

Seasonal Strategies in Insects

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Few insect species encounter environmental conditions which remain favourable for continuous growth, development, and reproduction throughout the year. Such species are said to be homodynamic: they have life cycles characterised by a lack of seasonally synchronised adaptations. Most species however, inhabit regions in which seasonal variations in environmental conditions impose a corresponding seasonal change in rate of development, alternating between periods of rapid growth and reproduction, and a period of rest or dormancy. Such heterodynamic life cycles are typical of temperate latitudes where seasonal adversities, such as low temperatures often combined with the absence of food, retard or completely inhibit development during winter. However, even in tropical latitudes, the alternation of a wet with a dry season can also result in specific life cycle adaptations linked temporally to these environmental changes.

This paper is concerned with those strategies found in insect life cycles which enable them to survive unfavourable, recurrent changes in their environment. In general, these comprise 2 basic strategies: a migration, and b dormancy.

Migration is well documented for Northern Hemisphere insects. It may consist simply of flight from emergence site to another place, where growth and reproduction can continue; or it may be combined with a dormancy state such as adult (reproductive) diapause. An example of the latter in North America is the monarch butterfly, *Danaus plexippus* (L.) which migrates and then enters an overwintering adult diapause (Urquhart 1976); and in Australia, the bogong moth, *Agrotis infusa* (Boisd.) which migrates and then enters an aestival (summer) adult diapause (Common 1954).

The second major seasonal strategy, that of dormancy, includes the following resting conditions.

- A Summer dormancies
 - a Heat torpor
 - b Quiescence
 - c Summer diapause (aestivation)
- B Winter dormancies
 - a Cold torpor
 - b Quiescence
 - c Winter diapause

The classification and definition of dormancies has formed the subject of many papers, but because of differences in the terminology and their interpretations, problems arise when attempting to describe accurately the type of dormancy found in a particular insect's life cycle. The more important publications in this field are listed in a separate bibliography. They are especially concerned with defining the differences between "quiescence" and "diapause" and the differences within the diapause syndrome itself. The following section attempts to give a simple, working definition of the dormancy categories outlined above, and to relate them to both Northern and Southern hemisphere conditions. To avoid repetition, only strategies for winter survival will be discussed, but the generalisations apply also to the summer dormancies.

Torpor and quiescence differ only in duration. Torpor is typically induced by sudden short spells of adverse weather which, although not severe enough to kill the insect, abruptly halt its activity and development; it may occur at any time of year and thus affect any life cycle stage, i.e., it is non-seasonal. Quiescence, by contrast, is of longer duration and is a common seasonal (i.e., phenological) adaptation in the life cycle of many insects. Quiescence can in turn be distinguished from diapause in that it is directly induced and terminated by surrounding environmental conditions, i.e., low temperatures induce, and return to warmer temperatures terminate the quiescent state. Purely extrinsic factors are involved in its onset and termination and these act directly on the metabolic rate, resulting in either a slowing down or a complete arrest of development. In univoltine species, only one stage of the life cycle will normally enter quiescence with the onset of winter. In multivoltine species however (e.g., the blowfly, which in New Zealand can overwinter in all stages) each of these stages is capable of surviving in quiescence.

Diapause is defined as a dormancy state with the following characteristics:

- 1 It is a seasonally specific adaptation in the life cycle, which persists for a certain minimum period of time regardless of surrounding environmental fluctuations.
- 2 In nearly all cases, it occurs in only one species-specific stage in the life cycle.
- 3 It is not induced in direct response to unfavourable conditions but is "anticipatory", i.e., it occurs *before* the onset of winter, while conditions still permit growth and development.
- 4 Daylength (photoperiod), in addition to temperature, has been shown to be involved in the timing and induction of most published examples of diapause.

From 3 and 4 above, it is postulated that in diapausing insects an internally operating "clock" mechanism is involved, which can measure daylength and hence discriminate season. On either side of a "critical daylength", species either switch into diapause, or continue with growth and development. Based on this photoperiodic response, diapausing insects have been classified as either long-day insects (which grow and develop under long daylengths but diapause under short daylengths) or short-day insects (which grow and develop under short daylengths but diapause under long daylengths).

