

## Key themes in the study of seasonal adaptations in insects II. Life-cycle patterns

Hugh V. DANKS\*

Group of Insect Physiology and Molecular Biology, Research Institute for Bioresources, Okayama University; Kurashiki 710–0046, Japan

and

Biological Survey of Canada (Terrestrial Arthropods), Canadian Museum of Nature; Ottawa, Canada K1P 6P4

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### Abstract

Recent work on selected topics of particular interest for understanding insect life-cycles is reviewed, including habitat patterns, kinds of variation, the spreading of risk and prolonged diapause, trade-offs and developmental plasticity, circannual rhythms, the concept of life cycles as developmental choices, and development or delay as the default response. Seasonal adaptations have a wider range of components than has often been appreciated. Variation in life-cycle traits, including the duration of development and the timing of emergence, can be wide, narrow, or discontinuous. Trade-offs encompass multiple simultaneous traits and are not always structured as might be expected. Diapause, cold hardiness, reproductive pattern, and other traits have evolved many times independently. Such complex interactions can be understood only by examining the detailed features of a species' habitat, because how developmental decisions are made and whether continuous development or delays are programmed reflect the predictability of habitats and the environmental signals they supply. Ecological context is important, not just mechanisms of adaptation. Therefore, although most previous studies have paid more attention to insect response than to habitat, interpreting the seasonal relevance of life-cycle patterns requires measurement and analysis for individual species of habitat characteristics and their variation, on a range of temporal and spatial scales, in much more detail than has been customary.

**Key words:** Life-cycles; diapause; variation; trade-off; habitat

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### INTRODUCTION

Insects respond to seasonal environments through a very wide range of coordinated life-cycle adaptations, such as growth rate and dormancy. This review highlights some themes that I consider to be of particular current interest, in order to draw attention to key subject areas and concepts and to integrate knowledge in the broad field of insect seasonal adaptations. Extensive background information, most of it not included here, is available in a number of earlier reviews (e.g. Tauber et al., 1986; Danks, 1987, 1994b, 2002; and others cited below). Therefore, I cite here chiefly selected recent examples. This paper, with an earlier one on patterns of cold-hardiness (Danks, 2005a), allows some general conclusions about the study of insect life cycles and about seasonal adaptations in gen-

eral.

### HABITAT PATTERNS

Several kinds of seasonal responses correspond with characteristics of the habitat. Key environmental features that have been recognized (Danks, 1999) include the prevalence of conditions adverse for insect survival (severity), differences through the year (seasonality), the amount of short-term variation within one season (unpredictability) and variations from year to year in a given seasonal parameter such as temperature (variability).

Seasonal responses also depend on whether organisms can predict future conditions by monitoring current environments. The availability and reliability of cues for monitoring depend especially on latitude and on habitat (Danks, 1987, chap. 6). For

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\* E-mail: [hdanks@mus-nature.ca](mailto:hdanks@mus-nature.ca)  
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example, photoperiod is very reliable and indicative especially at middle latitudes, and temperatures in highly buffered habitats have a relatively consistent seasonal pattern.

Habitats influence individual life cycles at several different scales. At a very large scale, latitudinal trends in climate lead to well-known geographical differences in life cycles and in the incidence, intensity and control of diapause. Although many geographic trends are complex (cf. Arnett and Gotelli, 1999), overall patterns of diapause are correlated especially with winter severity and duration of the growing season (e.g. Danks, 1987; Masaki, 1999). For example, whether a species has winter diapause, summer diapause or both depends on regional climatic patterns. Quiescence is supposed to reflect relatively mild seasonal climates or habitats, whereas diapause provides insurance against premature development if conditions might be favorable just before a period of certain adversity. Components of the growing season, especially accumulated heat as well as the timing of freezing temperatures or other adverse conditions, regulate the number of generations that is feasible in a given place. Contributing to and even confounding the large-scale patterns are historical elements such as Pleistocene glaciations, isolation and genetic drift (Armbruster et al., 1998; Bossart, 1998; Stone et al., 2001).

At an intermediate scale, topographic complexity, for example mountain ridges and valleys, influence the degree of dispersal and hence patterns of variation among populations (Wishart and Hughes, 2001). Dispersal abilities are especially relevant at this scale, because local selection favours specific life-cycle adaptations but interbreeding offsets local evolution, as well shown by Llewellyn et al. (2003) for aphids. Dispersal, range size, foodplant range-size, and other population factors therefore all interact with growing season and other local habitat features to determine the patterns of life-cycle adaptation (cf. Dennis et al., 2000).

Even at the scale of local habitats, the patterns of suitability that drive seasonal adaptations are difficult to quantify. Certainly, the direct influence of seasonal conditions and their year-to-year differences is well known, but more complex relationships are not. For example, the timing of bud burst in relation to egg hatch is critical for many species (e.g. Chen et al., 2003), yet the phenology of host

plants in different seasons may change in a different manner than that of their herbivores. The impact of asynchrony also depends on overall seasonal timing. For example, species feeding near the beginning or end of the season are especially sensitive to variation in the start or end of the season. Nor can they develop using any extra time that might be available to reach a larger size, because the quality of the leaves declines as the season advances. In contrast, species feeding in summer use leaves that do not change so rapidly in quality, and so could grow to a larger size if time is available (Fox et al., 1997; Kause et al., 2001; and see Trade-offs below).

Habitats affect life cycles on still smaller scales. For example, in one small population of butterflies, phenology could vary by up to 11 days according to the microdistribution of the larval population within the habitat (Weiss and Weiss, 1998).

Unpredictable habitats are especially difficult to characterize. Disturbances such as catastrophic fires, floods or drought typically occur many years apart, and less drastic but equally unpredictable changes significant to organisms take place on shorter time frames, for example in lake hydrology, salinity and nutrient level and in stream flow (e.g. Garcia et al., 1997; Lytle, 2002; Benbow et al., 2003). A key feature of habitats in the context of life cycles, therefore, is how variable they are, and how extreme and unpredictable this variation is beyond a strictly seasonal pattern. Therefore, even whether certain variables affect life cycles or not differs annually (Fleishman et al., 2000).

In summary, habitat features and variations must be considered as a core element of responses to seasonal environments, even though typical earlier work has emphasized instead the role of precise insect responses to the invariable astronomical cue of photoperiod.

## KINDS OF VARIATION

Patterns of variation are controlled by genetic differences, expressed through polymorphic traits, and by environmental cues that adjust ongoing responses (polyphenism or plasticity) (Danks, 1994b, 2002). In practice, both genetic and environmental responses are combined. I focus here on the kinds of variation in life-cycle traits in individuals in one place, rather than on any geographic differences.

Populations of individuals vary in a general way because of differences in genetic make up and in the conditions experienced, but usually these variations are normally distributed with a fairly narrow spread. Wider or more complex patterns are associated with natural habitats that vary seasonally or unpredictably. In particular, insects must find a balance between narrow and wide variations serving different ends. Narrow variations assist coincidence with optimal conditions of climate or food (especially when resources are temporally limited), enhance synchrony for mating and other intraspecific relationships, and coincide a resistant stage with predictable seasonal adversity. Wider variations may make more of the season available, but conversely may extend development or reproduction into periods with suboptimal conditions. In particular, wider variations serve to offset risk. Therefore, both symmetrical (normal) and asymmetrical distributions of development and emergence are known. More complex responses include multimodal variation and programmed developmental changes that alter the rate of development or suppress it through diapause.

