The elements of seasonal adaptations in insects

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Abstract—The many components of seasonal adaptations in insects are reviewed, especially from the viewpoint of aspects that must be studied in order to understand the structure and purposes of the adaptations. Component responses include dispersal, habitat selection, habitat modification, resistance to cold, dryness, and food limitation, trade-offs, diapause, modifications of developmental rate, sensitivity to environmental signals, life-cycle patterns including multiple alternatives in one species, and types of variation in phenology and development. Spatial, temporal, and resource elements of the environment are also reviewed, as are environmental signals, supporting the conclusion that further understanding of all of these seasonal responses requires detailed simultaneous study of the natural environments that drive the patterns of response.

Résumé—On trouvera ici une revue des multiples composantes des adaptations saisonnières des insectes, particulièrement des aspects à examiner afin de comprendre la structure et les buts de ces adaptations. Ces composantes incluent la dispersion, la sélection d'habitat, la modification d'habitat, la résistance au froid, à la sécheresse et aux restrictions de nourriture, les compromis, la diapause, les modifications du taux de développement, la sensibilité aux signaux environnementaux, les patrons de cycles biologiques (y compris les patrons multiples possibles chez une même espèce), ainsi que les types de variation dans la phénologie et le développement. La revue considère aussi les conditions d'espace, de temps et de ressources dans le milieu de même que les signaux environnementaux. En conclusion, la compréhension accrue de ces réponses saisonnières requiert une étude détaillée et simultanée des environnements naturels qui régissent les patrons de réponses.

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Introduction

The extensive literature about insect seasonality reveals great diversity and complexity in the adaptations that withstand seasonal adversity and synchronize development with the seasons. This paper reviews the basic structure of these adaptations, identifying the elements that are needed to characterize a given life cycle and hence serving too to identify the decisions needed in planning investigations. Treating this broad subject area in detail would require several books, but the aim here is to provide a

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shorter treatment that gives the necessary overview and essential details in one place, in the hope that such a treatment will be of value to a range of readers. The approach therefore is synoptic rather than comprehensive, but relevant literature, especially reviews and recent papers, is cited to lead into the wider literature on each topic. Specific practical aspects have been treated by Danks (1987*a*, chap. 14, 1996, 2000*c*).

Most accounts of insect seasonality focus immediately on the organisms' responses, such as photoperiodism. I begin instead with the important environmental context, because unravelling the responses requires an understanding of the characteristics and complexity of natural environments. Spatial, temporal, and resource-limited elements of the responses are then outlined, including the ways in which insects deal with seasonal adversity, followed by an account of the ways in which the responses are controlled and integrated.

Elements of the habitat

Habitats vary in space and time on a variety of different scales. Small-scale spatial influences, notably the role of microhabitats, are especially important for insects, but they operate in the context of much larger patterns (for example, compare Corbet 1972; Oke 1987; Bailey *et al.* 1997). Adaptations are a result of changes not just on seasonal time frames but also over longer and shorter intervals, and reflect too the evenness or predictability of the changes.

Habitats provide both resources (such as food) and constraints (such as cold winters). Depending on time and place, therefore, insects require a resistant stage during adversity and an active stage during conditions that can be exploited for development or reproduction. Habitats also differ in how visibly or reliably they provide signals from which current or future conditions can be assessed. Consequently, the analysis of insect habitats in the context of life cycles must address a range of elements: spatial and temporal frameworks, resources and limitations, and signal features.

Spatial framework

The spatial complexity of habitats is one template for the evolution of seasonal adaptations. At the largest scale, the presence and intensity of developmental delays such as diapause depend on regional patterns of climate. Such large-scale patterns may also have been modified by the historical processes of glaciation, isolation, and genetic drift (*e.g.*, Armbruster *et al.* 1998; Bossart 1998; Stone *et al.* 2001).

Intermediate spatial complexity, such as complex topography, influences dispersal and thus interpopulation variation in species with limited capacity for movement (Wishart and Hughes 2001). Certainly, there is much evidence for heritable variation in life-history traits for populations from different habitats, for example between closed woodlands and open landscapes that are warmer (Karlsson and Van Dyck 2005) or between habitats at different elevations (Sorensen *et al.* 2005). In particular, because local selection favours specific life-cycle adaptation but interbreeding offsets regional differentiation, knowing about dispersal, range size, and other factors that interact with local habitat features such as growing season and resource distribution helps scientists to interpret seasonal adaptations and voltinism (*cf.* Dennis *et al.* 2000; Llewellyn *et al.* 2003).

Habitat suitability at the local level comprises many elements beyond the general effects of climatic differences. For example, complex interactions with host-plant phenology are known. Host plants may or may not coincide with the seasons in the same way as their herbivores, creating differences in suitability from one place to the next. The fitness of many herbivores depends on the close synchrony of egg hatch with bud burst (*e.g.*, Chen *et al.* 2003) or on the quality of leaves at particular times of year. Leaf quality tends to decline rapidly after spring, and again towards the end of the season. Summer leaves vary less, increasing the range of developmental durations that are possible in species that feed during the middle of the season (*cf.* Fox *et al.* 1997; Kause *et al.* 2001).

Smaller scale influences are also known. For example, modelling for one butterfly population showed that locating larvae differently within the habitat can change phenology by up to 11 days (Weiss and Weiss 1998). Differences among microhabitats are also critical to winter survival. Thus, depending on locality and year, survival of the boll weevil *Anthonomus grandis* Boheman (Curculionidae) overwintering in litter varies from 0% to 100% (Pfrimmer and Merkl 1981). Differences in survival can depend on many very small-scale features, such as local vegetation (which holds up snow) and whether it dies back seasonally, and surface depressions (which accumulate water or snow and may reduce the impact of fires) (Danks 1991*b*).

Temporal framework

Habitat suitability, driven chiefly by climatic suitability, depends on how far conditions depart from those allowing development and on their seasonal pattern, but it depends also on the extent of variation both within and among years (Danks 1999). Differences in these parameters are exemplified by data for a small number of sample sites shown in Table 1. Of course, many more climate types and gradations have been recognized, including a range of alpine, desert, tropical, and oceanic climates (*e.g.*, Hodkinson 2005*a*; Oliver 2005; Turnock and Fields 2005). However, the sample locations in Table 1 serve to illustrate key habitat characteristics for insects.

Severity reflects temperatures that are too cold or too hot, heat sums inadequate for development, and moisture regimes that are too dry. For example, winter temperatures range, chiefly according to latitude, from extremely cold to warm, while summer temperatures range from cool to hot (Table 1). The effect of temporal variation in conditions depends on the average condition. For example, in the high Arctic, where mean maximum temperatures in summer are only a few degrees above 0 °C, day-to-day variation makes summer frosts very likely (*cf.* Table 1). This likelihood is up to 90% even in the warmest month (Danks 1993, Table 1). In turn, severe climates influence the occurrence of host plants and other foods. Coping with severity requires resistance such as cold hardiness, selection of microhabitats that are buffered against the extremes of heat, cold, or dryness, daily and annual timing of activity, and so on.

Timing and other adaptations are likewise required to allow for *seasonality*, conditions that change across an annual time frame so that typically they are suitable for development and reproduction only part of the time. Seasonal conditions are commonly assessed by seasonal differences and variations in temperature (*cf.* Table 1), but many other environmental factors influence suitability (see Resources and limitations).

Unpredictable short-term patterns include variation within a given month. Marked changes of this sort, for example sudden spells of hot or cold, drought or flooding, may be especially dangerous to synchronized cohorts. Again, their effect depends on the mean temperature (*cf.* Table 1).

Variability from year to year makes suitable habitats or resources different in amount or in timing from one year to the next, threatening species without ways to modify fixed modes of development. The effects of long-term extremes that differ greatly from the mean depend on the mean temperature. For example, subfreezing temperatures can occur in arctic summers (as noted above for the shorter term) and unusual heat in subtropical summers (Table 1). The consequences of inter-seasonal variability have seldom been quantified but may be more pervasive than is usually considered. For example, Östman (2005) concluded that large-scale year-to-year variations are more important to the survival and fecundity of carabid populations than are spatial variations over the shorter term. Likewise, the role of long-term climatic patterns (as opposed to more random variations), such as those driven by the El Ninõ or North Atlantic Oscillation effects (*cf.* Dettinger and Diaz 2000), has been assessed only in a limited way but can significantly alter insect phenology and other traits (Briers *et al.* 2004).

Climatic factors, especially the driving variables of temperature and precipitation, affect different habitats in different ways. Protected habitats change more slowly and have a narrower range of extremes than exposed ones (*cf.* Danks 1971*a*). Typical tropical streams have relatively steady flow, whereas at high latitudes seasonal differences in precipitation and evapotranspiration usually are more marked and contributions from winter snow and ice are delayed (Dettinger and Diaz 2000). In desert regions, rainfall is especially variable from year to year, and stream flow is more variable still (Dettinger and Diaz 2000). Moreover, stream flow varies on still smaller scales (Lytle 2002; Benbow *et al.* 2003).

Key characteristics of conditions at the level of habitat are therefore difficult to quantify because of their variability and unpredictability. For example, the "dryness" of deserts depends on the variability and predictability of rainfall as well as on its absolute amount (Noy-Meir 1973). Some variables affect life cycles in some years but not in others (*e.g.*, Fleishman *et al.* 1997). Similar intermittent influences are exerted by rare catastrophic events such as fires, flooding, and drought. For example, depending on the terrain and the stand type, the mean time

Table 1. Sample measures of severity, seasonality, unpredictability, and variability in zones with different

	Severity			
Zone	W mean air temp., °C	C mean air temp.,°C	Annual heat accumulation,* day-deg. above 0 °C	W mean precip., mm
1. High Arctic	4.6	–33.7[†]	250	21
2. Low Arctic	7.9	–26.5	633	53
3. North temperate central continental	19.3	–17.6	2210	60
4. North temperate eastern continental	20.7	–10.8	3067	78
5. North temperate maritime	15.4	–4.3	2128	89
6. South temperate continental	26.7	7.5	6237	131
7. Seasonal tropical	29.4[‡]	26.1[§]	9974	76
8. Wet tropical	25.8[†]	24.3	9261	261
9. Desert	20.9[¶]	15.4**	6470	0.1

Note: W, warmest month (typically July); C, coldest month (typically January). Summer is the warmest 6 months
Canada (52°N); 4, Ottawa, ON, Canada (45°N); 5, St. John's, NL, Canada (45°N); 6, Birmingham, AL, United States of
and Orvig (1970); Court (1974); Hare and Hay (1974); Miller (1976); Portig (1976); and Ratisbona (1976).

*Heat accumulations are indicative only, based on monthly mean screen-air temperatures.

[†] February.

[‡] May.

[§] December.

[‖] February–August (93% May–October).

[¶] January.

**July.

[††] October–May.

between fires in many boreal coniferous forests is only about 50 to 100 years, a shorter period than the intrinsic generation time of the trees (Danks and Foottit 1989). Variations in different habitats over intervals of more than one year include marked changes in salinity (*e.g.*, Garcia *et al.* 1997), nutrient level, and other features. How organisms cope with such intermittent challenges is therefore relevant to their success. They must not only follow annual cycles that accord with seasonality and withstand long periods each year with very low temperatures or limited rainfall, but also survive unpredictable events.

Resources and limitations

Among physical elements, temperature is the most critical habitat factor, tied closely to climates (see above) and effective through lower and upper limits and through heat accumulation. Lower developmental limits for insects average about 10 or 11 °C (Utida 1957; Honěk and Kocourek 1990) and in most temperate species upper limits lie between 20 and 35 °C (unpublished analysis). On average, species need about 350 day-degrees above the developmental threshold to complete the life cycle, but there are very wide variations among species (Honěk and Kocourek 1990; Danks 2006*c*). The impact of temperature is modified by habitat, and most other physical conditions and resources are integrated with other factors. For example, oxygen levels depend on flow rate and microhabitat (*e.g.*, Genkai-Kato *et al.* 2005). Even in simple situations, food availability integrates the seasonal supply of heat, light, water, and so on. Most biotic influences are complex because organisms interact with one another: the effects of parasites, predators, diseases, and competitors on seasonal suitability are dynamic as populations develop and interact. In some species biotic rather than physical factors cause most winter mortality, even where temperatures are low (*cf.* Pitts and Wall 2005).

Therefore, depending on the time of year, most habitats have positive elements when they provide resources and favour development and negative elements when physical conditions are untenable and resources are inadequate. Assessing the setting of individual species therefore has to take account of both constraints (adversity) and needs (suitability).

climates.