In addition to the above, the fact that diapause is under complex hormonal control whereas quiescence is more simply a function of temperature acting on the metabolic rate can, along with the above 4 characteristics, be useful in distinguishing between these two dormancy states.

If these characteristics are to be of practical value, it should be possible to devise experimental tests for distinguishing between diapause and quiescence under controlled laboratory condition. A final decision on the dormancy state present in a particular species must, however, also include accurate field observations. It should be possible to induce and terminate quiescence by lowering and raising the temperatures with no differences occurring between identical cultures maintained at the same temperatures under long days (i.e., LD 16:8) or short days (i.e., LD 8:16). If a difference in response is obtained between these two regimes, it suggests that a photoperiodic effect may be present. Numerous experiments designed to elucidate the nature of photoperiodic responses, particularly in diapausing insects, are to be found in the literature (see Beck 1968). Those given here are suggested merely as initial, elementary approaches which do not require highly sophisticated equipment. The choice of experimental approach also depends on whether the insect has a univoltine or multivoltine life cycle.

For multivoltine species, a first step would be to attempt to induce diapause in a summer (non diapausing) generation by maintaining a culture under short-days at winter simulating temperatures, e.g., LD 8:16, 12°C. Secondly,

it should be possible to avert diapause in the destined overwintering generation by maintaining it under long days at optimal temperatures, e.g., LD 16:8, 21°C. It is important to remember that photoperiodic induction (or its avoidance effect) may occur one or more stages before the diapausing stage. Thus it may be necessary to rear an entire generation under the potentially diapause-inductive or diapause-preventing light and temperature regimes.

If photoperiodic control is detected, further definitive experiments designed to determine the critical daylength can be carried out. This is the daylength at which the incidence of diapause in the population changes from a very high to a very low, or nil percentage. Work on the codling moth, *Laspeyresia pomonella* (L.), in the Northern Hemisphere nicely illustrates these experimental techniques and the photoperiodic control of its diapause. In different populations of this moth, as latitude increases the number of generations per year decreases, until it becomes univoltine at high latitudes. Correspondingly, the critical daylength also increases with increasing latitude so that diapause is induced earlier in the season the further north the population is found (Russ 1966). A similar trend is also reported in New Zealand (Wearing pers. comm.).

A more common "test" for diapause has been to attempt its termination (rather than its induction) by chilling, but for several reasons the usefulness of this experimental approach is open to doubt (Tauber and Tauber 1976). Certainly the widespread occurrence and demonstration of photoperiodic control of diapause (Danilevsky 1965; Beck 1968; Saunders 1976) emphasises the importance of utilising experimental techniques which include control of daylength as well as temperature.

There are, however, apparent exceptions to control of diapause through photoperiod among multivoltine species (e.g., tropical flesh-flies; Denlinger 1974) and univoltine species, particularly at high latitudes. Indeed, obligate diapause is regarded as being characteristic of such univoltine life cycles. For this reason perhaps, it has been defined by some authors as differing from facultative diapause in that it is under purely internal control and independent of external environmental influences. However, evidence of the polygenic nature of the genetic mechanism underlying diapause suggests that obligate species (in which all individuals in every generation enter diapause) appear to be under "rigid" internal control whereas facultative species are labile with respect to environmental influences, particularly temperature. Thus in facultative species, the percentage incidence of diapause may vary with each generation and can range from 0% to virtually 100%. Furthermore, de Wilde (1962) has commented "since the discovery of photoperiodism in insects, the number of cases showing obligatory diapause has shrunk remarkably". Thiele (1973) lists 15 species having obligatory diapause (termed "parapause", i.e., under purely internal control), but a comparison of this list with Saunders's (1976) table of species in which photoperiodic control of diapause has been demonstrated shows that only one of these 15 is still considered to have a diapause independent of photoperiodic control. However, other examples of obligate diapause under purely internal regulation do exist. In addition to the remaining valid case listed by Thiele, 2 are mentioned by de Wilde (1962), 2 by Danilevsky (1965) and 4 out of the approximately 230 species listed by Saunders (1976). In these insects, the inherited propensity for diapause appears to be triggered by factors other than photoperiod: either by a purely internal process solely dependent on "genetical triggering", or by other external factors such as temperature cycles (or thermoperiods). It is possible, therefore, that the occurrence of an obligate diapause in a univoltine species may be the outcome of 2 separate selection processes. On the one hand, such species or populations of a species may represent the extreme end of the facultative range of a parent species from which it has retained its photoperiodic control mechanism. Presumably **such** insects have undergone a post-Pleistocene northward spread from temperate