A typical narrow mode of variation is synchrony of emergence. In a few species it is controlled by simple temperature quiescence (Jenkins et al., 2001), but many species have more complex responses, including successively increasing temperature thresholds through which late larvae can catch up with earlier ones, and photoperiodically controlled growth rates and diapauses (Danks, 1994a; Aoki, 1999).

Life cycles adapt rapidly to local climates, to foodplants (Fordyce and Nice, 2003) and to laboratory conditions (Matos et al., 2002). The extent of variation is rapidly reduced in most laboratory colonies (e.g. Miyatake and Yamagishi, 1999). Moreover, the ease with which variation can be detected depends greatly on sample size, especially at the extremes (Danks, 2000 for temporal patterns; Gutiérrez and Menéndez, 1998 for flight periods in nature). Wide variation in developmental time and other life-history features is characteristic of some species (e.g. Aquino and Turk, 1997; Stiefel et al., 1997), especially in extreme habitats (Kawecki, 1995). In typical experiments, stress tends to increase variance, but the effects are complex (Krebs and Loeschcke, 1999). All of these effects suggest caution in experimental work, because natural vari-

ation is likely to be underestimated.

Skewed distributions in the development of populations are not unusual because individuals can be delayed by local circumstances, but cannot accelerate to a corresponding extent even if conditions are fully suitable. Such delays give a 'tail' after the main distribution. This effect is enhanced because early offspring are at a considerable demographic advantage, and therefore the main distribution tends to reflect relatively rapid development or oviposition. A second type of adaptive skew results from programmed delays in both development and reproduction that serve as insurance against unpredictable events (see Risk spreading).

In some species, saw-toothed clines of response are produced as local populations add or reduce a whole generation, rather than a partial one, within the available growing season (Masaki, 1978; Roff, 1980; Mousseau and Roff, 1989; Nylin and Svård, 1991; Ishihara, 1998). Such responses can be mediated by step-wise changes of critical photoperiod, for example (Gomi and Takeda, 1996). Other species respond by cohort-splitting, whereby advanced individuals emerge the same year but later ones delay until the next year, often through diapause (Danks, 1992; Townsend and Pritchard, 1998), producing a bimodal pattern of development, though not necessarily of seasonal emergence. Bimodal and multimodal responses may also reflect risk spreading.

Alternatively, the quality rather than the occurrence of individuals changes with time. For example, the size of eggs or the tendency to enter diapause can change as the mother ages (reviews by Danks, 1987; Mousseau and Dingle, 1991). Such changes lead to interesting interactions with natural conditions which themselves change with time. For example, later eggs of the grasshopper *Chorthippus brunneus* are larger (through an effect of maternal age), and thus presumably more fit, but earlier conditions are more favourable for the hatchlings (Cherrill, 2002). However, few of these interactions have been analysed in detail. Correlating changes in offspring quality with more comprehensive analysis of habitat conditions would be instructive.

## RISK SPREADING AND PROLONGED DIAPOUSE

In many species built-in variability of response spreads the population through time so that not all individuals are endangered by a given episode of adverse conditions. Such spreading of risk is visible in a wide range of environments, and individual differences interpreted as risk spreading (including very different pathways of development programmed by diapause, diapause intensity and other seasonal responses) have been reported many times, typically with a persistent genetic basis (see Danks, 1987; Masaki, 2002). Recent examples across various time frames include variable duration of pupal development in a geometrid moth (Tammaru et al., 1999), variable egg hatch of a bushcricket (Hockham et al., 2001), variable larval duration in a burnet moth (Wipking and Kuntz, 2000), and alternative routes among directly developing, dormant and mobile forms in a glycyphagid mite (Knülle, 2003). Sangpradub et al. (1999) found intraspecific variation in development rates, a wide range of simultaneous size classes, an ability to overwinter in different larval stages, and asynchronous extended flight periods in caddisflies from a temperate stream. Neal et al. (1997) interpreted the variable spring egg hatch of *Malacosoma* (which was independent of spring temperatures) as a means to offset potential losses of young larvae from late winter storms.

Most kinds of dormancy over annual or shorter time frames have significant variability, allowing organisms to respond not only to the adversity itself but also to its unpredictable occurrence, including year-to-year differences in the onset or end of the adverse season, such as the date of the first frost. Some instances respond to non-seasonal events, as in quiescent morphs of the mite *Tetranychus kanzawai* Kishida, which survive rainfall better than active morphs (Ikegami et al., 2000). Very conservative bet-hedging responses—partly associated with minimizing energy use when resources are limited—such as slow development, temperature-independent development, growth-rate compensation through the life cycle, extended reproduction and long adult life are known especially in certain beetles from several different families (Chaabane et al., 1997; Ehlert et al., 1997; Betz and Fuhrmann, 2001; Topp, 2003).

On longer time frames, prolonged diapause lasts through two or more adverse seasons. Prolonged diapause occurs especially in species from habitats that are unpredictable, such as deserts, the arctic and intermittently flowering or fruiting foodplants (Danks, 1987, Table 27, lists more than 140 species with prolonged diapause; Danks, 1992). However, it also occurs in more ordinary environments, suggesting that every environment has some degree of unpredictability (Danks, 1994a).

Recent work assembles longer term data (e.g. Powell, 2001, showed that *Yucca* moths can survive in prolonged diapause for 30 years; Tauber and Tauber, 2002), and considers how the patterns of a variable number of years spent in diapause are maintained. Prolonged diapause might be prompted by external conditions or cues, but such responses for the onset (as opposed to the end) of prolonged diapause have been verified in very few species (review by Danks, 1987). Alternatively, genetic polymorphism or evolutionarily stable strategies (ESS) would balance over time the selection for alleles conferring normal diapause versus those producing prolonged diapause. Finally, “stochastic polyphenism” (Walker, 1986) or “diversified bet-hedging” (e.g. Menu and Desouhant, 2002) would generate within-generation variability from a single genotype. Diversified bet hedging was claimed in the weevil *Curculio elephas* (Gyllenhal) (Menu et al., 2000; Soula and Menu, 2003), because although ESS or balanced polymorphism requires equal fitness in the long and the short life-cycle types (based on reproduction frequency, fecundity, mortality, etc.) the measured fitness of the 1- and 2-year types was not equal. However, short-term analysis excludes the occasional cost of failed 1-year cycles in unusual years, and certainly the level of prolonged diapause in most species is low or very low, reflecting its role as intermittent insurance rather than as an alternative of equal short-term fitness.

More detailed analyses of the basis and maintenance of prolonged diapause would be of great interest. Prolonged diapause probably has a complex genetic basis, by analogy with the maintenance of diapause itself, which often persists over many generations even under strong selection (Danks, 1987, Table 30). Analyses of prolonged diapause over many years are necessary to allow environmental effects to be integrated realistically.

## TRADE-OFFS AND DEVELOPMENTAL PLASTICITY

A basic tenet of life-history theory is that organisms must allocate limited resources among different traits, leading to “trade-offs”. These trade-offs constrain the ways in which life cycles can be constructed, because it is not possible to maximize every trait simultaneously. Therefore many attempts to assess the fitness of different life-cycle patterns have focussed on potential trade-offs, and an astonishing array of trade-offs has been validated for one species or another. Recent literature includes especially studies of developmental time, developmental rate or growth rate versus size, weight, fecundity, competitive ability, wing morph, resistance to heat shock and other adverse conditions, predator pressure and so on; of fecundity versus cold resistance, winter survival, wing morph or dispersal; and of the pattern of reproduction or egg production, or early fitness, versus survival, longevity or late fitness, as well as egg size versus egg number. A particular genetically determined balance of trade-offs can be modified by selection, but much work considers phenotypic responses within a season.