	Seasonality		Unpredictability	Variability	
Annual mean precip., mm (annual snow, cm)	Temp. difference W – C, °C	Precip. in summer, % of annual	W daily mean temp. range, °C (% of mean)	W extreme min. temp., °C (extreme max., °C)	C extreme min. temp., °C (extreme max., °C)
130 (68)	38.3	73	4.9 (107)	–2 (16)	–49 (–14)
380 (204)	34.4	58	7.6 (96)	–1 (24)	–45 (4)
352 (97)	36.9	72	14.5 (75)	2 (40)	–46 (9)
850 (219)	31.5	53	11.7 (57)	5 (37)	–36 (11)
1551 (380)	19.7	40	9.6 (62)	1 (29)	–23 (13)
1347 (3)	19.2	48	11.6 (43)	11 (41)	–13 (27)
1142 (0)	3.3	45[‖]	10.6	23 (34)	20 (31)
2869 (0)	1.5	49	9 (35)	20 (36)	16 (36)
2 (0)	5.5	10[††]	7.8	13 (30)	9 (22)

(typically April to September). Zone 1, Resolute, NU, Canada (75°N); 2, Iqaluit, NU, Canada (64°N); 3, Saskatoon, SK,
America (34°N); 7, Managua, Nicaragua (12°N); 8, Uaupés, Brazil (0°N); 9, Iquique, Chile (20°S). Data from Vowinckel

Signals

An important feature of habitats is how well they provide to insects signals that can be used to predict future conditions. Environmental signals used for this purpose seldom stem directly from the resources or conditions that limit seasonal activity, because to avoid adversity or to coincide with suitability, insects must generally predict rather than simply monitor seasonal changes. Therefore, except in habitats that are extremely well buffered, such as deeper soil layers, proximate rather than ultimate factors are used to control seasonal responses.

The most effective signals are reliable, frequent, and recognizable (Danks 1987*a*, chap. 6). Signals are reliable when well correlated with the seasons and not subject to short-term noise. Therefore, the cue of photoperiod, which is associated with invariable astronomical events, is the single most reliable environmental signal. Thermoperiod is driven largely by the same events and shares some of the same features. Food quality is often closely tied to the seasons. Many other factors, including temperature level and most biotic factors, are less reliable.

Frequent or continuous signals can be assessed regularly. Most major physical cues such as photoperiod, temperature, and moisture are in this category. Signals are easily recognized when sensors are available and when conditions change rapidly and evenly between levels that are well differentiated from one time of the season to another. Sensors are available for most potential cues. Photoperiod is highly recognizable even when the differences from day to day are relatively small, as at some times of year and at lower latitudes, because daylengths change very evenly. Many other signals, such as temperature, are less informative because they fluctuate widely from day to day. Although average temperatures show clear trends over the longer term, it is usually difficult for insects to integrate this information in ways that would allow a timely seasonal response.

Beyond intrinsic elements of the signals themselves, availability or visibility as influenced by the insect's habitat determines their value for predicting seasonal change. For example, the great intrinsic reliability, frequency, and recognizability of photoperiod are negated if species live in very dark places (such as the soil

Table 2. Essential elements of seasonal responses.

Seasonal constraint	Sample response	Sample action	Sample correlate
Spatial differences	Movement to less severe places	Migration; choice of overwintering habitats and microhabitats	Energy storage
Temporal differences	Life-cycle timing; response to year-to-year differences	Developmental patterns including different stages; phenological and reproductive patterns; diapause and other controls	Adjustments of timing using environmental signals
Availability of resources and suitability of environments	Differential resource use; habitat modification; resistance to adversity	Host-plant switches; construction of shelters, aggregation, *etc.*; tolerance of or resistance to cold, dryness, food limitation, *etc.*	Energy use and other correlates
Combined elements	Trade-offs	Many trade-offs, but multiple rather than one-to-one interactions hinder assessment	Size and time (but not always)

and inside some plant tissues) where signals cannot be detected even by sensors with very low thresholds.

In essence, insect responses are usually controlled by signals that provide information meaningful for a particular habitat. Consequently, for example, photoperiod is not used at the highest latitudes because temperature varies close to 0 °C and plays a dominant role there, so that even if changes in light intensity or solar elevation could be detected above the Arctic Circle in summer, the seasonal information these cues provide is less relevant than current temperature (*e.g.*, Danks and Oliver 1972*b*). Likewise, in some circumstances species from deserts with intermittent rainfall would be expected to use moisture, humidity, or food cues because those factors would most likely indicate suitable windows for development. Assessing habitat features for a given species in parallel with the characteristics of signals and their availability suggests what factors should be tested for potential roles as seasonal signals. Nevertheless, many insect species make small adjustments in their responses to main factors such as photoperiod by using other signals too (see below). Taking account of additional factors evidently has adaptive value, so testing a relatively wide range of conditions is usually wise.

Elements of the response

Insects respond to seasonal adversity and habitats that are intermittently favourable for development and reproduction in many different ways, as summarized in Table 2. Spatial differences in conditions are met by long-distance and short-distance movement. Temporal variations in favourability are met by specific patterns of timing of life-cycle components. Other adaptations serve to exploit resources and to modify or resist the environmental limitations. However, because these many elements may make opposing demands and it is not possible to optimize or maximize every feature simultaneously when resources are finite, trade-offs among various components of the response are usually required. The sets of responses in habitats that have extreme cold, dryness, salinity, or other challenges are especially instructive.

Spatial framework

The simplest way for insects to avoid or coincide with given conditions is to choose among available habitats through movement or specific selection. These responses occur on a wide range of scales, although small-scale choices are more prevalent than long-distance movements. Moreover, movements even at the largest scale end by targeting specific microhabitats, even though responses vary in how many steps and what time or distance is involved in displacements towards habitats suitable for development or overwintering. For example, the long fall migration of monarch butterflies (*Danaus plexippus* (Linn.)) (Nymphalidae) (Brower 1995, 1996) takes them to certain trees in certain forested habitats that offer favourable conditions for overwintering (Leong 1990; Brower *et al.* 2002). Adult *Baetis* mayflies (Ephemeroptera: Baetidae) disperse from their sites of emergence and oviposit elsewhere in microsites preferred for oviposition, but the subsequent survival of larvae — and hence the emergence of adults in the new areas — is affected by independent processes operating at the local level that are different from the influences on adults and their oviposition in the previous generation (Peckarsky *et al.* 2000).

Lady beetles and noctuid moths may fly considerable distances from the lowland habitats where they develop, but then choose specific aestivation shelters in which to aggregate (*e.g.*, Oku 1983). Most other species overwinter relatively close to their feeding habitats, but again they first move to suitable general habitats, for example from fields to field edges or woodlands, then enter microhabitats chosen on the basis of temperature, light, moisture, touch, and other factors (review by Danks 1991*b*; and see Nalepa *et al.* 2005). Such a process parallels other chains of behaviour in insects, such as dispersal, then landing, then host selection in aphids (Powell *et al.* 2006) and components of habitat selection and then host selection in parasitoids (Vinson 1976). Viewing seasonal movements as a series of steps (such as energy acquisition, long-distance movement, habitat selection, and microhabitat selection) helps to identify logical components for experimental investigation and analysis.

Extensive flight and the diapause that accompanies both long-distance and short-distance movement to escape adversity usually depend on the buildup of energy stores, typically in the form of lipids (information for many species is listed by Danks 1987*a*). In milder climates, favourable microhabitats, including artificial ones, may allow winter development that would not be feasible otherwise (*e.g.*, Takafuji 1994; Ohashi *et al.* 2005).

At the smallest scale, many species not only select microhabitats but also use adaptive behaviours, such as basking, body orientation, or hiding, especially for thermoregulation; many species maintain body temperature within a relatively narrow range, and finely tuned responses have been reported (Heinrich 1981, 1993). As might be expected, most behavioural elements are adapted locally (Samietz *et al.* 2005). Allied to these responses are melanism or dark colouration, which helps absorb solar heat, and hairiness, which helps retain it (Danks 1981; Gross *et al.* 2004).

Temporal framework

Insect life cycles consist of stages with different prominence and with different potentials for activity, resistance, and so on (Danks 2000*c*). These stages are timed according to a number of general patterns. The timing, especially for adults, can be described in terms of phenology, but phenological variables are surprisingly diverse and may be combined in different ways.

Typical metamorphosis includes stages that are immobile (eggs, or eggs and pupae), stages that feed (larvae, or larvae and adults), and stages that reproduce (adults). Delays or dormancies are interpolated into many life cycles (for sample reviews see Tauber *et al.* 1986; Danks 1987*a*). Although dormancy is common in immobile stages, as might be expected, it is known in any stage and indeed in insects as a whole appears to be more prevalent in larvae, which last the longest in most groups except beetles. Seeking of food resources, as well as wider dispersal, is most common in winged adults but also is common in larvae. The durations of activity and dormancy and the tendency to be dormant also reflect phylogeny. Thus, the diapause stage tends to be the same within genera and to some degree within families (Danks 1987*a*). For example, typical Orthoptera overwinter as eggs, chironomids as larvae, sarcophagids as pupae, and drosophilids as adults. In the many families of beetles in which the adult is long-lived and feeds extensively, adults usually overwinter (Danks 1987*a*), as in coccinellids (Hodek 1973). Major feeding stages — larvae in most groups — are typically prolonged, but in species that eat ephemeral foods such as dung, carrion, and fungal fruiting bodies, the larval stage is much abbreviated and then ordinarily is followed by prepupal or pupal, and rarely by adult, dormancy.

Different stages also have different abilities to withstand severe conditions. Dormant stages often require resistance. Such resistance is favoured in the resting stages of metamorphosis by the fact that in most species those stages have evolved some additional level of mechanical protection, because physical damage accumulates and cannot be repaired in immobile individuals. Protection includes the coverings of eggs and the cocoons of pupae (Danks 2002*a*, and see below). Many dormant, fully fed larvae or prepupae (Danks 1987*a*, Table 11) also resist adverse conditions inside cocoons or similar structures prior to metamorphosis to the pupa, for example in many Hymenoptera.

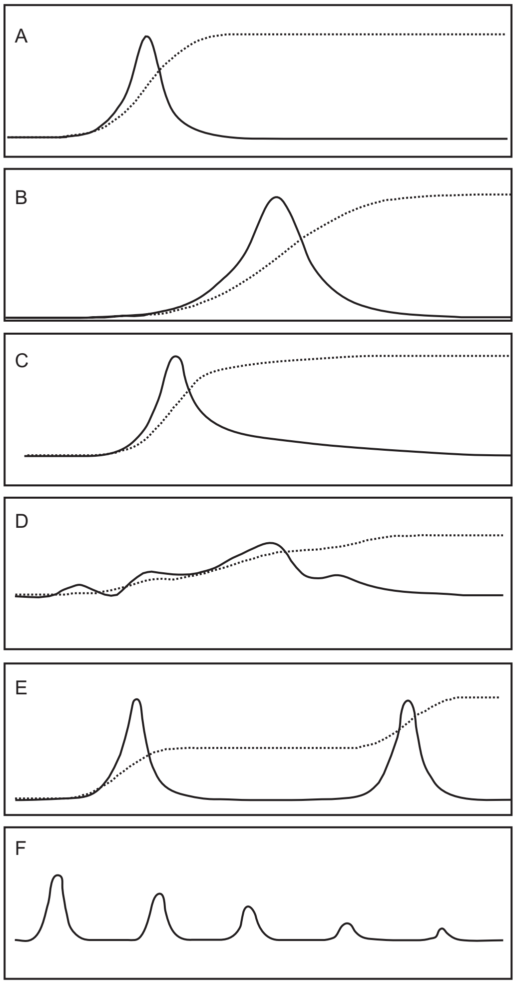
Other characteristics reflect the fact that the timing by which suitable resources can be exploited is easier in some stages than in others. Many species deposit eggs near buds, overwinter as partly grown larvae, or metamorphose in spring and thereby enter a key feeding stage when succulent new plant growth is available (*e.g.*, Masaki 1980). The timing of reproductive activity also accords precisely with the availability of suitable habitats. For example, many species are dormant in the stage (*e.g.*, pupa) immediately preceding reproduction, allowing rapid oviposition soon after emergence in the spring. This tendency is especially clear in habitats with an abbreviated growing season, where "spring species" (Corbet 1964*a*) predominate.

Finally, some species have complex life cycles with multiple periods of activity, reproduction, or dormancy or multiple stages that can enter dormancy. These integrated systems are discussed in a later section.