Table 1.—List of published studies on seasonal adaptations in endemic species in New Zealand.

Author and date	Study area	Species	Order and family	Number generations per year	Food source	Overwintering stages)	Author's description of seasonal strategy
Dale 1963	Canterbury Manawatu	<i>Pericoptus truncatus</i> (sand scarab)	Coleoptera: Scarabaeidae	2 or 3 year life cycle	driftwood zone and marram grass	prepupa	possibly an egg and a prepupal facultative diapause
Donovan 1958 1974	Auckland (37°S). N.Z. wide	<i>Leioproctus bolioni</i> (hairy colletid bee)	Hymenoptera: (a) Colletidae (30 spp.) (b) Halictidae (5 spp.)	1	manuka, kanuka, pohutukawa flowers	prepupa (a) larvae (b) fertilised adult females	quiescence, diapause (a) "hibernation" (b) "overwintering"
Gaskin 1975	Manawatu	<i>Orocrambus</i> spp. (10 spp.)	Lepidoptera: Noctuidae	1, or 2 or 1-2	indigenous and introduced grasses	last larval instars	quiescence, growth retardation
Harris 1974	Wellington	<i>Priocnemis nitida</i> (spider wasp)	Hymenoptera: Pompilidae	1	spiders	prepupa	diapause
Horak-Kaenel 1970	Nelson (41°S), Te Anau (45°S)	<i>Protodes carnifex</i>	Lepidoptera: Tortricidae	1	<i>Nothofagus cliffortioides</i> (beech)	1st instar in cocoon on under- surface on leaf egg	quiescence
McIntyre 1969	Christchurch (43°S), Kaikoura (42.5°S)	<i>Pteronemobius</i> sp.	Orthoptera: Gryllidae	1 1-2	pasture grasses and herbage		Obligate diapause (Christchurch) facultative (Kaikoura)
Parkes 1972	Hamilton, Kawhia (coastal) (38°S)	<i>Pteronemobius</i> sp.	Orthoptera: Gryllidae	1 (Hamilton) 2 or more (Kawhia)	pasture grasses and herbage	Hamilton: eggs, few adults, Kawhia: all stages	Hamilton; facultative diapause. Kawhia: slow, all year breeding
Richards 1973	Auckland	<i>Deinacrida heteracantha</i> , <i>D. fallai</i> (wetas)	Orthoptera: Stenopelmatidae	2, years	native, and in introduced shrub and tree foliage	<i>D. heteracantha</i> : some eggs; various nymphal instars and adults <i>D. fallai</i> : various nymphal instars and adults	<i>D. heteracantha</i> Winter diapause in nymphal instars and possibly some eggs. <i>D. fallai</i> : "less intense" nymphal diapause
Spitzer 1970	Manawatu (40°S)	<i>Persectania aversa</i> (southern army worm) and other noctuids	Lepidoptera: Noctuidae	2-3 2, to many	grasses and seed crops	various, several at least. All stages in <i>P. aversa</i>	General growth retardation with possible quiescence.
Wightman 1974	Christchurch (43°S)	<i>Costelytra zealandica</i> (grass grub)	Coleoptera: Scarabaeidae	1 or 2 years	grasses and herbage	larvae and pupae	larval quiescence (hibernation)
Wilkinson 1964	Otago (47°S)	<i>Metacrias strategica</i> (mountain tiger moth)	Lepidoptera: Arctidae	1-2	grasses and herbage	larvae and pupae	larval quiescence (hibernation)
Young 1970	Christchurch (43°S)	<i>Sigara arguta</i> (water boatman) <i>Anisops assimilis</i> (back swimmer)	Hemiptera: Corixidae, Notonectidae	1, and part second	aquatic plants; invertebrates	adults	ovarian regression in later summer plus migration to overwintering habitat