Trade-offs directly relevant to life-cycle patterns include diapause or its duration, because of the stored energy needed to survive diapause, versus post-diapause fitness (Ishihara and Shimada, 1995; Kroon and Veenendaal, 1998; Ellers and Alphen, 2002). Size and developmental rate are commonly traded off, because normally individuals cannot grow very large if they develop very quickly (cf. Danks, 1994a). However, recent work shows that such trade-offs by no means follow simple expectations. Moreover, what kinds of trade-offs might be recorded depends on laboratory procedures (Danks, 2000), including rearing density (cf. Prasad et al., 2001; Prasad and Joshi, 2003).

Whether trade-offs or differential resource allocations are even possible depends on the acquisition of resources in the first place. Consequently, trade-offs may not be visible if the input or availability of resources is too variable (Messina and Slade, 1999; Brown, 2003; Messina and Fry, 2003). Laboratory experiments suggest that time and size trade-offs are restricted to stressful situations (Fischer and Fiedler, 2002), or at least that trade-offs tend to disappear in uncrowded condi-

tions (Cortese et al., 2003). For example, abundant food can disable other trade-offs. Both earlier emergence and larger adults are possible when food is of high quality (Wissinger et al., 2004). Larger larvae of the moth *Lobesia botrana*, produced from larger eggs, perform better only in more difficult food conditions (Torres-Vila and Rodríguez-Molina, 2002).

Conversely, low temperature and poor food may depress both size and growth rate, as might be expected, but some traits are unexpectedly neutral or independent of one another. For example, reproductive investment and the offspring size/number trade-off may evolve independently (Frankino and Juliano, 1999). Resistance to heat and resistance to cold are independent (Hercus et al., 2000). Development time may not be traded off with size or weight (see below). Some traits are canalized or kept constant: for example, some blepharocerids grow at the same rate over a range of temperatures from 0°C to 16°C (Frutiger and BuerGISser, 2002).

Other relationships are the reverse of those expected, as for developmental time and size in a gerrid (Klingenberg and Spence, 1997). Klingenberg and Spence (1997) concluded that in this instance size itself is not adaptive, but coevolves in correlation with other traits.

A major problem in studies of trade-offs is that in natural populations multiple life-cycle features trade off simultaneously, not the simple pairs customarily studied under controlled conditions. Size, for example, affects other trade-offs (Roff et al., 2002), even to the extent of dominating all other relationships (e.g. Morse and Stephens, 1996). Longevity versus egg production trade-offs are different for long-winged and short-winged individuals of a cricket (Tanaka and Suzuki, 1998). In *Drosophila*, fecundity trades off with longevity but the correlation with energy saved is not exact (Djawdan et al., 1996). Egg size versus egg number trade-offs can be obscured by variation due to ambient conditions (Ernsting and Isaaks, 2000). Indeed, even the nature of trade-offs can be altered by temperature; for example, development time in *Drosophila* increased when individuals were selected for longevity at high temperatures, but when a cold-resistant line was selected for longevity at low temperatures, developmental time decreased (Norry and Loeschcke, 2002). Selection on some traits reveals other, sometimes unexpected, correla-

tions when more than a few traits are studied simultaneously (Miyatake, 1998).

In summary, the trade-offs or sets of trade-offs are dynamic, so that different allocations have different values, and how size and other features are influenced depends on many other components. Therefore, the various contributors to fitness interact in a complex hierarchy (compare the discussions of Danks, 1994a; Nylin and Gotthard, 1998; Carroll et al., 2003; Hoffmann et al., 2003; Bradshaw et al., 2004).

Awareness of such complexities has been especially useful in identifying how life cycles are structured in nature. One of the most valuable conclusions from recent work is that, just as trade-offs may be restricted to stressful situations in the laboratory (see above), whether seasonal time is limited or not—"time stress"—determines the structure of potential trade-offs. For example, when short photoperiods signal that the end of the season is approaching, development may accelerate in order to allow safe entry into diapause before the winter, or to allow emergence in time for reproduction, with varying influences on size and growth rate (Carrière et al., 1996; Leimar, 1996; Gotthard, 1998, 2001; Nylin and Gotthard, 1998; Gotthard et al., 1999, 2000; De Block and Stoks, 2004). When resources are limited, some species reduce developmental time with the same growth rate and so reduce size; others reduce size somewhat but maintain the same duration of development; yet others take longer to develop, but maintain size. When resources are not limited, some such trade-offs are not necessary. Which strategy is followed may also depend on sex, because in general size is more valuable to females (maintaining fecundity), but at least in protandrous species time is more valuable to males (enhancing the likelihood of mating) (e.g. Kleckner et al., 1995; Zonneveld, 1996; Fischer and Fiedler, 2000, 2001). Therefore, trade-offs among development, growth rate, size and other traits integrate the specific value of time, against a background of resource availability and allocation. Moreover, despite its demographic value, growth rate is not routinely maximized (Margarf et al., 2003; Tammaru et al., 2004), unlike some earlier expectations, so that individuals retain room for manoeuvre in responding to environmental circumstances.

Such adaptive variations in growth rate and other

traits confirm that the presence and nature of any trade-offs depend on the features of individual species in specific environments, so that broad ecological approaches are needed to understand life cycles. In contrast, most studies of specific trade-offs in the laboratory are confined to a few components, and most mathematical models provide relatively limited insights because they lack empirical validation. As pointed out by Nylin and Gotthard (1998), a key challenge is to discover how the plasticity of response manifested by multiple trade-offs is maintained in nature, presumably by long-term environmental variation. As indicated above, understanding the maintenance of prolonged diapause poses a similar challenge.

## CIRCANNUAL RHYTHMS

Circannual rhythms, controlled chiefly by seasonal photoperiodic signals, are well known in vertebrates (e.g. Dunlap et al., 2004), but in insects most of the possible endogenous annual timers that have been claimed prove to have other explanations such as induction in the maternal generation (review by Danks, 1987, pp. 187–190).

Well documented is the circannual rhythm of the dermestid beetle *Anthrenus verbasci* (Linn.) (Blake, 1958, 1959), recently reported on in some detail by Nisimura and Numata (2001, 2002, 2003). The period of the rhythm is 37–40 weeks under constant short days, its Zeitgeber is a change in photoperiod, and the phase can be shifted by appropriate treatments.

The search for and study of other species with similar responses would be rewarding, including other species of *Anthrenus* (e.g. *A. sarnicus* Mroczkowski: Coombs and Woodroffe, 1983), and species in seasonal habitats where development is always univoltine. It seems unlikely that a response of evident adaptive value in seasonal environments would be so rare in insects compared with the many well-known responses controlled by photoperiod and temperature on a seasonal but not endogenous annual basis.