The seasonal occurrence of stages (phenology), including the temporal pattern of adult emergence, can be characterized by features such as the *onset* of emergence, its *duration*, the *synchrony* of individuals, any *skew* from normality, and variations including *irregularities* and *modalities*. Easiest to describe are the phenological patterns of species with normally distributed emergence that takes place over a short period (Fig. 1A) or over a longer interval (Fig. 1B).

Other species have more complex patterns. For example, skew (Fig. 1C) is common, giving a tail after the main distribution. Often it reflects only the fact that some individuals can be delayed by local conditions, whereas even when conditions are fully suitable no individual can develop much faster than the norm. However, in other instances the skew is adaptive, with relatively small but significant numbers of late emergents providing insurance against catastrophes that might befall the main population (risk spreading; see Types of variation below).

Fig. 1. Sample stylized phenological patterns (solid lines) with cumulative equivalents (dashed lines, shown at a different scale). (A) Unimodal, narrow normal. (B) Unimodal, wide normal. (C) Unimodal, skewed. (D) Irregular. (E) Bimodal, equal. (F) Multimodal, skewed. For additional information see text.



Irregular phenology (Fig. 1D) arises by more than one route. Emergence highly dependent on weather that intermittently falls below the temperature threshold for emergence results in irregular recruitment of adults. Similar patterns are shown by traps that rely on activity influenced by weather. Alternatively, emergence in individual microhabitats might be normally distributed, but sections of the population in habitats with different conditions emerge at slightly different times. Combined emergence by individuals in different microclimates can therefore give an irregular pattern (Baker 1980). In ponds with different mean temperatures, the same species of aquatic insects emerge at different times (Danks and Oliver 1972*a*; Corbet and Danks 1973).

Bimodal emergence (Fig. 1E) arises in several ways. Separate generations give separate peaks. In many species, developmental decisions (see Control and integration below) accelerate emergence or allow emergence or activity under one condition but retard or prevent it in members of the same cohort under another, producing phenological peaks separated by an unsuitable season, for example in spring and fall (*cf.* Masaki 1980, Fig. 1) or in successive years (cohort splitting: *e.g.*, Pritchard 1979; Danks 1992; Kiss and Samu 2005). Multimodal patterns have several causes too, but of particular interest are skewed patterns (Fig. 1F), such as prolonged diapause between years, that — like genetically programmed bimodal patterns — appear to be a way of spreading risk (see Types of variation below). The various emergence patterns shown in Figure 1 are paralleled by patterns of oviposition after emergence, with the added possibility of delayed onset.

Careful measurements and analyses are required to identify the different patterns. Important information about life cycles and their relationship to natural environments may be missed if experiments are too short, observations are too limited, or data are improperly grouped (Danks 2000*c*). Also important is the variability of these parameters from one year to the next. Warm, cold, or dry seasons may change the pattern of emergence or advance or delay its onset, often considerably, for example by 10 days for mosquitoes in the high Arctic (Corbet and Danks 1973) and by one month for black flies at the tree line (Ide *et al.* 1958). Moreover, the retarding or accelerating effect of a given season is not the same for all species. Winter snow accumulations and cool or cloudy weather during the spring thaw do not affect low-lying aquatic habitats in the same way as dry elevated habitats blown free of snow. Assessing the significance of phenological patterns may thus require several years of data from natural habitats.

Resources and limitations

In addition to spatial and temporal coincidence, adaptations that facilitate the acquisition of resources include adjustments of metabolism or activity to enhance development and reproduction, in response to physical conditions or food. At the same time, environmental limitations may prevent normal growth and development, and many other adaptations serve to modify local conditions or to resist adversity. Moreover, trade-offs balance allocations for different purposes when resources are limited.

Modification of adverse conditions

Many species actively *modify* local conditions to reduce the impact of adverse seasons, as opposed to simply seeking out favourable microsites. These modifications include excavating substrates, constructing shelters, inducing responses in plants or hosts, and aggregating (including sociality), as well as modifications made by parents that improve conditions for their progeny (reviews by Danks 2002*a*, 2004*b*).

Many insects dig into the soil for overwintering, the chamber often strengthened by a silk lining. There they are buffered against winter temperatures. Other species overwinter in less robust but still protective substrates, such as plant stems. Excavations also protect against dry conditions, and some species adjust the depth and location of burrows according to desiccation stress (*e.g.*, Rasa 1999). Seasonal flooding is offset by a resin lining in nests of some bees (Roubik and Michener 1980).

Some species that eat leaves construct shelters during feeding, especially by tying leaves together with silk. They include both solitary and communal species. In aquatic habitats, shelters such as the cocoons of chironomid larvae and the cases of caddisfly larvae typically are made from saliva and material incorporated from the substrate.

The most durable cocoons are made by dormant stages. Indeed, overwintering generations normally construct more robust cocoons with thicker walls than do intervening nondormant generations of the same species (sample species are listed by Danks 1987*a*, Table 6). These cocoons provide mechanical protection not just against abrasion but also against more severe stresses (Danks 1971*b*, 2004*b*). The cocoons may act as a humidity buffer (*e.g.*, Tagawa 1996), protect against water (Sagné and Canard 1984), or stop ice from reaching the body surface, preventing freezing by inoculation (Sakagami *et al.*

1985). Although most cocoons have limited effects on temperature, some darkly coloured or specialized cocoons absorb solar heat and thus accelerate development (Kevan *et al.* 1982; Lyon and Cartar 1996). Cocoons and other shelters also deter many generalist predators during the active season (Dillon 1985; Gross 1993).

The galls induced seasonally by insects on plants also protect against some generalist enemies, and they give mechanical protection, desiccation resistance, and so on (Danks 2004*b*, pp. 14–15). Some parallel benefits arise through use or modification by parasitoids of host structure or behaviour (Hippa and Koponen 1984; Horton and Moore 1993).

Some but by no means all aggregations serve to increase temperature (Benton and Crump 1979; Klok and Chown 1999) and reduce water loss (Yoder *et al.* 1992*a*). Some reduce predation especially by reinforcing aposomatic colouration or chemical repellents (Vulinec 1990). A few condition the food (*e.g.*, Marchenko and Vinogradova 1984) or overwhelm host defences (Grégoire 1985) and thus accelerate development. The most striking benefits of aggregation are seen in colonies of social insects able not only to construct a protective nest but also to condition internal temperature, moisture, food supply, and so on (Southwick 1987) and to protect against predators through structure, repellents, and coordinated defensive behaviour (Jeanne 1975).

Finally, substantial seasonal benefits follow from modification by parents of the habitats in which their eggs are deposited and their larvae develop. Eggs of some species are protected by placement, concealment, or robust coverings such as oothecae (*cf.* Richards and Davies 1977, p. 321), paralleling the protection afforded to active stages by their own efforts such as burrowing and cocoon making. Depending on the species, protection of eggs in the oviposition site, retention of eggs inside the mother during development, or parental care provided to larvae can prevent ice inoculation, flooding, and desiccation; reduce predation, parasitism, and even diseases; and supply food resources (Danks 2002*a*, p. 17).

Resistance to adversity

Many types of adversity can prevent the activity or threaten the survival of insects. For example, adaptations are known in response to anoxia (Nagell and Brittain 1977; Hoback and Stanley 2001; Hodkinson and Bird 2004) as well as to ice scour, spring spates, floods, and other extremes or disturbances (*e.g.*, Mendl and Müller 1978; Clifford *et al.* 1979; Lytle 2002; Prowse and Culp 2003). However, information is most abundant about how insects withstand cold, dryness (often with high temperatures), and lack of food.

Cold

Insects survive the cold of winter by a wide array of adaptations that have been reviewed many times (for recent updates and salient references see Bale 2002; Danks 2005). Elements of these responses are shown in Table 3.

Insects can be injured at low temperatures above 0 °C ("chilling injury") — see Turnock and Fields (2005) and references cited therein. Injury from cold appears to be associated with a breakdown of membrane structure and membrane-based ion gradients (Ramløv 2000; Košt'ál *et al.* 2004; Zachariassen *et al.* 2004*a*); compromised protein structure and enzyme function have also been suggested. Corresponding adaptations to low temperatures, including temperatures below 0 °C, include modification in the saturation of membrane fatty acids to maintain function at lower temperatures (*e.g.*, Bennett *et al.* 1997; Košt'ál and Šimek 1998; Ohtsu *et al.* 1998). Shock proteins (Craig *et al.* 1993), produced in response to chilling or heating, are also presumed to protect against low temperatures (*cf.* Denlinger *et al.* 1991; Relina and Gulevsky 2003); typically they act as molecular chaperones that help in protein transport, folding and unfolding, assembly and disassembly, and aggregation processes. Nevertheless, it has proved difficult to associate the occurrence or reduction during cold hardiness or diapause of shock proteins or other molecules (or the upregulation or downregulation of responsible genes) with their detailed function (Storey and Storey 1999), despite many recent studies. Indeed, there are many interspecific differences (compare, for example, Hayward *et al.* 2005 and Tachibana *et al.* 2005; see also Jung and Lee 2005; Kayukawa *et al.* 2005; Michaud and Denlinger 2005) and even differences between winter diapause and summer diapause in the same species (Chen *et al.* 2005).

At temperatures below 0 °C, most species remain unfrozen because they supercool. Several systems are used in the same or different species to prevent freezing. Ice formation is most likely when molecules can assemble in the appropriate configuration (that of the ice crystal)

Table 3. Common mechanisms of direct resistance to cold in insects.

Mechanism	Sample systems or substances
Survive chilling	
Protect membranes or membrane function	Membrane transition temperature lowered by changing composition of fatty acids
Protect proteins, enzymes, and other functions	Potential roles of shock proteins and other molecules
Prevent freezing	
Lower haemolymph melting point	Manufacture of low-molecular-weight solutes, including glycerol, other polyhydric alcohols, sugars, some other substances; some species manufacture multiple solutes
Lower haemolymph freezing point	Antifreeze proteins lower the freezing point (this action is enhanced by glycerol and other molecules)
Prevent inoculative freezing	Some antifreeze proteins prevent ice inoculation
Reduce nucleation sites	Adaptations in structural proteins, *etc.*
Eliminate nucleators	Empty gut
Mask nucleators	Nucleators or nucleation sites masked by nucleation inhibitors
Reduce water available for the freezing process	Associate water with cell constituents ("bound water", *etc.*); dehydrate passively by readily losing water through the cuticle to surrounding ice
Survive freezing	
Limit supercooling to reduce impact of freezing events	Manufacture of nucleating proteins; cuticular structure readily allowing inoculation
Reduce amount and rate of formation of ice	Manufacture low-molecular-weight cryoprotectants
Protect membranes or membrane function	See above; also, protection provided by association of various cryoprotectants with membranes
Protect other functions	See above
Rapid cold hardening	Enhanced resistance caused by brief cooling beforehand
Prevent recrystallization during thaw	Manufacture of antifreeze proteins; manufacture of specific recrystallization inhibitors (known in nematodes)
Modify water status	Unreactive glassy states mediated especially by carbohydrates such as trehalose
Dynamic adjustments	
Seasonal adjustment of cryoprotectants	Solutes and antifreeze proteins change through the winter in some species, changing supercooling points and other features
Rapid cold hardening	See above
Freezing-induced change in supercooling points	Freezing exposure lowers supercooling points in some species
Linkages with diapause	Diapause is a prerequisite for some elements of cold hardiness in some species
Seasonal adjustment of mitochondria	Mitochondria reduced during winter cold and inactivity
Ongoing repairs	Warmer intervals permit injury caused by cold exposures to be repaired in some species
Interaction between antifreeze proteins	Enhances action

Note: Indirect methods such as seasonal inactivity, site selection, and cocoon construction are treated elsewhere.

around a physical nucleus, and indeed in the absence of such a nucleus freezing is unlikely until water molecules are moving very slowly at the homogeneous nucleation temperature, which is about –40 °C (Vali 1995). The incidence of freezing is therefore reduced by eliminating nucleators. This can be done through modification of the tissues (as by the design of structural proteins, *cf.* Zachariassen *et al.* 2004*b*), by eliminating certain molecules (*e.g.*, Neven *et al.* 1986), and by evacuating the gut (because typical ingested food has potent nucleators). Some species may even moult to eliminate gut nucleators (Worland 2005). Nucleators and nucleation sites can also be masked by inhibitory molecules (*cf.* Wilson *et al.* 2003).

Supercooling is enhanced too by solutes of low molecular weight, chiefly polyhydric alcohols and sugars (examples are listed by Lee 1991 and Ramløv 2000), which can reach multimolar concentrations in overwintering insects. These substances lower melting and freezing points by colligative action, so that their effects are additive. Many species have more than one kind of solute, for example both glycerol and sorbitol.

