinism, responsiveness to cues) can depend genetically on a small number of alleles (Chapter 9), and physiologically on adjustments in the timing of release of a few major neuroendocrine substances (Chapter 13). This finding confirms that diapause traits are relatively easily controlled and changed. Such potentially labile internal control in part explains why their manifestations have become so complex and can differ so strikingly among related species.

A review such as this, which emphasizes dormancy, may tend to overvalue dormancy at the expense of other traits. Especially at lower latitudes, responses to seasonality can include alternatives to dormancy. These alternatives include variability in the duration of development (Denlinger and Shukla 1984; Nilssen 1980) as well as habitat selection and seasonal migration. Diapause, like other adaptations, is a means of synchronizing the life cycle with favourable events, and not simply a means of avoiding unfavourable ones. A foodplant suitable for a limited period could be exploited, for example, either by the restriction of oviposition to a given plant stage (as in many Lepidoptera) coupled with adequate powers of dispersal, or by larval dormancy in one place. Species that live in — or move during the adverse season into — deep lakes or other stable habitats might require no dormant period in response to temperature (although food supplies from above might be seasonally limiting there).

Natural patterns of variation, which often are underemphasized, are particularly instructive in understanding the structure of dormancy responses. These patterns, like diapause itself, are related to seasonal certainty, which influences especially the placement and duration of the reproductive period in accordance with the likelihood of successful reproduction at any given time of year. Adaptive syndromes therefore respond to the average, the normal range, and the predictability of various environmental circumstances, and include variation as a means of spreading risk; very few insect populations, so to speak, have all their eggs in one temporal basket. The structure of alternative responses (polymorphisms of various types discussed in Chapter 9), and of genetic mechanisms by which programmes for the alternatives are retained in the population, should occupy increasing attention in future studies of diapause.

A question such as "What is dormancy?" is therefore too simple. Dormancies are a major part of integrated responses controlling the life cycle, involving arrests, delays, and alterations of development (see Table 45). Past analyses of dormancy and diapause have tended to treat these components as separate entities comprehensible by classifying information on response; if not into types of diapause, at least into types of response to photoperiod and other factors. Attempts at a wider analysis of life-cycle syndromes (in the vertebrates as well as the invertebrates) have tended on the other hand to emphasize reproductive effort between successive generations by

Table 45. Summary of some variables in the seasonal control of the life cycle

Variables	Some options for control
<i>Seasonal programme</i>	
Phenology	Various seasonal positions of feeding and reproductive stages; overlapped generations
Voltinism	Two or more years per generation, univoltine, two or more generations per year; partial generations; generations developing continuously
Stage sensitive to modifiers	Previous generation(s), present generation; egg (any stage of embryonation), larva (any instar), prepupa, pupa, adult (pharate; pre-reproductive or reproductive)
Stage responsive to modifiers	[As above]
Number of responses per generation	Continuous; one; several (e.g. multiple dormancies in the same or different stages)
Nature of response	Switch of developmental pathway, serial responses, graded response
Rate of development	Arrest, or change of rate, in response to season
Seasonal correlates or consequences	Structure, behaviour, food storage, resistance, various physiological traits
<i>Modifiers</i>	
Intrinsic features of individual response	Sex, strain, etc. (combined with external influences)
External factors	Response (see Number and nature of responses, Rate of development, and Seasonal correlates above) to various cues and conditions; displacement (see below)
Displacement into different conditions	Migration; microhabitat choice
Nature of physiological machinery for response	Signal receptors, biological clocks, endocrine systems

means of models that summarize any effect of diapause through its effect on fecundity, voltinism and other simple population statistics (cf. Stearns 1977).

I believe that the understanding of dormancy can best be advanced by analysis at a level between these two: by interpreting life cycles from the standpoint of *different pathways* for development, which are selected partly by internal programmes, and partly by the effects of external circumstances on internal systems. For any given species, the most meaningful conceptual framework for the analysis of dormancy is therefore a "flow chart" of these life-cycle options; and in such schemes the ways in which the developmental switches are operated (by internal and external means) can be studied in detail to explain life cycles in nature. Such an ecological approach would help to underpin the extensive evolutionary discussions that have recently been developed, perhaps prematurely, whilst also expanding the study of dormancy beyond the chiefly physiological viewpoints previously emphasized. A comprehensive view of insect dormancy therefore must have a primarily ecological orientation.