## LIFE CYCLES AS MULTIPLE DEVELOPMENTAL CHOICES

Many species cope with seasonal environments through life cycles that allow a series of alternative

developmental choices. Each individual follows a particular life-cycle pathway by making successive developmental decisions, such as whether or not to enter diapause, whether or not to become quiescent, and whether to develop slowly or rapidly. Many alternative pathways are possible when there are multiple decision points through the life cycle; each individual can then optimize its chance of survival by adjusting the duration of immature development, the time of metamorphosis to the adult, or the timing of reproduction according to its genetic program and especially in response to ongoing environmental information. Of course, the response to a given environment can change through the life cycle, so that short photoperiods might have one effect in early instars and the opposite effect in later instars (e.g. Khaldey, 1977).

By plotting out the alternatives, investigators can visualize the responses and discover their seasonal pattern. For example, the life cycle of the northern dragonfly *Aeshna viridis* Eversmann (data of Norling, 1976 as plotted by Danks, 1991) is complex but proves to be made up of relatively simple choices between diapause, non-diapause, and developmental-rate alternatives. Short days induce a larval diapause (ended by long days) in several of the later instars, and it is most intense and so lasts longer in the latest instars. In smaller larvae, long rather than short days induce a less intense diapause. Diapause is especially likely when younger larvae are exposed to a change from short to long days; but when diapause is not induced in these larvae, the same short-day to long-day change accelerates growth. These alternative responses to photoperiod, coupled with responses to temperature, serve to synchronize emergence and limit it to early summer, allowing life cycles of exactly two or three years, but not of other durations. Development of middle-instar larvae is delayed by diapause in summer so that they cannot emerge in fall. Advanced larvae enter a long diapause in fall, preventing premature emergence. In the spring the development of later (but not earlier) stages is stimulated so that they emerge the same summer.

Complex and continuous responses to photoperiod and temperature in many other species serve similar purposes, and can be understood by plotting the various alternative developmental pathways. Detailed examples are illustrated by Danks (1991, 1994a), including complex pathways plotted

from the data of previous investigators on eggs of orthopterans, on larvae of dragonflies, earwigs and moths, on larvae and pupae of butterflies and on deutonymphs of mites. A relatively limited number of basic responses is repeated in different species, but they are assembled into coherent sets that cope effectively with the natural seasonal changes and challenges experienced by each species.

It would be very helpful to see more life-cycle data presented in this broader framework of life-cycle pathways, and more investigations conducted to expose the nature of the alternative decision points. Experiments using multiple simultaneous treatments are required to do this, rather than isolated photoperiodic response curves. For example, Wardaugh's (1986) account of the 18 alternative life-cycle pathways in the grasshopper *Chortocetes terminifera* (Walker), governed chiefly by egg diapause and quiescences mainly under environmental control, relied on a very large number of different experimental treatments. More limited experiments are less likely to provide satisfactory answers. The need for labour- and equipment-intensive experiments means that proposals to do work of this sort may not be feasible if they are only partly funded, although partial funding has become a common tendency in many jurisdictions. However, the context provided by examining life-cycle pathways more comprehensively is often the only way to reveal the adaptive nature of the component responses.

## DEFAULT RESPONSES

The concept of *defaults* (e.g. Danks, 2002), i.e. what responses take place automatically unless prevented, clarifies how the seasonal program responds to habitat. Life cycles with active defaults—in which *development* is automatic—are associated with habitats that are usually suitable for activity and also supply environmental signals able to predict reliably when conditions will deteriorate. Development is stopped by specific signals only if the need arises.

Life cycles with passive defaults—in which *delay* is automatic—are found in species from habitats that often become unsuitable, and moreover where environmental signals do not reliably predict the future adversity. In these species, the default system stops development in a more-or-less

resistant stage, or at least before the vulnerable adult stage, unless conditions specifically signal it to continue. Conservative passive responses of this sort, such as a fixed diapause, or development confined to a very narrow band of temperature, insure individuals against sudden environmental adversity. Of course, in safe environments passive responses would unduly limit the opportunities for development, just as active responses in severe habitats would be more likely to endanger developing individuals.

Many difficulties in understanding life cycles have arisen from the existence of passive systems. In particular, so-called "obligate" diapause has usually been seen as an inevitable programmed arrest in development, but in fact these adaptations merely reflect the fact that resumption of the developmental program requires an environmental signal such as a change in photoperiod, temperature, or food (Danks, 1987, Table 23; Worland et al., 2000). Most species that develop actively include one or more key control points such as diapause, usually induced by the environment; in some other species the control is interpolated passively. The key driving variable, once again, is the nature of the habitat.

## CONCLUSIONS

Insects control their life cycles through active development and passive delays using environmental information of different sorts and to different degrees to accelerate or retard development in one or more life stages. As a result, the adaptations are extremely complex. Variation in life-cycle traits, including the duration of development and the timing of emergence, can be wide, narrow, or discontinuous. Trade-offs encompass multiple simultaneous traits, but are not always present nor structured as might be expected, especially when seasonal time is limited. Even single traits can serve many alternative or simultaneous purposes. For example, delayed development may contribute to diverse goals such as conserving energy, protecting against adversity, synchronizing individuals with one another or with food resources, optimizing the timing of reproduction, preventing development at risky times of year, and monitoring environments for longer periods (Danks, 2002).

Therefore, the key variables for understanding

life cycles are those of the environment, and the key orientation is to the detailed features of a species' habitat. As introduced above, these features act across a wide range of spatial and temporal scales, from continents to microhabitats and from days to years. Such an ecological orientation suggests helpful ways to view life-cycle patterns. Visualizing developmental pathways in the form of successive decision points shows how ecologically relevant decisions are made, especially in reference to habitat conditions. The predictability of habitats as well as the predictive power of signals that can be monitored dictate whether active life-cycle controls (requiring specific habitat signals to induce delays), passive controls (requiring specific signals to allow development to resume), or genetically programmed variations are more effective.

Moreover, the most important factor selecting for a given life cycle may not be the obvious one. Some high arctic insects overwinter exposed because starting development early in the summer is more important than winter insulation: overwintering in sheltered places would protect them from cold, but more importantly it would slow down the spring thaw (Danks, 2004). In other cold environments, acquiring heat through the summer may be more important than withstanding winter cold (Bird and Hodkinson, 1999). Observed trade-offs in some species (see above) give parallel lessons, confirming the many ways in which habitat features dictate life-cycle patterns.

Consequently, it is not enough to consider only the detailed mechanisms or functional parts of seasonal adaptations, because study of the parts alone does not explain the ecological relevance of the whole. For example, daily and seasonal biological clocks differ in the nature of the timing information they record, in the breadth of effective cues, in receptive pigments and their location, and in other components, as summarized by Danks (2003, 2005b). However, most recent attention has been paid to the molecular mechanism by which the circadian cycle is driven and its potential linkage with the seasonal photoperiodic clock, despite the fact that it is the purpose and not the potential timing mechanism of the seasonal clock that enables insect responses to be interpreted (Danks, 2005b). Photoperiodic responses are informative chiefly because they allow survival in seasonal environments (purpose), and not because they might have some



sort of linkage with circadian timing systems (mechanism). Once again, it is the context provided by detailed knowledge of the environment that allows us to understand life cycles, through the annual patterns of regional climate, the seasonal availability of energy, the habitat conditions experienced by individual species, the predictive value of available cues, and so on.