Larger antifreeze proteins (review by Duman 2001) lower the freezing point but not the melting point by inhibiting ice formation (*cf.* Kristiansen and Zachariassen 2005). This action is enhanced by other antifreeze proteins together with certain solutes of low molecular weight (*e.g.*, Li *et al.* 1998; Duman 2002; Duman and Serianni 2002; Wang and Duman 2005, 2006). Some of the antifreeze proteins found in superficial tissues or around the gut appear to prevent inoculation by ice (Olsen *et al.* 1998). Antifreeze proteins are also known to inhibit recrystallization of ice during post-freezing temperature changes or thawing (Duman 2001). Cells can be injured by such reorganizations of ice crystals and not only by the initial formation of ice. At least some invertebrates have specific recrystallization inhibitors, which are smaller than typical antifreeze proteins (Ramløv *et al.* 1996).

The freezing process depends on the supply of water molecules, and so closer association of water with biological molecules or surfaces reduces the likelihood of freezing. Such changes are responsible for significant winter reductions in the amount of “freezable water” or “osmotically inactive water”, also termed “bound water” (Block 2002; Wolfe *et al.* 2002; Block and Zettel 2003). The cold hardiness of several species in extreme environments includes marked dehydration (*e.g.*, Danks 1971*b*; Ring and Danks 1994; Bennett *et al.* 2005).

Some soil organisms with permeable integuments, including some earthworms, enchytraeids, and springtails, remain unfrozen by progressive dehydration through the cuticle to surrounding ice. This loss concentrates solutes in the body fluids to a level at which the fluids will not freeze (Holmstrup and Zachariassen 1996; Holmstrup *et al.* 2002). A similar phenomenon has been reported for stonefly eggs, which dehydrate and supercool below –29 °C while surrounded by ice (Gehrken and Sømme 1987).

Another set of insects survives actual ice formation in the body. Such freezing-tolerant species typically limit the degree of supercooling because the very rapid ice formation that takes place in highly supercooled solutions increases the extent of injury compared with slow freezing. Proteins that ensure nucleation are manufactured by many freezing-tolerant species (review by Duman 2001; Lundheim 2002). Some other freezing-tolerant species survive only if frozen by inoculation (review by Duman *et al.* 1991; Riihimaa 1996), suggesting that they lack ice nucleators but that the cuticular structure offers no resistance to inoculation. Low-molecular-weight cryoprotectants in freezing-tolerant species serve to decrease the amount of ice formed at a given temperature and to slow its rate of formation (Ramløv 2000). Relationships of tissue freezing with anoxia have also been considered, because freezing impedes oxygen delivery (*e.g.*, Morin *et al.* 2005).

Freezing tolerance is associated in some species with a change in the state of water to form a homogeneous glass, which prevents all molecular diffusion and reactions and thus inhibits metabolic processes as well as solute crystallization. Glasses form, typically by dehydration, in the presence of certain carbohydrates at high concentration. Trehalose is the best known glass former, mediating glasses at relatively high and ecologically relevant temperatures (Ring and Danks 1998; Danks 2000*a*).

Also known to enhance cold hardiness is rapid cold hardening, typically in active stages: relatively brief exposures to mild cold enhance subsequent resistance to more severe cold (overview by Danks 2005). Rapid cold hardening occurs in a range of taxa. Moreover, it can give additional protection in cold-acclimated or winter individuals (Powell and Bale 2005 for an aphid) or additional freezing tolerance (Lee *et al.* 2006*a* for an antarctic midge). Production of shock proteins and cryoprotectants is associated with rapid cold hardening in some species (Qin *et al.* 2005; Yoder *et al.* 2006*a*) but not in others (Lee *et al.* 2006*a*). Changes in membrane lipid composition or fluidity have also been reported (Overgaard *et al.* 2005; Lee *et al.* 2006*b*). These differences suggest that rapid cold hardening involves several different processes, but we do not know their functioning in detail.

Evidence is also accumulating as to how other elements and pathways are involved in cold hardiness, such as cholesterol (Yi and Lee 2005) and membrane transport of cryoprotectants and water (Izumi *et al.* 2006), although again the details remain to be worked out. Nor are some other potentially allied responses understood. For example, recovery from chill coma is complex (Macdonald *et al.* 2004). Cold hardening that reduces mortality from cold does not reduce chill-coma recovery times (Rako and Hoffmann 2006). However, rapid cold hardening may reduce the chill-coma temperature (Shreve *et al.* 2004).

A major conclusion that can now be drawn about insect cold hardiness is that many of its features are dynamic (Danks 2005). Cold hardiness is not a static condition instituted for the winter, but a series of complex developmental and metabolic patterns. For example, some species adjust cryoprotectant levels in fall and spring and even during winter (Baust and Nishino 1991). Cold hardiness levels vary both over the long time frame of winter and over much shorter intervals (*cf.* rapid cold hardening). For example, the type of cold hardiness may change between chilling-susceptibility and freezing-susceptibility according to life stage and acclimation (Carrillo *et al.* 2005). Freezing exposure lowers the supercooling point of individuals in subsequent exposures in a few species (Bale *et al.* 2000, 2001; Brown *et al.* 2004). The effects of cold across different temperature ranges and with different times of exposure interact, for both chilling and freezing injury, and there is some repair of cold injury during warmer spells (Nedvěd *et al.* 1998; Renault *et al.* 2004; review by Turnock and Fields 2005). Diapause is linked to cold hardiness to different degrees. Even here, the relationships are complex and diapause and cold hardiness are not simply codependent. Rather, in several species at least some aspects of the diapause program are prerequisites for some aspects of cold hardiness (Denlinger 1991; Šlachta *et al.* 2002; Hodkova and Hodek 2004; review by Danks 2005). Susceptibility to cold shock may also depend on diapause status (Pitts and Wall 2006).

These many differences among species are not surprising. Different species have evolved different life-cycle programs, cold hardiness, and other adaptations. For example, antifreeze proteins appear to have evolved independently in collembolans and insects (Graham and Davies 2005). Because habitat and water relations as well as temperatures affect overwintering conditions in a complex way, conclusions about the evolution of different types of cold hardiness are not well developed (Danks 2005), although, as might be expected, freezing tolerance is more prevalent in insects from colder climates (Turnock and Fields 2005).

Other dynamic aspects of cold hardiness that have been reported but as yet are little understood include mitochondrial degradation during winter (Kukal *et al.* 1989; Levin *et al.* 2003), the effects of fluctuating temperatures on survival, interactions between antifreeze compounds that enhance their collective action (see above), and changes in supercooling points on a daily basis (Worland and Convey 2001; Sinclair *et al.* 2003). Ecological interactions figure in many of these adaptations. For example, insects may select low-temperature habitats when there are frequent freeze–thaw transitions in order to allow a cold-hardy state to be maintained (Hayward *et al.* 2003). Understanding all of these elements therefore depends on integrating knowledge about the specific ecophysiological adaptations with knowledge of patterns in the environmental challenges they have been selected to overcome.

Dryness

Many natural systems are seasonally dry, especially in summer, and droughts can have significant and long-term effects on ecosystems (Humphries and Baldwin 2003; Lake 2003). Even many winter habitats are very dry, and adaptations to cold and desiccation overlap (Ring and Danks 1994, 1998; see also Worland and Block 2003; Williams *et al.* 2004).

Several different adaptations enhance survival when water is in short supply, especially in dormant individuals that cannot move to find it (review by Danks 2000*a*). These adaptations serve to limit water loss, acquire water, or tolerate water loss, as summarized in Table 4. Such characteristics can be selected relatively rapidly (Chown and Klok 2003*a*).

A main suite of adaptations in dry environments limits the loss of body water, which is a function of body size because the surface to volume ratio is larger in small individuals. Inactivity during dormancy conserves water (Benoit *et al.* 2005). Many species reduce cuticular permeability through thick sclerotization, often with an impermeable surface wax layer (review by Edney 1977; Alarie 1998), which is much thicker during dormancy (Danks 1987*a*, p. 23; Yoder *et al.* 1992*b*, 1995; Kaneko and Katagiri 2004; Nelson and Lee 2004). The level of saturation of epicuticular hydrocarbons is lower in diapause individuals of some species (Kaneko and Katagiri 2004). Spiracular losses through respiration are also greatly reduced by the lowered metabolism of diapause individuals (*e.g.*, Williams and Lee 2005). Structural modifications such as sunken and protected spiracles or spiracles opening into subelytral chambers reduce such losses too (Greenslade 1981; Draney 1993; Hadley 1994; Byrne and Duncan 2003). Cyclical opening of the spiracles (especially in diapause individuals) is also supposed to reduce water loss by keeping spiracles closed except for short bursts to allow gas exchange (*e.g.*, Kanwisher 1966; many subsequent papers; Jõgar *et al.* 2004), although there has been discussion of whether it actually evolved for that purpose or instead stemmed from the hypoxic and hypercapnic environments characteristic of underground burrows, where it would favour carbon dioxide release (Lighton 1996, 1998). However, discontinuous gas exchange does not appear to favour release of carbon dioxide relative to loss of water (Gibbs and Johnson 2004), it has evolved independently several times, and it does conserve water in dormant individuals and those from extreme habitats (see below). Such a system is feasible only because tracheal oxygen continues to be available in insects down to very low partial pressures. Water is also conserved by excretion with minimal use of water (Edney 1977).

Water in the body is partly controlled by solutes, which increase the osmotic pressure and lower the vapour pressure, helping to resist desiccation. Solutes also enable transfer of water among compartments within the body: active transport of ions causes water to follow. Sodium and chloride are the major inorganic ions, but others participate to different degrees in different taxa. In particular, the osmotically active substances in advanced endopterygote insects are small organic molecules (such as amino acids), and sodium and chloride play relatively small roles (review by Hadley 1994). These different systems must influence the routes and types of damage to cells during desiccation. Some species, especially while dormant, allow haemolymph concentrations of osmoeffectors to increase greatly during dehydration, but other species osmoregulate, typically by removing ions from the haemolymph and sequestering them in the fat body (Hadley 1994; Bjerke and Zachariassen 1997).

Active individuals usually can acquire water relatively easily, by drinking, by eating moist food, and perhaps by metabolizing suitable food (review by Hadley 1994). Both nondormant and dormant individuals of several taxa have structures to absorb liquid water (*e.g.*, egg hydropyles), and moreover structural and physiological adaptations are used by some species to acquire water. The cuticle of some desert beetles condenses water, which runs down the tilted body to the mouth (Parker and Lawrence 2001). Special structures and hygroscopic secretions have evolved in many different groups of insects and arachnids that allow water to be absorbed down to very low partial pressures (Knülle 1984), and even from air well below saturation. These secretions typically rely on high concentrations of potassium ions for rectal absorption in insects using structures derived from the excretory system. The hygroscopic fluid that facilitates oral absorption in other insects and mites may derive from the salivary glands (review by Hadley 1994).

In the springtail *Folsomia candida* (Willem) (Isotomidae), water can be absorbed through the permeable cuticle following a rapid increase in osmolytes such as myoinositol and glucose (Bayley and Holmstrup 1999). The possibility that insects can metabolize water from stored reserves has often been suggested (compare Dautel 1999 for ticks), but the details of such a process and the relationships between energy and water production are not well understood.

Finally, a few species tolerate loss of water, reducing to as little as 30% of the original fresh weight (review by Edney 1977). Tolerating water loss is normally effective only in the short term. High initial water content favours survival when drying conditions are not extreme (*e.g.*, Miller 1968). In response to drying, water may be moved among body compartments by active

Table 4. Common mechanisms of direct resistance to dehydration in insects (after Danks 2000*a*).

Mechanism	Sample systems or substances
Limit loss	
Increase size	Larger insects have a lower surface/volume ratio and so lose water more slowly than small ones
Reduce activity	Inactivity reduces respiratory loss
Seal cuticle	Additional or thicker wax coatings reduce cuticular permeability
Evolve modified spiracles	Sunken spiracles protected by hairs and other structures reduce water loss during respiration; subspiracular tracheal pressure cycles also may conserve water
Close spiracles	Spiracular closing inhibits spiracular water loss; cyclic gas exchange may reduce water loss in dormant insects
Sequester solutes, osmoregulate, *etc.*	Biochemical adjustments alter the relationships (incuding vapour pressure) of body water fractions in ways that enhance dehydration resistance
Acquire water	
Drink	Normally only active individuals drink water or solutions
Eat food containing water	Normally only active individuals eat
Absorb liquid water	Some species have specific structures to absorb water, including egg hydropyles and the ventral tubes of springtails
Absorb or condense water vapour	Some species have specific structural and physiological adaptations to extract water vapour from air
Metabolize water from food	Metabolism produces water, but it is seldom known that such metabolism is linked to water balance
Metabolize water from stored reserves	As above; the relative contribution of energy and water from different substrates varies
Tolerate loss	
Maintain high water content	Greater losses can be tolerated from a higher starting point
Survive low water content	Compartmentalizing water, regulating osmotic effects, making more water osmotically inactive, and other biochemical adaptations permit tissues to survive when water is withdrawn
Enter anhydrobiosis	Metabolism ceases after a period of preparation: complex sequence of adaptations including protective substances, notably trehalose

Note: Indirect methods such as seasonal inactivity, site selection, and cocoon construction are treated elsewhere.

transport of ions, as well as by the osmotic changes induced directly by drying.