or sub-tropical latitudes. Alternatively, in a few species an obligate diapause may have resulted from selection pressures operating on an indigenous, non-migratory population in particular environments in which daylength fails to act as either a clear indicator of season, or as in the case of certain subterranean insects, may even be virtually absent. In such circumstances, the development of an associated photoperiodic control mechanism would have been impossible.

Most studies on seasonal adaptations in insects such as migration and diapause have been carried out in the Northern Hemisphere where these are of common occurrence. Unfortunately little comparable work has been undertaken in New Zealand. In 1967 Dumbleton was the first to compare and contrast the differences in seasonal overwintering adaptations in the Northern Hemisphere and in New Zealand. He pointed out that past and present climatic severity in the Northern Hemisphere has resulted in a high incidence of diapause (and deciduousness) in its fauna and flora, whereas our relatively mild maritime climate would have had little effect in selecting for the same seasonal mechanism in our endemic fauna and flora. As an illustration of this he cites our high incidence of native evergreen plants, and goes on to suggest a very low incidence of diapause in our insects. A survey of studies on the phenology of our native insects should indicate whether or not actual overwintering strategies are consistent with this hypothesis, remembering that it is mainly applicable to terrestrial, phytophagous insects. A paper on this subject including a preliminary assessment of published studies on overwintering in endemic insects has already been published (Roberts 1977). Table 1 shown here includes 4 more studies. Yet for several reasons it still remains incomplete.

Firstly, some field observations of seasonal adaptations are unpublished: Cowley (pers. comm.) reports that complete growth arrest in a single overwintering stage (e.g., diapause) is unknown for any of our approximately 150 endemic Trichoptera species.

Secondly, several studies report the insect simply as "overwintering", or "hibernating", or in "dormancy", so that it is impossible to determine whether diapause or quiescence occurs. In addition, some authors use "diapause" indiscriminately instead of the more general term dormancy. For example, the "diapause" said to occur in giant wetas (Richards 1973) is considered more likely to be a low temperature induced quiescence as there is a lack of strict seasonal synchronisation in life cycle development combined with the ability of several different nymphal instars and adults to overwinter, rather than there being only a single, specific overwintering stage. This opinion is supported by observations made on alpine wetas. At least 3 or even 4 different developmental stages of *Hemideina maori* (Pictet & Saussure) were collected by Sutherland (1964) at 4700 feet altitude in Central Otago during autumn. The contrast between the overwintering adaptations of this species in alpine conditions during winter and its counterparts in the Northern Hemisphere are noted. In fact Sutherland reached a similar conclusion to Dumbleton and suggested that "in New Zealand all stages of insects must be hardier, and probably grow whenever the environment permits, summer or winter".

Thirdly, the endemicity of some of our "native" insects, e.g., *Pteronemobius* spp., is sometimes difficult to determine (Ramsay, pers. comm.), and hence the origin of their diapause mechanism must also remain uncertain.

Of the 11 examples listed in Table 1, 5 are described as overwintering in quiescence; 3 more have either a quiescence or a diapause; and in 3 cases a diapause is stated to be present. In some instances it is important to note that selection pressures other than those of macroclimatic adversity may be involved. Insects with unstable habitats and/or a seasonally discontinuous food supply (e.g., the spider wasps, the sand scarab, and the aquatic Hemiptera) may have evolved a different sort of survival mechanism, e.g., diapause, from that which appears to be present in the majority of our native insects.

Despite the comparative paucity of studies specifically concerned with seasonal strategies in our endemic insects, and the difficulties posed by some of the definitions of overwintering dormancies, present evidence strongly suggests that in New Zealand with our relatively mild winters and the ready availability of a year-round evergreen food supply, endemic phytophagous insects are seldom likely to require a diapause mechanism to ensure their survival during the less favourable season of the year.

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