Of course, the phylogenetic history of a group or species does determine the core structure of seasonal responses (e.g. Saulich and Sokolova, 2000 for the seasonal cycles of noctuid moths), but perhaps more striking is the large number of traits linked to habitat or its seasonal components that have evolved many times independently. These traits include not only diapause (review by Danks, 1987, p. 290) and cold hardiness (Danks, 2005a), but also reproductive pattern (e.g. Guillet and Vancassel, 2001), paedogenesis (Wyatt, 1967; Hodin and Riddiford, 2000), wing reduction (e.g. Hunter, 1995; Desender, 2000), parental care (e.g. Machado and Raimundo, 2001), gall structure (e.g. Stone and Cook, 1998), and so on. Bradshaw and collaborators (Bradshaw et al., 1998, 2000, 2003a, b, 2004; Bradshaw and Holzapfel, 2001) suggest from work on the pitcher-plant mosquito *Wyeomyia smithii* that photoperiodic responses such as critical photoperiod are readily modified by selection, whereas other elements of the response, including thermal adaptations and the mechanism for monitoring daylength, respond much more slowly. Investigating the evolution of photoperiodic and thermal responses in widely distributed species from less specialized habitats would be valuable.

Recently, much of the work on seasonal adaptations has concentrated on very specific mechanisms. Nevertheless, how different responses are integrated to provide coherent, seasonally relevant developmental trajectories can be understood only by reference to ecological demands. A broad ecological approach based on the role of habitat is required to understand seasonal adaptations in real environments. Moreover, specific detailed data are needed: regional photoperiods and mean monthly air temperatures are by no means sufficient.

Therefore, in the same way as for patterns of cold hardiness (Danks, 2005a), to interpret insect life-cycle patterns it is necessary to study habitats as well as insect responses. For any individual species, habitat characteristics and their variation

in time and space must be measured and analysed in much more detail than has been usual when studying insect life cycles.

## REFERENCES

- Aoki, T. (1999) Larval development, emergence and seasonal regulation in *Asiagomphus pryori* (Selys) (Odonata: Gomphidae). *Hydrobiologia* 394: 179–192.
- Aquino, A. L. and S. Z. Turk (1997) Ciclo vital de *Leptysma argentina* Bruner 1906 (Acrididae: Leptysminae: Leptysmini). Variabilidad en el esquema reproductivo e reproducción. *Acta Entomol. Chilena* 21: 93–99.
- Armbruster, P., W. E. Bradshaw and C. M. Holzapfel (1998) Effects of postglacial range expansion on allozyme and quantitative genetic variation of the pitcher-plant mosquito, *Wyeomyia smithii*. *Evolution* 52: 1697–1704.
- Arnett, A. E. and N. J. Gotelli (1999) Bergmann's rule in the ant lion *Myrmeleon immaculatus* DeGeer (Neuroptera: Myrmeleontidae): Geographic variation in body size and heterozygosity. *J. Biogeogr.* 26: 275–283.
- Benbow, M. E., A. J. Burky and C. M. Way (2003) Life cycle of a torrenticolous Hawaiian chironomid (*Telmatogeton torrenticola*): Stream flow and microhabitat effects. *Ann. Limnol.* 39: 103–114.
- Betz, O. and S. Fuhrmann (2001) Life history traits in different life forms of predaceous *Stenus* beetles (Coleoptera, Staphylinidae), living in waterside environments. *Neth. J. Zool.* 51: 371–393.
- Bird, J. M. and I. D. Hodkinson (1999) Species at the edge of their range: The significance of the thermal environment for the distribution of congeneric *Craspedolepta* species (Sternorrhyncha: Psylloidea) living on *Chamerion angustifolium* (Onagraceae). *Eur. J. Entomol.* 96: 103–109.
- Blake, G. M. (1958) Diapause and the regulation of development in *Anthrenus verbasci* (L.) (Col., Dermestidae). *Bull. Entomol. Res.* 49: 751–775.
- Blake, G. M. (1959) Control of diapause by an 'internal clock' in *Anthrenus verbasci* (L.) (Col., Dermestidae). *Nature* 183: 126–127.
- Bossart, J. L. (1998) Genetic architecture of host use in a widely distributed, polyphagous butterfly (Lepidoptera: Papilionidae): Adaptive inferences based on comparison of spatio-temporal populations. *Biol. J. Linn. Soc.* 65: 279–300.
- Bradshaw, W. E., S. Fujiyama and C. M. Holzapfel (2000) Adaptation to the thermal climate of North America by the pitcher-plant mosquito, *Wyeomyia smithii*. *Ecology* 81: 1262–1272.
- Bradshaw, W. E. and C. M. Holzapfel (2001) Phenotypic evolution and the genetic architecture underlying photoperiodic time measurement. *J. Insect Physiol.* 47: 809–820.
- Bradshaw, W. E., C. M. Holzapfel and T. E. Davison (1998) Hourglass and rhythmic components of photoperiodic time measurement in the pitcher plant mosquito, *Wyeomyia smithii*. *Oecologia* 117: 486–495.
- Bradshaw, W. E., M. C. Quebodeaux and C. M. Holzapfel (2003a) Circadian rhythmicity and photoperiodism in