A few species can tolerate extreme drying to less than 5% water content when they enter an anhydrobiotic state. Anhydrobiosis is known in several small invertebrates such as crustaceans, rotifers, tardigrades, and nematodes, in springtails, and in the chironomid midge *Polypedilum vanderplanki* (Hinton) (Greenslade 1981; Crowe *et al.* 1992; Watanabe 2006). The adaptations required are highly specific, involving relatively slow water loss, which is often favoured by behaviour or surface changes, accompanied by a cascade of biochemical and other adjustments that require metabolic activity, including trehalose production (Ring and Danks 1994; Kikawada *et al.* 2005). However, in *P. vanderplanki* isolated fat body tissues manufacture trehalose and can enter the anhydrobiotic state without any central control (Watanabe *et al.* 2005). Once in anhydrobiosis, the organisms are remarkably resistant to both natural and artificial extreme conditions (Jönsson 2003), and the time spent in this state is not counted as part of the developmental program (Ricci and Covino 2005).

The various adaptations for dehydration resistance, including anhydrobiosis, confirm the dynamic nature of water relations in insects from dry environments. Sequential or reversible adjustments of water status can be integrated through absorption or osmoeffectors, for example. Water in insects is in several different states that are largely or partly interdependent (Danks 2000*a*). Indeed, as was concluded for cold hardiness, most adaptations to dry environments appear to reflect ongoing metabolic adjustments, not just entry into some sort of inert state. Even the unreactive state of anhydrobiosis depends on prior specific metabolic sequences.

Food limitation

Survival when food is limited can be enhanced by eating what is available rather than a restricted diet, and by tolerating starvation (Table 5). Many predators change diets seasonally, eating any common species of the right size that they can catch. Some herbivorous species also change food plants in a seasonal pattern; this is most easily demonstrated when there is a strict seasonal alternation between hosts, as in many aphids that alternate between perennial overwintering hosts and ephemeral summer food plants. Many but not all species in challenging environments such as the Arctic eat a range of food plants rather than only one (review by Danks 1987*b*). Moreover, many arctic species are generalist saprophages or predators that can survive in areas where less widespread foods are restricted (Danks 1981, 1990, *etc.*).

Many species prolong their development if food is limited or of poor quality, and others delay reproduction in the absence of suitable adult food. For example, typical anautogenous biting flies develop eggs only after they acquire a blood meal.

Starvation can be withstood by reducing metabolism. Of course, species in diapause do this, but also predators such as spiders almost halve their metabolic rates without dormancy when starved, and may switch to metabolizing fat (*e.g.*, Anderson 1974; Tanaka and Itô 1982). Such abilities are also well developed in species such as ticks and bugs that feed on vertebrate blood (*e.g.*, Moreira and Spata 2002). The high arctic moth *Gynaephora groenlandica* (Wocke) (Lymantriidae) also adjusts metabolism according to food supply (Bennett *et al.* 1999). Such species can survive for many months without food.

A major route for withstanding starvation is the accumulation of extensive reserves, typically lipids stored in the fat body, to supply energy in the absence of feeding. Some adult insects cannot feed, and any that are not short-lived then rely on food stores carried through from the larval stage. There is a great deal of information about starvation resistance and trade-offs between stored reserves and other features (including cold hardiness, for example) within and among species of *Drosophila* (*e.g.*, van Herrewege and David 1997; Chippindale *et al.* 1998; Hoffmann and Harshman 1999; Hoffmann *et al.* 2003, 2005*a*, 2005*b*), but there has been less analysis of similar phenomena in other species of insects. Findings for *Drosophila* show especially that energy metabolism is complex and varies among species, so that a range of responses to food limitations would be expected at the metabolic level, depending on the habitats and life styles of different insect species.

Other metabolic problems may have to be solved by insects that are inactive for very long periods in the absence of food. For example, adults of the shield bug *Parastrachia japonensis* Scott (Cydnidae) appear to recycle uric acid from the midgut as an amino acid source, by means of symbiotic bacteria (Kashima *et al.* 2006).

Table 5. Common mechanisms of direct resistance to food limitation in insects.

Mechanism	Sample systems or substances
Use available supplies	
Widen food range	Wide range of food plants
Widen habitat	Generalized saprophagy in soil habitats
Eat what is present	Change diet seasonally
Tolerate starvation	
Reduce energy use	Prolonged development, delayed reproduction, and other resource allocations
Reduce energy requirements	Reduced metabolic rate
Store reserves	Accumulate extensive reserves, especially lipids in fat body

Note: Indirect methods such as seasonal inactivity are treated elsewhere.

Trade-offs

Resources are normally limited, but organisms can allocate resources among different traits to maximize fitness. The differential allocation of resources — trade-offs — gives insight into how life cycles are constructed and what types of life cycles are possible in particular circumstances. Genetic programmes can incorporate set trade-offs (such as the allocation between energy stored in eggs and energy devoted to flight), and also trade-offs can change within a season in response to current conditions, by phenotypic plasticity. For example, females of the bean weevil *Bruchidius dorsalis* (Fahraeus) (Coleoptera: Bruchidae) lay larger eggs when their offspring will encounter harder seeds, producing larger larvae that can drill farther into the seeds (Takakura 2004). Of course, both genetic and environmental factors are involved; in one study of stress resistance in *Drosophila*, differences among environmental conditions were one-and-a-half times greater than the heritable (genetic) ones (Hoffmann *et al.* 2005*a*). The main features of trade-offs are summarized in Table 6.

The assessment of trade-offs is by no means simple, for several reasons (*cf.* Danks 1994, 2002*b*, 2006*b*). Resources that are never surplus (“constraints”) cannot be traded off (discussion by Danks 2002*b*, pp. 133–134). Allocations essential to survival are protected, so that they are unlikely to be traded off. Development that is not modified in response to circumstances is said to be canalized; for example, growth of some blephariceridsis insensitive to temperature changes (Frutiger and Buergisser 2002). Even behavioural traits may depend on the conditions experienced, integrating the availability of resources with many subsequent life-cycle features. For example, in the cricket *Teleogryllus commodus* (Walker) (Gryllidae), more fecund females exercise greater mate choice (Hunt *et al.* 2005). Such trade-off decisions can influence subsequent population dynamics. In the mite *Sancassania berlesei* (Michael) (Acaridae), the level of maternal investment (through an egg number – egg protein trade-off mediated by the mother’s age as well as her food supply) influences how populations will develop over several generations because of ongoing competitive effects (Benton *et al.* 2005).

Trade-offs can be made effectively only when there is some stability of the resources being acquired, and they tend to be obscured when conditions are very variable (*e.g.*, Messina and Slade 1999; Messina and Fry 2003). Conversely, when food reserves are especially abundant, the trade-offs normally required may not be necessary, so that trade-offs between size and time are not observed (*e.g.*, Cortese *et al.* 2003; Wissinger *et al.* 2004). Even when limitations make some sort of trade-off essential, the features expected to trade off or to coincide may instead be independent of one another (though they may trade off with other elements). For example, instances of independence between offspring production and reproductive investment (Frankino and Juliano 1999), resistance to heat and resistance to cold (Hercus *et al.* 2000), and time and size (Nylin 1994; Klingenberg and Spence 1997; Vorburger 2005) are known. Some of these disconnects reflect the fact that the components potentially trading off do not have equivalent weight. Size may modify and even overwhelm other trade-offs (Morse and Stephens 1996; Roff *et al.* 2002). In particular, multiple factors trade off simultaneously, with complex reaction norms (*e.g.*, Stillwell and Fox 2005; Fischer *et al.* 2006), and the simple one-to-one relationship

Table 6. The main features of trade-offs.

Feature	Components	Details	Examples
Limits	Constraints	Resources that are only at minimum levels cannot be traded off	Limited food determines final size directly
	Energy	Energy is the common limiting currency	Both long-distance dispersal and immediate high fecundity are not usually possible
	Canalization	Development may be canalized to be inflexible	Growth rate is insensitive to temperature
Complexity	Major elements	Certain elements are especially important in most trade-offs	Customarily emphasized are size or weight, developmental time or rate, growth rate, survival, fecundity, and longevity
	Other elements	Many other resources potentially can be traded off	Other elements include competitive ability, wing morph, resistance to heat, cold, and other adverse conditions, predator pressure, wing morph or dispersal, reproductive pattern, early and late fitness, egg size versus egg number, and diapause duration versus post-diapause fitness
	Simultaneous trade-offs	Many elements are integrated at once (unlike typical 1:1 laboratory tests)	All of the components listed above are in dynamic balance
Flexibility	Many pathways	The factors in a potential trade-off can relate in many different ways	Trade-offs are effected through various metabolic and other pathways
	Traits below maximum	Developmental and reproductive traits are not necessarily at their maximum levels, even under temporal constraints	Growth rate is not routinely maximized

between a pair of factors selected for study in the laboratory and seen to be traded off may not represent a natural situation. Most attention has been paid to key measures of fitness such as duration or rate of growth or development and egg production or fecundity, which have been examined especially in relation to size, resistance to adverse conditions, competitive ability, wing morph, and fitness elsewhere in the life cycle, but there are many other potential interactions. For example, developmental rate and size can influence immune function (Rantala and Roff 2005). Therefore, studies of multiple traits reveal complex correlations, some of them unexpected (Miyatake 1998). Developmental time in *Drosophila* increased in individuals selected for longevity at high temperatures, but decreased when cold-stress-selected lines were selected for longevity at low temperatures (Norry and Loeschcke 2002). Some trade-offs or correlations, such as stress resistance and longevity or developmental rate and growth rate, break down after prolonged laboratory selection (Archer *et al.* 2003; Phelan *et al.* 2003).

The complex and dynamic nature of trade-offs now revealed (Danks 1994; Nylin and Gotthard 1998) is helpful for interpreting life cycles. “Stressful” situations force trade-offs, and stress can come from the limitation of several kinds of resources, including not just energy but also time. When time to complete development is limited, for example, trade-offs take different forms according to species: reduce developmental time and reduce size; maintain developmental time and reduce size; or increase developmental time and maintain size (references in Danks 2006*a*). However, in yet other species or circumstances time is not limited, and such trade-offs are not necessary. Moreover, we also know that growth is not routinely kept at the maximum possible rate (Margraf *et al.* 2003; Tammaru *et al.* 2004), despite an expectation derived chiefly from stable, nonseasonal laboratory situations that the net reproductive rate will be maximized. Instead, individuals retain some flexibility of growth rate, a trait that would widen the range of options available for dealing with environmental challenges.

The recent analysis of trade-offs shows even greater complexity than had been envisaged earlier. These complexities stem from the differences among real environments and the ways in which multiple features interact. Understanding environmental features and their variations therefore is one key to interpreting trade-offs. Useful insights might come too from study of physiological and endocrine regulation of the responses (*cf.* Davidowitz *et al.* 2005; Zera 2005). Another key need is to discover how the ability to respond appropriately through phenotypic plasticity is maintained (Nylin and Gotthard 1998; Danks 2006*a*). Long-term study of genetic mechanisms and variations therefore is required too (see Types of variation below).

Responses in extreme habitats

Habitats in which conditions become unpredictably extreme as well as seasonally extreme offer particular sets of challenges, and it is instructive to see how insects cope with them. Such environments include regions such as the Arctic and deserts as well as individual habitats that are temporary or saline. Moreover, some environmental elements are shared among challenging habitats. For example, the high Arctic is very dry and therefore is a cold desert, bodies of water in desert habitats are often temporary, and in deserts both terrestrial and aquatic habitats may be saline because of evaporation.