- the pitcher-plant mosquito: Adaptive response to the photic environment or correlated response to the seasonal environment? *Am. Nat.* 161: 735–748.
- Bradshaw, W. E., M. C. Quebodeaux and C. M. Holzapfel (2003b) The contribution of an hourglass timer to the evolution of photoperiodic response in the pitcher-plant mosquito, *Wyeomyia smithii*. *Evolution* 57: 2342–2349.
- Bradshaw, W. E., P. A. Zani and C. M. Holzapfel (2004) Adaptation to temperate climates. *Evolution* 58: 1748–1762.
- Brown, C. A. (2003) Offspring size-number trade-offs in scorpions: An empirical test of the van Noordwijk and de Jong model. *Evolution* 57: 2184–2190.
- Carrière, Y., A. M. Simons and D. A. Roff (1996) The effect of the timing of post-diapause egg development on survival, growth, and body size in *Gryllus pennsylvanicus*. *Oikos* 75: 463–470.
- Carroll, S. P., M. Marler, R. Winchell and H. Dingle (2003) Evolution of cryptic flight morph and life history differences during host race radiation in the soapberry bug, *Jadera haematoloma* Herrich-Schaeffer (Hemiptera: Rhopalidae). *Ann. Entomol. Soc. Am.* 96: 135–143.
- Chaabane, K., M. Loreau and G. Josens (1997) Growth and egg production in *Abax ater* (Coleoptera, Carabidae). *Pedobiologia* 41: 385–396.
- Chen, Z., K. M. Clancy and T. E. Kolb (2003) Variation in budburst phenology of Douglas-fir related to western spruce budworm (Lepidoptera: Tortricidae) fitness. *J. Econ. Entomol.* 96: 377–387.
- Cherrill, A. (2002) Relationships between oviposition date, hatch date, and offspring size in the grasshopper *Chorthippus brunneus*. *Ecol. Entomol.* 27: 521–528.
- Coombs, C. W. and G. E. Woodroffe (1983) The effect of temperature upon the longevity, fecundity and circannual development of *Anthrenus sarnicus* Mroczkowski (Coleoptera: Anthrenidae). *J. Stored Prod. Res.* 19: 111–115.
- Cortese, M. D., F. M. Norry, R. Piccinalli and E. Hasson (2003) Direct and correlated responses to artificial selection on developmental time and wing length in *Drosophila buzzatii*. *Evolution* 56: 2541–2547.
- Danks, H. V. (1987) *Insect Dormancy: An Ecological Perspective*. Biological Survey of Canada (Terrestrial Arthropods), Ottawa. 439 pp.
- Danks, H. V. (1991) Life-cycle pathways and the analysis of complex life cycles in insects. *Can. Entomol.* 123: 23–40.
- Danks, H. V. (1992) Long life cycles in insects. *Can. Entomol.* 124: 167–187.
- Danks, H. V. (1994a) Diversity and integration of life-cycle controls in insects. In *Insect Life-cycle Polymorphism: Theory, Evolution and Ecological Consequences for Seasonality and Diapause Control* (H. V. Danks ed.). Kluwer Academic Publishers, Dordrecht, pp. 5–40.
- Danks, H. V. (ed.) (1994b) *Insect Life-cycle Polymorphism: Theory, Evolution and Ecological Consequences for Seasonality and Diapause Control*. Kluwer Academic Publishers, Dordrecht. 376 pp.
- Danks, H. V. (1999) Life cycles in polar arthropods—Flexible or programmed? *Eur. J. Entomol.* 96: 83–102.
- Danks, H. V. (2000) Measuring and reporting life-cycle duration in insects and arachnids. *Eur. J. Entomol.* 97: 285–303.
- Danks, H. V. (2002) The range of insect dormancy responses. *Eur. J. Entomol.* 99: 127–142.
- Danks, H. V. (2003) Studying insect photoperiodism and rhythmicity: Components, approaches and lessons. *Eur. J. Entomol.* 100: 209–221.
- Danks, H. V. (2004) Seasonal adaptations in arctic insects. *Integr. Comp. Biol.* 44: 85–94.
- Danks, H. V. (2005a) Key themes in the study of seasonal adaptations in insects I. Patterns of cold hardiness. *Appl. Entomol. Zool.* 40: 199–211.
- Danks, H. V. (2005b) How similar are daily and seasonal biological clocks? *J. Insect Physiol.* 51: 609–619.
- De Block, M. and R. Stoks (2004) Life-history variation in relation to time constraints in a damselfly. *Oecologia* 140: 68–75.
- Dennis, R. L. H., B. Donato, T. H. Sparks and E. Pollard (2000) Ecological correlates of island incidence and geographical range among British butterflies. *Biodiv. Conserv.* 9: 343–359.
- Desender, K. (2000) Flight muscle development and dispersal in the life cycle of carabid beetles: Patterns and processes. *Bull. Inst. R. Sci. Nat. Belg. Entomol.* 70: 13–31.
- Djawardan, M., T. T. Sugiyama, L. K. Schlaeger, T. J. Bradley and M. R. Rose (1996) Metabolic aspects of the trade-off between fecundity and longevity in *Drosophila melanogaster*. *Physiol. Zool.* 69: 1176–1195.
- Dunlap, J. C., J. J. Loros and P. J. DeCoursey (eds.) (2004) *Chronobiology. Biological Timekeeping*. Sinauer, Sunderland, Mass. 382 pp.
- Ehlert, R., W. Topp, S. Thiernemann and B. Brett (1997) Phenotypic plasticity in *Choleva agilis* to maintain fitness in an unpredictable environment (Coleoptera: Cholevidae). *Entomol. Gen.* 21: 145–159.
- Ellers, J. and J. J. M. van Alphen (2002) A trade-off between diapause duration and fitness in female parasitoids. *Ecol. Entomol.* 27: 279–284.
- Ernsting, G. and A. Isaaks (2000) Ectotherms, temperature, and trade-offs: Size and number of eggs in a carabid beetle. *Am. Nat.* 155: 804–813.
- Fischer, K. and K. Fiedler (2000) Sex-related differences in reaction norms in the butterfly *Lycaena tityrus* (Lepidoptera: Lycaenidae). *Oikos* 90: 372–380.
- Fischer, K. and K. Fiedler (2001) Sexual differences in life-history traits in the butterfly *Lycaena tityrus*: A comparison between direct and diapause development. *Entomol. Exp. Appl.* 100: 325–330.
- Fischer, K. and K. Fiedler (2002) Life-history plasticity in the butterfly *Lycaena hippothoe*: Local adaptations and trade-offs. *Biol. J. Linn. Soc.* 75: 173–185.
- Fleishman, E., A. E. Launer, S. B. Weiss, J. M. Reed, C. L. Boggs, D. D. Murphy and P. R. Ehrlich (2000) Effects of microclimate and oviposition timing on prediapause larval survival of the Bay checkerspot butterfly, *Euphydryas editha bayensis* (Lepidoptera: Nymphalidae).

- J. Res. Lepid.* 36 [1997]: 31–44.
- Fordyce, J. A. and C. C. Nice (2003) Contemporary patterns in a historical context: Phylogeographic history of the pipevine swallowtail, *Battus philenor* (Papilionidae). *Evolution* 57: 1089–1099.
- Fox, C. W., K. J. Waddell, F. R. Groeters and T. A. Mousseau (1997) Variation in budbreak phenology affects the distribution of a leafmining beetle (*Brachys tessellatus*) on turkey oak (*Quercus laevis*). *Ecoscience* 4: 480–489.
- Frankino, W. A. and S. A. Juliano (1999) Costs of reproduction and geographic variation in the reproductive tactics of the mosquito *Aedes triseriatus*. *Oecologia* 120: 59–68.
- Frutiger, A. and G. M. Buergeiser (2002) Life history variability of a grazing stream insect (*Liponeura cinerascens minor*; Diptera: Blephariceridae). *Freshwat. Biol.* 47: 1618–1632.
- García, C. M., R. García-Ruiz, M. Rendon, F. X. Niell and J. Lucerna (1997) Hydrological cycle and interannual variability of the aquatic community in a temporary saline lake (Fuente de Piedra, Southern Spain). *Hydrobiologia* 345: 131–141.
- Gomi, T. and M. Takeda (1996) Changes in life-history traits in the fall webworm within half a century of introduction to Japan. *Funct. Ecol.* 10: 384–389.
- Gotthard, K. (1998) Life history plasticity in the satyrine butterfly *Lasiommata petropolitana*: Investigating an adaptive reaction norm. *J. Evol. Biol.* 11: 21–39.
- Gotthard, K. (2001) Growth strategies of ectothermic animals in temperate environments. In *Environment and Animal Development* (D. Atkinson and M. Thorndyke eds.). BIOS Scientific Publishers, Oxford, pp. 287–303.
- Gotthard, K., S. Nylin and C. Wiklund (1999) Seasonal plasticity in two satyrine butterflies: State-dependent decision making in relation to daylength. *Oikos* 84: 453–462.
- Gotthard, K., S. Nylin and C. Wiklund (2000) Individual state controls temperature dependence in a butterfly (*Lasiommata maera*). *Proc. R. Soc. Lond. B* 267: 589–593.
- Guillet, S. and M. Vancassel (2001) Dermapteran life-history evolution and phylogeny with special reference to the Forficulidae family. *Evol. Ecol. Res.* 3: 441–447.
- Gutiérrez, D. and R. Menéndez (1998) Phenology of butterflies along an altitudinal gradient in northern Spain. *J. Zool.* 244: 249–264.
- Hercus, M. J., D. Berrigan, M. W. Blows, A. Magiafoglou and A. A. Hoffmann (2000) Resistance to temperature extremes between and within life cycle stages in *Drosophila serrata*, *D. birchii* and their hybrids: Intraspecific and interspecific comparisons. *Biol. J. Linn. Soc.* 71: 403–416.
- Hockham, L. R., J. A. Graves and M. G. Ritchie (2001) Variable maternal control of facultative egg diapause in the bushcricket *Ephippiger ephippiger*. *Ecol. Entomol.* 26: 143–147.
- Hodin, J. and L. M. Riddiford (2000) Parallel alterations in the timing of ovarian ecdysone receptor and ultraspiracle expression characterize the independent evolution of larval reproduction in two species of gall midges (Diptera: Cecidomyiidae). *Dev. Genes Evol.* 210: 358–372.
- Hoffmann, A. A., J. G. Sørensen and V. Loeschcke (2003) Adaptation of *Drosophila* to temperature extremes: Bringing together quantitative and molecular approaches. *J. Therm. Biol.* 28: 175–216.
- Hunter, A. F. (1995) The ecology and evolution of reduced wings in forest Macrolepidoptera. *Evol. Ecol.* 9: 275–287.
- Ikegami, Y., S. Yano, J. Takabayashi and A. Takafuji (2000) Function of quiescence of *Tetranychus kanzawai* (Acari: Tetranychidae), as a defense mechanism against rain. *Appl. Entomol. Zool.* 35: 339–343.
- Ishihara, M. (1998) Geographical variation in insect developmental period: Effect of host plant phenology on the life cycle of the bruchid seed feeder *Kytorhinus sharpianus*. *Entomol. Exp. Appl.* 87: 311–319.
- Ishihara, M. and M. Shimada (1995) Trade-off in allocation of metabolic reserves: Effects of diapause on egg production and adult longevity in a multivoltine bruchid, *Kytorhinus sharpianus*. *Funct. Ecol.* 9: 618–624.
- Jenkins, J. L., J. A. Powell, J. A. Logan and B. J. Bentz (2001) Low seasonal temperatures promote life cycle synchronization. *Bull. Math. Biol.* 63: 573–595.
- Kause, A., I. Saloniemi, J.-P. Morin, E. Haukioja, S. Hanhimäki and K. Ruohomäki (2001) Seasonally varying diet quality and the quantitative genetics of development time and body size in birch feeding insects. *Evolution* 55: 1992–2001.
- Kawecki, T. J. (1995) Expression of genetic and environmental variation for life history characters on the usual and novel hosts in *Callosobruchus maculatus* (Coleoptera: Bruchidae). *Heredity* 75: 70–76.
- Khaldey, Ye. L. (1977) The biology, phenology and photoperiodic reaction of *Forficula tomis* (Dermaptera, Forficulidae). *Entomol. Obozr.* 56: 721–730 (in Russian) (English translation in *Entomol. Rev.* 56(4): 6–12).
- Kleckner, C., W. A. Hawley, W. E. Bradshaw, C. M. Holzapfel and I. J. Fisher (1995) Protandry in *Aedes sierrensis*: The significance of temporal variation in female fecundity. *Ecology* 76: 1242–1250.
- Klingenberg, C. P. and J. R. Spence (1997) On the role of body size for life-history evolution. *Ecol. Entomol.* 22: 55–68.
- Knülle, W. (2003) Interaction between genetic and inductive factors controlling the expression of dispersal and dormancy morphs in dimorphic astigmatic mites. *Evolution* 57: 828–838.
- Krebs, R. A. and V. Loeschcke (1999) A genetic analysis of the relationship between life-history variation and heat-shock tolerance in *Drosophila buzzatii*. *Heredity* 83: 46–53.
- Kroon, A. and R. L. Veenendaal (1998) Trade-off between diapause and other life-history traits in the spider mite *Tetranychus urticae*. *Ecol. Entomol.* 23: 298–304.
- Leimar, O. (1996) Life history plasticity: Influence of photoperiod on growth and development in the common blue butterfly. *Oikos* 76: 228–234.
- Llewellyn, K. S., H. D. Loxdale, R. Harrington, C. P. Brookes, S. J. Clark and P. Sunnucks (2003) Migration and genetic structure of the grain aphid (*Sitobion avenae*) in