The adaptations of arctic and subarctic insects to the long cold winters, short cool summers, and variability of the region have been reviewed several times (*e.g.*, Downes 1965; Danks 1981, 1990, 2004*a*; Hodkinson 2005*b*). The severe winters are met by cold hardiness and habitat choice, as might be expected, but even so there are unusual cold hardiness adaptations in some species (Danks 2000*b*, 2004*a*), such as very low supercooling points (Ring 1981, 1983), freezing tolerance despite very low supercooling points (Ring 1982), and freezing tolerance despite an absence of the usual cryoprotectants (Ring 1981, 1983). Different species show different patterns of relationship between water, freezing, and desiccation (Block 2002), but both small cryoprotectants such as glycerol (Ring 1983) and antifreeze proteins (Duman *et al.* 2004) are widely distributed. As might be expected, cold hardiness of some species persists year round (*e.g.*, Kukal 1991; Sinclair and Chown 2005*a*).

Adaptations to the short cool arctic summer include activity at low temperatures, selection of warm habitats and microhabitats (*e.g.*, Böcher and Nachman 2001), and melanism and hairiness (review by Danks 1981; Danks *et al.* 1994). Selection of habitats with suitable moisture regimes is also important (Hayward *et al.* 2004). Basking behaviour is well developed in adults (Kevan and Shorthouse 1970; Kevan 1975, 1989) and even larvae (Kevan *et al.* 1982; Kukal 1991) and is enhanced by melanism and hairiness. Hairiness and similar structures that retain a boundary layer of air also play an important role in resisting desiccation (Bennett *et al.* 2001). Some biting flies do not feed on blood (hosts are in short supply or are hard to find) and others do so facultatively only if hosts are available (Corbet 1964*b*).

Some species have abbreviated life cycles with relatively rapid development during summer and reach the same overwintering stage each year. For example, high arctic mosquitoes overwinter as drying-resistant and freezing-resistant eggs that hatch early in spring, and subsequent larval and pupal development are rapid (Corbet and Danks 1973). Other species, including those that are large, feed each summer and overwinter several times in different larval stages. Such life cycles can last for many years (Butler 1982; Lantsov 1982; Kukal and Kevan 1987; Morewood and Ring 1998; Søvik and Leinaas 2003; Søvik 2004; review by Danks 1981). Slow development may stem not only from cool temperatures as such but from prolonged or repeated exposures to cold, which might necessitate repair (Sinclair and Chown 2005*b*).

Species with annual or longer life cycles typically emerge early in the year, maximizing the period for feeding and reproductive activity during the warm season. Many high arctic species carry this tendency to the extreme, emerging only if they have completed growth the previous year ("absolute spring species": Danks and Oliver 1972*a*) and deferring until the next season any individuals not emerging as early as possible. Some such responses, as well as life cycles that include a moult to the next instar each spring (Danks and Byers 1972; Søvik *et al.* 2003), appear to be controlled by diapauses (*e.g.*, Birkemoe and Leinaas 1999). They reflect strict life-cycle control at critical stages, even if flexible behaviour and development are permitted at other times (Danks 1999).

A final set of adaptations in arctic species responds to long-term variability such as below-average temperatures over several years. Prolonged diapause in some individuals (see below) and deferred emergence in cool years (Oliver 1968; MacLean 1973) allow part of the population to avoid a summer season that may be unsuitable. In several taxa, parthenogenesis is more common in the Arctic than in other regions, and this has been interpreted as buffering populations against change, thus protecting well-adapted genotypes against rapid responses by selection over only a few years that might prove deleterious over the longer term (Downes 1965; Danks 1981, 2004*a*).

A number of lessons can be drawn from the range of adaptations in arctic species. First, the species respond to multiple simultaneous influences, including interspecific interactions even in this depauperate zone. For example, there are complex timing and other interactions among insects and plants (Danks 1987*b*). Second, success can follow from several different routes, for example both abbreviated and prolonged life cycles. Third, the key selective forces are not necessarily the most obvious ones. Many species choose the habitats that will thaw earliest, even if that increases their exposure to winter cold. Some caterpillars overwinter exposed on high arctic ridges (Danks 1981), and high arctic mosquitoes deposit eggs only in the sites that will thaw first in spring (Corbet and Danks 1975). When the season is very short, therefore, time can be more important than severity. Fourth, life cycles are characterized by both flexibility and fixity: strict programming is needed at some times to ensure that reproduction coincides with favourable conditions, and the simple ability to grow whenever it is warm enough is not sufficient (Danks 1999).

Finally, microhabitats are especially important, leading to very small-scale responses. The key influence is insolation, which warms insect habitats by as much as 10 or 20 °C above ambient temperature (Sørenson 1941; Corbet 1972). The warmed surface of the ground, plant clumps, and shallow waters are the most important habitats for arctic insects. As a result, cloudiness influences insect habitat temperatures, so that moisture regimes are important both directly and through their effects on temperature. Indeed, in the northwestern high Arctic, with small islands in an extensive ocean, it might even be supposed that any effects of climatic warming on insect habitat temperatures will be more than offset as sea ice melts: the moisture available from greater expanses of open ocean water will lead to increasing cloud cover that blocks the sun (Danks 2004*a*).

Many adaptations are known in arthropods inhabiting hot deserts that are characterized by high temperatures and extreme dryness, often exacerbated by strong winds, sand storms, absence of shade, and impenetrable soils (sample reviews by Cloudsley-Thompson 1975, 1991, 2001; Crawford 1981; Seely 1989; Costa 1995; Sømme 1995; Heatwole 1996; Punzo 2000; see also adaptations to dryness above). A few species (*e.g.*, leaf miners and gall formers) live in relatively moist microhabitats (Wiesenborn 2000), but most species avoid the worst conditions by sheltering in burrows or crevices during the day and emerging only during the cooler night (Henschel 1998). Such temporal and spatial restrictions are often enhanced by endogenous circadian rhythms (*e.g.*, Alpatov *et al.* 1999). Wider searching activity may be confined to more humid periods (Rasa 1994). Seasonal dormancy is common and most species time reproductive activity with cooler or wetter periods. When these are irregular, individuals of many species hatch, pupate, or emerge in direct response to rainfall (*cf.* Denlinger 1986 for tropical insects).

Typical desert species mitigate conditions by specific behaviours such as body orientation and stilting, as well as by structural features. Although some darkly coloured species bask when it is cool but avoid or orient away from direct sunshine when it is hot, and others limit heating through pale colours (Hamilton 1975), it has also been claimed that the primary roles of colour in desert animals are not thermal but for warning or camouflage (Cloudsley-Thompson 1979).

Despite a range of adaptive behaviours, most desert species must nevertheless resist extremes of heat and dryness by physiological means except during favourable periods. A few species are resistant to temperatures up to 50 °C (Hadley 1975). Water is conserved by impermeable cuticles, especially additional lipid layers (Edney 1977), but some species can also tolerate considerable losses of water (Zachariassen 1996) that would prove lethal to most temperate species (for other adaptations to dryness see also above). In particular, although many species restrict water loss through the cuticle, desert tenebrionid beetles also markedly reduce respiratory loss through the spiracles by lowering metabolism. This adaptation reduces cellular gradients of sodium and hence amino acids, but the very high efficiency of rectal reabsorption in these insects allows the resulting extracellular amino acids to be recovered rather than excreted (Zachariassen 1996). Cyclical respiration (see adaptations to dryness above) seems likely to be significant, especially in dry habits such as deserts where most species have been able to reduce losses through the cuticle itself to very low levels. The life cycles of desert insects are coordinated to the conditions, but depending on the species and its habitat both rapid or slow development and multivoltine or univoltine cycles occur (Punzo 2000).

In any event, insects from deserts respond to the conditions there in ways that reinforce some of the generalizations drawn from insects in arctic habitats. For example, multiple elements of ecology, behaviour, structure, physiology, and development are coordinated. Although convergent adaptations are common, successful development and reproduction can be attained in more than one way, so that desert insects show a range of voltinism, fecundity, and other features. Nevertheless, although adaptations in such extreme environments are coordinated and often in extreme form, survival in desert insects, as in arctic ones, depends not on striking new features but on adaptations known from elsewhere that enable these small animals to live in terrestrial habitats (Seely 1989).

Pools or streams that dry out seasonally or intermittently provide especially harsh conditions to their typical occupants, which are adapted to aquatic habitats (sample reviews by Williams 1996, 1997). As water is removed, the habitats warm up, the concentration of ions increases, and the oxygen content decreases. Different kinds of temporary habitats vary especially in the duration and season of drying and in features of the surrounding terrain (*e.g.*, Wiggins *et al.* 1980). The relatively small scale of these interactions allows many species to move to nearby permanent bodies of water during the dry period. Indeed, larger species fly actively and may even overwinter in permanent ponds, exploiting temporary ponds only during the active season. Very small species such as mites tend to use dispersing insect hosts or vertebrate vectors to reach alternative habitats.

Several species withstand drought *in situ* by means of more or less impermeable coverings, burying into the substrate, specialized cocoons (*e.g.*, Grodhaus 1980), and physiological adaptations including anhydrobiosis. They may survive in the dried habitat all year or only part of it (Wiggins *et al.* 1980). Specialized behaviours are involved in the choice of habitats for survival *in situ* as well as movement to suitable waters elsewhere. As in other extreme habitats, life cycles may be rapid or slow. Many species inhabiting temporary ponds complete their life cycles before the habitat dries, but others have prolonged development and survive the dry season in dormancy.

A number of other widely distributed habitats are extreme in one or more respects, although there is less detailed information about the specific adaptations of their insects. For example, bogs are characterized by extreme acidity, limited nutrients, cool conditions, low oxygen, and high water tables, and a limited but significant fraction of the fauna is confined to or more abundant in these habitats (Spitzer and Danks 2006). Specialists even live inside the pitchers of insectivorous plants (*e.g.*, Giberson and Hardwick 1999).

Salt marshes and seashores experience high salinity and inundation by tides, and (in addition to diet changes) species that live there tend to have enhanced tolerance of salt (*e.g.*, Giberson *et al.* 2001) or tolerance of submergence by seawater (*e.g.*, Sei 2004), and their activity is synchronized with the tides (Foster 2000). Just as in the Arctic, mosquito eggs are positioned precisely in the oviposition habitat. The salt marsh species *Aedes sollicitans* (Walker) places them high enough to exclude daily flooding but in range of the higher lunar tides that occur every 2 weeks (Knight and Baker 1962; Crans 2004). In areas subject to wave action, the availability of sheltered microhabitats is especially important (Pugh and Mercer 2001). Again, therefore, adaptations in coastal insects are both ecological, such as habitat choice and timing, and physiological, such as osmoregulation.

Information from these different extreme habitats confirms several generalizations about insect adaptations. Species can cope with extreme conditions only by multiple simultaneous adaptations of ecology and physiology. There is no single "required" adaptation, but three main kinds of responses help to solve the problems posed by difficult conditions: movement, as among ponds or into sheltered or otherwise favourable habitats; resistance, such as cold hardiness and drought tolerance; and life-cycle or behavioural adaptations, including circadian rhythms or opportunistic behaviour, dormancies, and rapid or prolonged development. Consequently, different suites of multiple adaptations are found in different species.

Control and integration

The timing of insect life cycles in relation to the seasons is controlled through the assembly and integration of many external and internal elements. These components are summarized in Table 7. The ways in which development is modified, notably by changes in developmental rate or by interruption of development, form the basis of the responses. Environmental cues such as photoperiod and how and when they are received and integrated allow the developmental modifications to be controlled in relation to seasonal information. Overall patterns of development are structured through the number and duration of delays and how they are integrated into one or more alternative life-cycle programs. Such programs may include the movement of insects from one habitat to another. Examining patterns of variation helps in the interpretation of many of the responses.

Developmental modifications

Development can be modified (Table 7) by a change in rate or by interruption. Quiescence interrupts development in direct response to ambient conditions that are not suitable (*e.g.*, too cold for development) and is used for seasonal control in some species (*e.g.*, *Dendroctonus*: Powell and Jenkins 2000; Powell and Logan 2005). However, most species interrupt development in a programmed diapause stage, which typically anticipates unfavourable conditions and is insensitive to otherwise favourable conditions until after a delay. Moreover, the duration of this delay varies (diapause intensity; see below). Although such interruptions in development have attracted the most attention, programmed adjustment of the duration of development by slowed or accelerated growth is also extremely common in insects.

Developmental modifications are governed in different ways in different species; they include both fixed genetic and environmentally controlled plastic responses and range from a single one-time response to the continuous adjustment of developmental rates throughout at least the larval stages (Danks 1994). Most species continue to develop unless delays are induced by specific signals (Danks 2002*b*). There are many typical instances of this sort whereby winter diapause is induced by short photoperiods. Such an "*active*" default allows development at any time unless a reliable signal of impending unsuitability is received. On the other hand, in many species from habitats that are intermittently unfavourable or in which environmental signals do not reliably predict future unsuitability, "*passive*" responses are more

Table 7. Control elements and integration.