- Britain related to climate and clonal fluctuation as revealed using microsatellites. *Mol. Ecol.* 12: 21–34.
- Lytle, D. A. (2002) Flash floods and aquatic insect life-history evolution: Evaluation of multiple models. *Ecology* 83: 370–385.
- Machado, G. and R. L. G. Raimundo (2001) Parental investment and the evolution of subsocial behaviour in harvestmen (Arachnida: Opiliones). *Ethol. Ecol. Evol.* 13: 133–150.
- Margraf, N., K. Gotthard and M. Rahier (2003) The growth strategy of an alpine beetle: Maximization or individual growth adjustment in relation to seasonal time horizons? *Funct. Ecol.* 17: 605–610.
- Masaki, S. (1978) Seasonal and latitudinal adaptations in the life cycles of crickets. In *Evolution of Insect Migration and Diapause* (H. Dingle ed.). Springer-Verlag, Berlin, New York, pp. 72–100.
- Masaki, S. (1999) Seasonal adaptations of insects as revealed by latitudinal diapause clines. *Eur. J. Entomol.* 93: 281–302.
- Masaki, S. (2002) Ecophysiological consequences of variability in diapause intensity. *Eur. J. Entomol.* 99: 143–154.
- Matos, M., T. Avelar and M. R. Rose (2002) Variation in the rate of convergent evolution: Adaptation to a laboratory environment in *Drosophila subobscura*. *J. Evol. Biol.* 15: 673–682.
- Menu, F. and E. Desouhant (2002) Bet-hedging for variability in life cycle duration: Bigger and later-emerging chestnut weevils have increased probability of a prolonged diapause. *Oecologia* 132: 167–174.
- Menu, F., J.-P. Roebuck and M. Viala (2000) Bet-hedging diapause strategies in stochastic environments. *Am. Nat.* 155: 724–734.
- Messina, F. J. and J. D. Fry (2003) Environment-dependent reversal of a life history trade-off in the seed beetle *Callosobruchus maculatus*. *J. Evol. Biol.* 16: 501–509.
- Messina, F. J. and A. F. Slade (1999) Expression of a life-history trade-off in a seed beetle depends on environmental context. *Physiol. Entomol.* 24: 358–363.
- Miyatake, T. (1998) Genetic changes in life history and behavioral traits during mass-rearing in the melon fly, *Bactrocera cucurbitae* (Diptera: Tephritidae). *Res. Popul. Ecol.* 40: 301–310.
- Miyatake, T. and M. Yamagishi (1999) Rapid evolution of larval development time during mass-rearing in the melon fly, *Bactrocera cucurbitae*. *Popul. Ecol.* 41: 291–297.
- Morse, D. H. and E. G. Stephens (1996) The consequences of adult foraging success on the components of lifetime fitness in a semelparous, sit and wait predator. *Evol. Ecol.* 10: 361–373.
- Mousseau, T. A. and H. Dingle (1991) Maternal effects in insect life histories. *Annu. Rev. Entomol.* 36: 511–534.
- Mousseau, T. A. and D. A. Roff (1989) Adaptation to seasonality in a cricket: Patterns of phenotypic and genotypic variation in body size and diapause expression along a cline in season length. *Evolution* 43: 1483–1496.
- Neal, J. W., Jr., J. L. Chittams and J.-A. Bentz (1997) Spring emergence by larvae of the eastern tent caterpillar (Lepidoptera: Lasiocampidae): A hedge against high-risk conditions. *Ann. Entomol. Soc. Am.* 90: 596–603.
- Nisimura, T. and H. Numata (2001) Endogenous timing mechanism controlling the circannual pupation rhythm of the varied carpet beetle *Anthrenus verbasci*. *J. Comp. Physiol. A* 187: 433–440.
- Nisimura, T. and H. Numata (2002) Evaluation of the frequency demultiplication hypothesis of circannual pupation rhythm in the varied carpet beetle *Anthrenus verbasci* (Coleoptera: Dermestidae). *Biol. Rhythm Res.* 33: 255–260.
- Nisimura, T. and H. Numata (2003) Circannual control of the life cycle in the varied carpet beetle *Anthrenus verbasci*. *Funct. Ecol.* 17: 489–495.
- Norling, U. (1976) Seasonal regulation in *Leucorrhinia dubia* (van der Linden) (Anisoptera: Libellulidae). *Odonatologica* 5: 245–263.
- Norry, F. M. and V. Loeschcke (2002) Temperature-induced shifts in associations of longevity with body size in *Drosophila melanogaster*. *Evolution* 56: 299–306.
- Nylin, S. and K. Gotthard (1998) Plasticity in life-history traits. *Annu. Rev. Entomol.* 43: 63–83.
- Nylin, S. and L. Svård (1991) Latitudinal patterns in the size of European butterflies. *Holarct. Ecol.* 14: 192–202.
- Powell, J. A. (2001) Longest insect dormancy: *Yucca* moth larvae (Lepidoptera: Prodoxidae) metamorphose after 20, 25 and 30 years in diapause. *Ann. Entomol. Soc. Am.* 94: 677–680.
- Prasad, N. G. and A. Joshi (2003) What have two decades of laboratory life-history evolution studies on *Drosophila melanogaster* taught us? *J. Genet.* 82: 45–76.
- Prasad, N. G., M. Shakarad, D. Anitha, M. Rajamani and A. Joshi (2001) Correlated responses to selection for faster development and early reproduction in *Drosophila*: The evolution of larval traits. *Evolution* 55: 1363–1372.
- Roff, D. A. (1980) Optimizing development time in a seasonal environment: The ‘ups and downs’ of clinal variation. *Oecologia* 45: 202–208.
- Roff, D. A., S. Mostoway and D. J. Fairbairn (2002) The evolution of trade-offs: Testing predictions on response to selection and environmental variation. *Evolution* 56: 84–95.
- Sangpradub, N., P. S. Giller and J. P. O’Connor (1999) Life history patterns of stream-dwelling caddis. *Arch. Hydrobiol.* 146: 471–493.
- Saulich, A. Kh. and I. V. Sokolova (2002) Seasonal adaptations in noctuid moths (Lepidoptera, Noctuidae). *Entomol. Obozr.* 81: 529–546 (in Russian) (English translation in *Entomol. Rev.* 82(9): 1127–1141).
- Soula, B. and F. Menu (2003) Variability in diapause duration in the chestnut weevil: Mixed ESS, genetic polymorphism or bet-hedging? *Oikos* 100: 574–580.
- Stiefel, V. L., J. R. Nechols and D. C. Margolies (1997) Development and survival of *Anomoea flavokansiensis* (Coleoptera: Chrysomelidae) as affected by temperature. *Environ. Entomol.* 26: 223–228.
- Stone, G., R. Atkinson, A. Rokas, G. Csóka and J.-L. Nieves-Aldrey (2001) Differential success in northwards range

- expansion between ecotypes of the marble gallwasp *Andricus kollari*: A tale of two lifecycles. *Mol. Ecol.* 10: 761–778.
- Stone, G. N. and J. M. Cook (1998) The structure of cynipid oak galls: Patterns in the evolution of an extended phenotype. *Proc. R. Soc. Lond. B* 265: 979–988.
- Tammaru, T., S. Nylin, K. Ruohomäki and K. Gotthard (2004) Compensatory responses in lepidopteran larvae: A test of growth rate maximisation. *Oikos* 107: 352–362.
- Tammaru, T., K. Ruohomäki and I. Saloniemi (1999) Within-season variability of pupal period in the autumnal moth: A bet-hedging strategy? *Ecology* 80: 1666–1677.
- Tanaka, S. and Y. Suzuki (1998) Physiological trade-offs between reproduction, flight capability and longevity in a wing-dimorphic cricket, *Modicogryllus confirmatus*. *J. Insect Physiol.* 44: 121–129.
- Tauber, M. J. and C. A. Tauber (2002) Prolonged dormancy in *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae): A ten-year field study with implications for crop rotation. *Environ. Entomol.* 31: 499–504.
- Tauber, M. J., C. A. Tauber and S. Masaki (1986) *Seasonal Adaptations of Insects*. Oxford University Press, New York. 411 pp.
- Topp, W. (2003) Phenotypic plasticity and development of cold-season insects (Coleoptera: Leiodidae) and their response to climatic change. *Eur. J. Entomol.* 100: 233–243.
- Torres-Vila, L. M. and M. C. Rodríguez-Molina (2002) Egg size variation and its relationship with larval performance in the Lepidoptera: The case of the European grapevine moth *Lobesia botrana*. *Oikos* 99: 272–283.
- Townsend, G. D. and G. Pritchard (1998) Larval growth and development of the stonefly *Pteronarcys californica* (Insecta: Plecoptera) in the Crowsnest River, Alberta. *Can. J. Zool.* 76: 2274–2280.
- Walker, T. J. (1986) Stochastic polyphenism: coping with uncertainty. *Fla. Entomol.* 69: 46–62.
- Wardaugh, K. G. (1986) Diapause strategies in the Australian plague locust (*Chortoicetes terminifera* Walker). In *The Evolution of Insect Life Cycles* (F. Taylor and R. Karban eds.). Springer-Verlag, New York, pp. 89–104.
- Weiss, S. B. and A. D. Weiss (1998) Landscape-level phenology of a threatened butterfly: A GIS-based modeling approach. *Ecosystems* 1: 299–309.
- Wipking, W. and J. Kurtz (2000) Genetic variability in the diapause response of the burnet moth *Zygaena trifolii* (Lepidoptera: Zygaenidae). *J. Insect Physiol.* 46: 127–134.
- Wishart, M. J. and J. M. Hughes (2001) Exploring patterns of population subdivision in the net-winged midge, *Elporia barnardi* (Diptera: Blephariceridae), in mountain streams of the south-western Cape, South Africa. *Freshwat. Biol.* 46: 479–490.
- Wissinger, S., J. Steinmetz, J. S. Alexander and W. Brown (2004) Larval cannibalism, time constraints, and adult fitness in caddisflies that inhabit temporary wetlands. *Oecologia* 138: 39–47.
- Worland, M. R., W. Block and G. Grubor-Lajsic (2000) Survival of *Heleomyza borealis* (Diptera, Heleomyzidae) larvae down to  $-60^{\circ}\text{C}$ . *Physiol. Entomol.* 25: 1–5.
- Wyatt, I. J. (1967) Pupal paedogenesis in the Cecidomyiidae (Diptera) 3—A reclassification of the Heteropezini. *Trans. R. Entomol. Soc. Lond.* 119: 71–98.
- Zonneveld, C. (1996) Being big or emerging early? Polyandry and the trade-off between size and emergence in male butterflies. *Am. Nat.* 147: 946–965.