Element	Components or alternatives
Developmental modifications	
Type of modification	Developmental rate, quiescence, or diapause
Type of response	Single or continuous, fixed or plastic
Default developmental response	Active development or passive delay
Default response after delay	Standard rate or accelerated rate
Variability	Little variation, normally distributed *vs.* wide or discontinuous variation, programmed
Sensitivity to environmental signals	
Type of sensitivity	Insensitive, intermittently sensitive to continuously responsive
Effective cues	None to many; cues include photoperiod, temperature, food, moisture, and others
Type of sensitivity	Qualitative or quantitative, fixed or changing through stage
Sensitive stage	One to many stages; various relationships to responsive stage
Life-cycle patterns	
Type of life-cycle control	Direct or indirect control, single or multiple factors and influences
Number of dormancies	One, multiple, or successive
Number of components in a single dormancy	One, few, or many
Duration of dormancy	Short, long or very long, fixed or variable
Number of successive diapause inductions possible in same stage	One or more
Duration of life cycle, voltinism	Days to years, <1 to many generations/year
Number of alternative life-cycle routes	None to many (fixed or simple life cycle *vs.* complex life cycle with multiple pathways)
Time budgeting	Time gained, conserved, monitored, or wasted

common. In these instances delay is the default option, and active development has to be induced by environmental suitability or reliable temporal signals (Danks 2002*b*, 2006*a*). For example, a number of short days followed by a number of long days — a completely unambiguous signal that summer is coming — are needed for reproductive development to occur in some carabid beetles and other insects (Thiele 1975; review by Danks 1987*a*, Table 23). Comparable alternatives occur in the completion of diapause. Many species resume development as inhibition diminishes with time at a standard rate (“horotelic”), but in other species the inhibition can be removed faster as a result of external signals (“tachytelic”) (Hodek 1981, 1983; Košt’ál *et al.* 2000).

Passive responses, in which development requires particular sequences of environmental conditions, give rise to individuals that fail to develop during simple experiments. Such results have led to the erroneous belief that the delays termed “obligate diapause” are inevitable and qualitatively different from other environmental responses. In fact, these “obligate” responses are rare.

Sensitivity to environmental signals

Environmental signals are used in many ways to control seasonal development (Table 7). Relatively few species are insensitive to environmental information, and even some of those believed to be insensitive to photoperiod, for example, prove to be sensitive only to particular changes that are not always included in laboratory protocols (see passive responses in the preceding section). Many species are sensitive at only one stage or for only a limited part of one stage. In other species, more stages are sensitive (see below). A few species integrate environmental information continuously throughout the life cycle and adjust development accordingly. For example, complex ongoing reactions of growth rate and diapause in response to photoperiod and temperature program the life cycle in the dragonfly *Aeshna viridis* Eversman (Aeshnidae) (Norling 1971; Danks 1991*a*).

Although photoperiod is the best known cue, different species use different environmental information. Photoperiod, light intensity, temperature level, thermoperiod, food, moisture, density, mating, and chemical cues have all been reported to influence diapause induction in one species or another (Danks 1987*a*, 1994, Table 2), and even the presence of predators may have an effect (Kroon *et al.* 2005). Many of these cues, especially temperature, also influence the progress of diapause (diapause development). And, although it has been less studied, growth rate is controlled not only by the direct action of temperature level and density or food limitation, but also by many factors that act as cues, including photoperiod and density (Danks 1987*a*, Tables 33, 36) as well as light intensity, temperature, food, moisture, and chemical signals (Danks 1987*a*, 1994). Moreover, these environmental elements typically interact and responses to more than one of them are integrated. The best known interaction is that between photoperiod and temperature (Danks 1987*a*; Saunders 2002).

Life style and habitat determine which cues are most informative for a given species. For example, production of dispersing or dormant stages depends on food or density in environments where the conditions of the food can deteriorate rapidly, as for some aphids and mites (*e.g.*, De Barro 1992; Corente and Knülle 2003).

Species also differ in how the signals are perceived or summed. Many species respond to whether photoperiods are above or below a critical length, but the length of the photoperiod has no influence other than its position above or below that critical length. However, an increasing number of species have been reported to show quantitative responses, whereby the degree of response accords with the actual duration of the photoperiod or the level of the temperature. This phenomenon was even held to be typical rather than exceptional by Zaslavski (1988, 1996). Quantitative responses have been reliably reported for the rate of growth (Suzuki and Tanaka 2000), the incidence of diapause (Kimura 1990), the intensity of subsequent diapause (Nakamura and Numata 2000; Kalushkov *et al.* 2001), and the intensity during diapause (Nakamura and Numata 2000). Moreover, in many species the response to a particular signal changes through development, even within the same stage. Commonly, this results from differences in sensitivity (see below) but in addition the response itself can change. For example, long photoperiods that stimulate rapid growth in young larvae slow growth in older ones (examples reviewed by Danks 1991*a*). Even in a single species, responses can be all-or-none as well as graded, the number of instars can vary, and responses can change through development (Tanaka *et al.* 1999). Diapause development in insects typically reduces the sensitivity to photoperiod or reduces the critical photoperiod (discussion by Danks 1987*a*, pp. 154–155).

Finally, the effective use of environmental signals depends on the stage or stages of sensitivity and how close they are to the stage that responds. Despite great variations among species and exceptions to normal tendencies, several generalizations can be made about this sensitivity (*cf.* Danks 1987*a*, pp. 80–81). First, sensitivity tends to be greater in active stages exposed to the environment and with better developed sense organs, and hence larvae and adults are more often or more markedly sensitive than eggs or pupae. Second, most often the sensitive stage only just precedes the stage that responds, a timing that is not surprising because cues as to future conditions typically are most reliable closer to the time for which prediction is needed. Third, many species add (not substitute) sensitivity in earlier stages as well, thereby monitoring conditions over a longer period, which might compensate for variation and allow ambiguous signals to be resolved. In such instances sensitivity typically increases towards the end of the sensitive stage so that more weight is given to the most recent experience, but alternative information received earlier is available if current signals are neutral or ambiguous. Theoretically, the tendency to use recent cues would be offset by the fact that early determination gives more time for the food storage and other metabolic adjustments required to survive diapause. This requirement, and the need to integrate cues over a finite interval (*e.g.*, a certain minimum number of short daylengths), extends the duration of the sensitive period in many species, even though it ends just before the developmental decision it governs.

Nevertheless, these generalizations are by no means universal. Larvae of the moth *Cydia pomonella* (Linn.) (Tortricidae), which feed inside apples, have early, not late, sensitivity (*e.g.*, Jermy 1967; Peterson and Hamner 1968), presumably because photoperiodic cues are masked inside the food source later in life. The sensitive and responsive stages are widely separated in a few spectacular examples, of which the best known is the sensitivity of eggs of the silk worm *Bombyx mori* Linn. (Bombycidae) for egg diapause in the next generation (Kogure 1933; many subsequent papers).

The fact that multiple cues are integrated in different ways in different species means that experimental designs that are too simple may cause relevant factors to be undervalued. Ancillary cues are easy to overlook if there is an undue preoccupation with photoperiods. Often the stage(s) of response cannot be determined accurately without multiple, rather than the usual simple, experimental switches from one regime to another during development.

Life-cycle patterns

Life cycles are patterned (Table 7) by the timing and duration of substages. In some species the substages are controlled relatively simply, for example by the direct effects of temperature, but in most species in seasonal environments more complex control is exerted by multiple token stimuli such as photoperiod.

Species also differ in how many dormancies intervene in the life cycle. Dormancy in the broadest sense can include adjustments of growth rate (see above) as well as diapause and quiescence (Danks 1987*a*). Typical species have a single diapause during the adverse season, but many other patterns are known (Masaki 1980; Danks 1987*a*). In typical species, one or more dormancies enforce a life cycle of exactly one year. Some species have multiple diapauses across several years (Nishizuka *et al.* 1998 for *Lepisma*; Ingrisch 1986 for grasshopper eggs). Moreover, each dormant period may consist of several phases, each of them potentially under environmental control. Thus diapause development consists of two or more stages (*e.g.*, Nomura and Ishikawa 2000) and ovarian diapause comprises multiple steps (*e.g.*, Košt'ál and Šimek 2000). Development then proceeds very differently according to the pattern of conditions (Higaki and Ando 2005). Such stages are linked, both because an earlier phase must be completed before a later phase can begin and because the occurrence of one phase may modify subsequent development. For example, in some species (but not in all) diapause-destined larvae grow more slowly (*e.g.*, Danks 1987*a*, Table 34; McGregor 1997), females that have experienced diapause during development are less fecund (*e.g.*, Ishihara and Shimada 1995; Bradshaw *et al.* 1998; review by Danks 1987*a*), and fast or slow later growth can compensate for slow or fast early growth (Volney and Liebhold 1985).

Dormancy lasts for a short or long fixed time in some species, but in most species its induction and end depend on environmental conditions. Extended periods of diapause have attracted the most attention (see below), but actually there are many ways of extending development in addition to a long single diapause, including slow development, dispersed reproductive effort, and repeated diapause, as shown for several species of beetles (Topp 2003). Some species even undergo repeated interruptions of development in the same stage, as exemplified by multiple quiescences and diapauses in eggs of some grasshoppers (Wardhaugh 1980; Ingrisch 1986). Successive reinductions of diapause are known in adults of several Heteroptera (Hodek 1971; references in Danks 2002*a*). Other species have diapause as successive control points in the life cycle at several different stages (Danks 1991*a*; Tanaka and Zhu 2004).

Given these many possible ways to introduce delay into the life cycle, some very long life cycles are known in which one completed generation can last for many years. Very long life cycles are associated in particular with poor-quality food and cold environments, but also with unpredictable circumstances (Danks 1992). Moreover, many species adjust the life cycle continually or at intervals in response to environmental cues, so that different alternative routes including very long durations are possible in a single species (*e.g.*, Danks 1991*a*). For example, egg development of the grasshopper *Chortoicetes terminifera* (Walker) (Acrididae) has no fewer than 18 alternative routes, modified by the presence and duration of diapauses and quiescences in several stages under the control of photoperiod, temperature, and moisture (Wardhaugh 1986; see Danks 1991*a*). Development of the mite *Lepidoglyphus destructor* (Shrank) (Glycyphagidae) reflects genetic and environmental inputs that bypass the hypopal stage (resting deutonymph) or interpolate it for a period of a few days to many months (Knülle 1991*a*, 1991*b*; see Danks 1994). Other species use different pathways to integrate other

Table 8. Summary of the types of variation involved in seasonal patterns.

Type of variation	Description of variation	Sample responses	Sample correlates
Basic elements			
Individual variation	Individual differences	Normality, skew	Genetic and environmental variation
Type of response	Stochastic *vs.* adaptive	General variation *vs.* specific evolved response	See below
Change in response	Amount and speed of change in the pattern of variation	Variance changes rapidly or slowly	Selective pressure
Temporal spread			
Narrow	Restricted	Synchronous emergence	Restrictive temperature threshold; multiple thresholds; laboratory selection
Broad	Wide, continuous	Prolonged emergence; staggered development	Long suitable season; laboratory stress
Discontinuous	Discrete modes	Split cohorts; sawtooth clines; prolonged diapause	Continuous change in growing season but unit change in no. of generations; unpredictable annual resources
Coincident variation	Temporal and other changes are integrated	Seasonal change in quality	Resources change through the season

adaptations with the time of year that adults emerge. For example, the butterfly *Pararge aegeria* (Linn.) (Nymphalidae) couples larval diapause, pupal diapause, or direct development that results in emergence during different seasons with sex-related morphological differences associated with flight and thermoregulation (Van Dyck and Wiklund 2002).

Species budget time to take account of seasonality, resource levels, and so on. When an extra generation is not feasible in any event even with spare time (because of seasonal resources or other constraints), some species simply waste the extra time through very slow growth or stationary moults, thereby maintaining appropriate seasonal synchrony (see also Trade-offs). At the other end of the spectrum, species may gain time by adaptations that include developing rapidly in all stages, exploiting rich food, eliminating stages, reducing resource investment by reducing size, fecundity, longevity, and structural complexity, accelerating development through such means as basking and rapid reproduction, and choosing the most suitable, especially the warmest, microhabitats. Multiple coincident adaptations of this sort allow extremely rapid development especially in species of very small size, giving generation times as short as 4 days (for detailed examples see Danks 2006*c*).

Types of variation

Patterns of variation provide important information about the control of seasonal responses especially in relation to environmental variation (see Table 8).

Background patterns of variation reflect differences among individuals and can be characterized from normality, skew, and other typical statistics. Individual differences stem from small genetic variations among individuals as well as from small differences in the conditions that each individual may experience even in the same habitat, in insects especially because of differences from one microhabitat to the next or from one part of the microhabitat to another.

From the perspective of seasonal adaptations, the most interesting differences are between variations that simply reflect this background of general individual variation and variations that have evolved to provide advantages in particular environmental circumstances, as explained below. Finally, the rate at which patterns of variation respond to selective forces gives additional insights into how environments affect the evolution of the patterns.

The roles of individual variation in evolved responses can be reviewed by recognizing three overall patterns of variation: narrow, broad but continuous, and discontinuous (compare Fig. 1). Variations restricted to a short time period, a small size range, and so on normally accord with predictable environments that may be suitable for a relatively short period (for the current or next generation), although synchrony has other advantages such as coincidence of individuals for reproductive activity. Narrow variations often are under environmental or seasonal control, such as a single temperature threshold. The diapause of many species serves to accumulate individuals in exactly the same stage by the end of winter; emergence is thus delayed until spring and brought under the direct control of heat accumulations. In turn, emergence in spring of several species requires a relatively high temperature that synchronizes the appearance of adults.

In some species multiple thresholds and differences among stages enhance synchrony. For example, in some dragonflies young larvae develop at a lower temperature than older larvae and so catch up during spring (Lutz 1968, 1974). In chironomid midges temperature thresholds increase successively through larval activity, growth, pupation, and emergence (Danks and Oliver 1972*a*). Other species use photoperiod too to synchronize development, as in some of the life-cycle pathways already noted. In addition, but with less explanatory relevance, laboratory experiments sometimes enhance synchrony because only individuals with a certain pattern of development are favoured by the culture conditions. Such biases may select for a laboratory strain with an unduly narrow range of variation (Miyatake and Yamagishi 1999; Danks 2000*c*).

Broad but continuous patterns of variation can exploit wider spatial, temporal, or nutritive resources. Species of several taxa are characterized by wide variations in development (*e.g.*, Aquino and Turk 1997; Stiefel *et al.* 1997). Very long emergence and subsequent oviposition into habitats that remain suitable all summer is characteristic of many aquatic insects in temperate and tropical habitats ("summer species" of Corbet 1964*a*). When development is staggered (from the long duration of oviposition or through developmental variation), resources are less likely to be overloaded. Caution is required in laboratory experiments, however, because inadequate conditions cause unnatural delays and increase variation in the duration of development. These limitations stem not only from the quantity or quality of food for larvae, but also from temperatures, light intensity, ancillary food, and so on that are required for normal reproductive activity (*e.g.*, Danks 2000*c*).

Discontinuous patterns of variation such as bimodal emergence, cohort splitting, and diapause by a fraction of the population for more than one year are especially instructive for understanding seasonal responses. A few of these patterns reflect short-term environmental control, such as two pulses of emergence in warm weather separated by a lull during a cold spell (*cf.* Fig. 1D above). However, most broad and discontinuous patterns of variation appear to reflect ways to overcome the unpredictability of natural environments (Danks 1983, 1987*a*, chap. 9). Such bet-hedging or risk-spreading responses occur in a wide range of taxa and environments. For example, pupal development in the moth *Epirrita autumnata* (Borkhausen) (Geometridae) lasts from 1 to 3 months, a variance that would be adaptive in spreading the risk of mortality from low temperatures and predation (Tammaru *et al.* 1999). Eggs of the bush cricket *Ephippiger ephippiger* (Fiebig) (Tettigoniidae) hatch over a very long interval as a result of maternal influences, including maternal age, on diapause; this variation has been interpreted as providing insurance against the low predictability of future environmental conditions (Hockham *et al.* 2001). Larvae of the burnet moth *Zygaena trifolii* (Esper) (Zygaenidae) vary widely in the duration of pre-diapause development and consequently in the instar in which diapause occurs, and the variation is genetically based (Wipking and Kurtz 2000). It appears to reflect the temporal and spatial unpredictability of the habitats of this species. *Glycyphagus* mites produce directly developing, dormant phoretic, and dormant sedentary forms under complex genetic and environmental control (Knülle 2003): genetic variation spreads risk, and current response to food levels adjusts the proportions of the different forms. The blue butterfly *Scolitantides orion* (Pallas) (Lycaenidae) accumulates diapause pupae from each summer generation, not just from the final one, maximizing the number of generations whilst insuring against failures (Trankner and Nuss 2005).

Egg hatch varies widely and erratically in stoneflies from unpredictably wet streams in Australia (Hynes and Hynes 1975). For example, eggs of *Dinotoperla serricauda* Kimmins (Gripopterygidae) began to hatch only after more than 30 weeks following their collection and continued to hatch for 70 more weeks. Extended hatch is characteristic of temperate *Isogenoides* species (Sandberg and Stewart 2004). Wide genetic variations in the date of egg hatch in the moth *Malacosoma americanum* (Fabr.) (Lasiocampidae) (independent of temperature) appear to offset the risk of loss of young larvae due to storms in late winter (Neal *et al.* 1997).

The desert bee *Perdita portalis* Timberlake (Andrenidae) commits only about half the pupae to development even under optimal conditions; also, individuals of low body weight are more likely to emerge, and emergence occurs directly in response to high humidity (Danforth 1999). Some attempts have been made at theoretical analysis of strategies for delayed development (*e.g.*, Bradford and Roff 1997), so far with limited resolution for the examples of most interest that include genetically determined polymorphisms (contrast Hopper 1999, who excluded such examples).

In many species, some individuals enter diapause for more than one adverse season (Danks 1987*a*, Table 40), with decreasing proportions of the population remaining in diapause through successive years. In extreme cases these prolonged diapauses can last for 30 years or more (Powell 2001 for yucca moths). Typical species come from habitats that are unpredictable, such as the Arctic, deserts, plants with intermittent fruiting, and so on, but prolonged diapause also occurs at low levels in many species from more ordinary environments.

Prolonged diapause appears to have a complex genetic basis (Danks 2006*a*). Therefore, although it ends in some species in response to environmental cues (*e.g.*, Masaki 2002; Higaki 2006), the onset appears to be genetically programmed in most species, either by genetic polymorphism comprising different genotypes in long-term balance or by stochastic polyphenism (Walker 1986) generating variability from a single genotype (also termed coin-flipping plasticity or diversified bet hedging: Menu and Debouzie 1993; Menu and Desouhant 2002; Menu *et al.* 2000). Because prolonged diapause affects only a small proportion of the population in most species and typically is adaptive over very long time frames (necessitating a way to "protect" the variation), its proper analysis in the context of unpredictable environments will be very difficult. Analysis of prolonged diapause in parasitoids of hosts that enter prolonged diapause (Koziol 1998; Corley and Capurro 2000; other examples in Danks 1987*a*, Table 27) would also be informative.

Multiple features of seasonal responses can be integrated through patterns of variation. For example, resources that change through the season can be exploited by programmed changes in individual quality. These changes are mediated by the age of the mother in a number of species (review by Mousseau and Dingle 1991), but the effects on fitness of such complex interactions are very difficult to quantify and interpret (and see Trade-offs). For example, young larvae of the grasshopper *Chorthippus brunneus* (Thunberg) (Acrididae) find better conditions early in the season, but the later eggs and hence hatchlings are larger (Cherrill 2002). Maternal fitness in this species is greater with many small eggs when conditions are good but greater with few large eggs when conditions are poor, near the edge of the range (Hassall *et al.* 2006).

In summary, the extent of individual variation differs widely among species and for different aspects of the response. In particular, some characteristics have narrow, normally distributed variations that synchronize populations with favourable environments, while others show wide or multimodal variations adaptive especially to environmental unpredictability. All of these patterns of variation reinforce the conclusion that seasonal adaptations reflect the nature of environments and the ways that they vary on a range of scales.

Geographical as opposed to individual patterns of variation also provide insights into environmental pressures. Very common are clines of response, with gradual changes in size or other features with latitude. Increase in size with latitude appears to be driven by temperature, because insects developing more slowly at lower temperatures are often larger (but see Walters and Hassall 2006); however, decrease in size with latitude accords with season length, as shorter seasons limit further growth (review by Blanckenhorn and Demont 2004). The clines can also be modified by factors such as food availability (Chown and Klok 2003*b*).

These clinal patterns depend on voltinism, because multivoltine species are not constrained (except near the end of the season) in the same way as univoltine ones (Blanckenhorn and Demont 2004). Bivoltine populations may develop faster than univoltine ones to achieve the second generation (Burke *et al.* 2005). In particular, resources such as growing season change gradually across space, whereas a seasonal response may be possible only in the discrete units of a generation. Hence, for example, the size of individuals may decline with growing season up to the point that a generation is lost because the season is now too short to complete the extra generation successfully. Size then increases dramatically before its slow decline resumes. Such sawtooth geographic clines have been shown in many orthopteroids and also in butterflies, beetles, and other taxa (*e.g.*, Masaki 1978; Roff 1980; Nylin and Svärd 1991; Ishihara 1998).

Conclusions

Understanding seasonal adaptations requires a broad view of the effects of temporal, spatial, and resource patterns. Although it is easier to work with only part of this huge conceptual territory, as most scientists have done, real organisms integrate a great array of factors simultaneously. Such a framework leads to great complexity of selective pressures and responses. Consequently, even a single trait can relate to multiple seasonal functions. For example, as pointed out by Danks (2002*a*), slow development can help to conserve energy, protect against adversity, synchronize individuals with one another or with food, optimize the timing of reproduction, prevent development at risky times of year, and monitor environments for longer periods to allow more reliable developmental decisions. All of these roles have been demonstrated in various species, and slow development typically serves more than one role simultaneously. The opposite trait, extremely rapid development, can help to accelerate population growth, exploit ephemeral or limited resources, and escape natural enemies or approaching climatic adversity and can serve other roles in special cases (for example, where males are parasitic on their own females). In particular, and reinforcing the complexity just noted, abbreviated life cycles have been achieved in many ways, including small size, rapid development, elimination or reduction of stages, and microhabitat choice (see Life-cycle patterns above).

Coupled with the challenging complexity of seasonal adaptations is the fact that usually the same selective forces from the environment can be overcome in many different ways. For example, temporary adversity can be met through diapause, changed developmental rate, resistance, or other means. Hence, it is not possible to tabulate any simple set of “seasonal responses”. Despite the complexity, seasonal adaptations nevertheless fall into recognizable geographical and temporal patterns such as the various clinal responses, life-cycle sequences, and sets of adaptations to adversity already summarized in preceding tables. Such summaries confirm that it is feasible to analyze the patterns at very broad as well as narrow scales. Likewise, it is necessary to examine relatively complex systems and simultaneous trade-offs. Life cycles can be patterned by many successive or simultaneous developmental options (see Life-cycle patterns above). The effects of responses to the environment may ripple through several generations (Mondor *et al.* 2005 for the effects of predation).

This review confirms that the key to understanding all of the adaptations lies in the specific nature of the environment (*cf.* Table 1). The seasonal responses of movement, habitat selection, habitat modification, and resistance to cold, dryness, and food limitation all stem from environmental pressures. Limitation of environmental resources forces the wide variety and great complexity of trade-offs. Environments are implicated in the patterns of variation. Especially striking is the contrast between equable habitats with reliable signals and varying and unpredictable ones inhabited by species showing a variety of patterns of variation that serve as bet-hedging strategies.

Detailed knowledge about environments is therefore required. This point has been made for many years about cold-hardiness studies, for example (*e.g.*, Danks 1978, 1996, 2006*a*). Even so, most studies of cold hardiness still focus only on physiological and biochemical adaptations without the detailed information about the conditions experienced and their patterns of natural variation that would help to explain the nature and incidence of the physiological and biochemical adaptations. Most studies of life-cycle adaptations likewise lack parallel environmental data. In contrast, knowledge of spring weather patterns, for example, has allowed the variability of spring hatch or emergence to be interpreted as a means of insuring against harsh interludes early in the season (*e.g.*, Bradshaw 1973; Neal *et al.* 1997). By the same token, we can understand how seasonal adaptations such as prolonged diapause are maintained and governed in a given species only through the long-term analysis of habitat variability for that species.

These observations reinforce the value of wider approaches than have been customary. I conclude that further progress in analyzing all of the aspects of seasonal adaptations reviewed in this paper depends especially on detailed simultaneous analyses of natural environments.

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