

The Diversity and Evolution of Insect Life Cycles

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Abstract. Insect life cycles and their control are extremely diverse and complex. They can be studied in several ways, including the analysis of ecological correlations (according to habitat, region and species), trade-offs and modelling. Many existing studies of all of these types are available, and a number of generalizations about how life-cycle adaptations evolve can be drawn from them: similar environmental challenges can be solved in many different ways; similar responses can evolve independently; responses evolve in combination; a single response may contribute to many functions; the same response may serve different functions; each species has a unique set of responses; life cycles structure different resources; expected trade-offs are not inevitable; selection is a long-term process; and the nature of environments is the key to understanding life cycles. These generalizations show especially the great extent of complexity, parallel evolution and overlap in the responses of different species, as well as the great importance of environmental resources and conditions in structuring the responses.

Although some such generalizations ought to be self-evident, they have often been overlooked. Enumerating them helps to demonstrate that great care is necessary for planning relevant studies. In particular, the generalizations suggest that future work on insect life cycles will be most fruitful if it is done in a broader context than most previous studies: by analyzing genetic and environmental components and their interactions at the same time; by assessing how life cycles structure the resources of time, space and energy; by measuring natural environmental conditions and their variation in more detail and in relation to specific life cycles; by conducting comprehensive work on individual species; and by developing long-term multifaceted studies rather than doing further elementary experiments.

Key words: Insects, life-cycle, evolution, trade-offs, selection, diapause.

Introduction

Insects structure their life cycles differently in response to the many constraints on development that are imposed by natural environments. As a result, there are very many complex, integrated life-cycle controls and life-cycle pathways. For example, environmental factors are used in many different ways by one or another species as shown in Table 1, which summarizes the information available in the literature (cf. Danks, 1987). Environmental factors can modify several components of development, including the onset of diapause (diapause induction), the processes after diapause begins (diapause development), and the rate of growth. Moreover, they can act in one or both of two ways (Table 1): as regulators that determine development directly, such as slower development at lower temperatures; or as cues or environmental

Table 1. Synopsis of environmental factors influencing seasonal development in insects.

Factor	Stage of development influenced		
	Diapause Induction	Diapause Development	Growth Rate
Photoperiod	+	+	+
Light intensity	+	+	×
Temperature level	+	+	*
Thermoperiod	+		?
Food	+	—	×
Moisture/Humidity	+	(+)	×
Density	+		*
Mates/mating	+	+	
Chemicals	+	+	×

+, acting as regulator; ×, acting as cue; *, acting as regulator or cue, or as both.

From *Insect Life-cycle Polymorphism*, 1994, p. 17, Diversity and integration of life-cycle controls in insects, H. V. Danks, table 2, ©1994 Kluwer Academic Publishers. With kind permission from Kluwer Academic Publishers.

tokens that act indirectly as seasonal signals.

This paper seeks to draw some broad generalizations about the diversity and evolution of life cycles from the huge amount of information about insect responses that is now available.

Individual Life Cycles

Several factors, acting together or in sequence, normally control the life cycle of each species. For example, in the catopid beetle *Catops nigricans*, larval growth rate is determined by temperature and photoperiod, the subsequent adult aestivation diapause is

obligatory or genetically programmed, and the duration of that diapause depends on photoperiod and temperature (Topp, 1990). In the dragonfly *Aeshna viridis*, the occurrence and intensity of mid-instar larval diapause both depend on photoperiod, larval growth rate depends on photoperiod, temperature and change in photoperiod, while the incidence of late-instar larval diapause as well as its intensity depends on photoperiod (Norling, 1971). These and other examples (Danks, 1994a) show that major developmental decisions in any given organism are controlled by a complex series of factors, which can be both environmental and genetic.

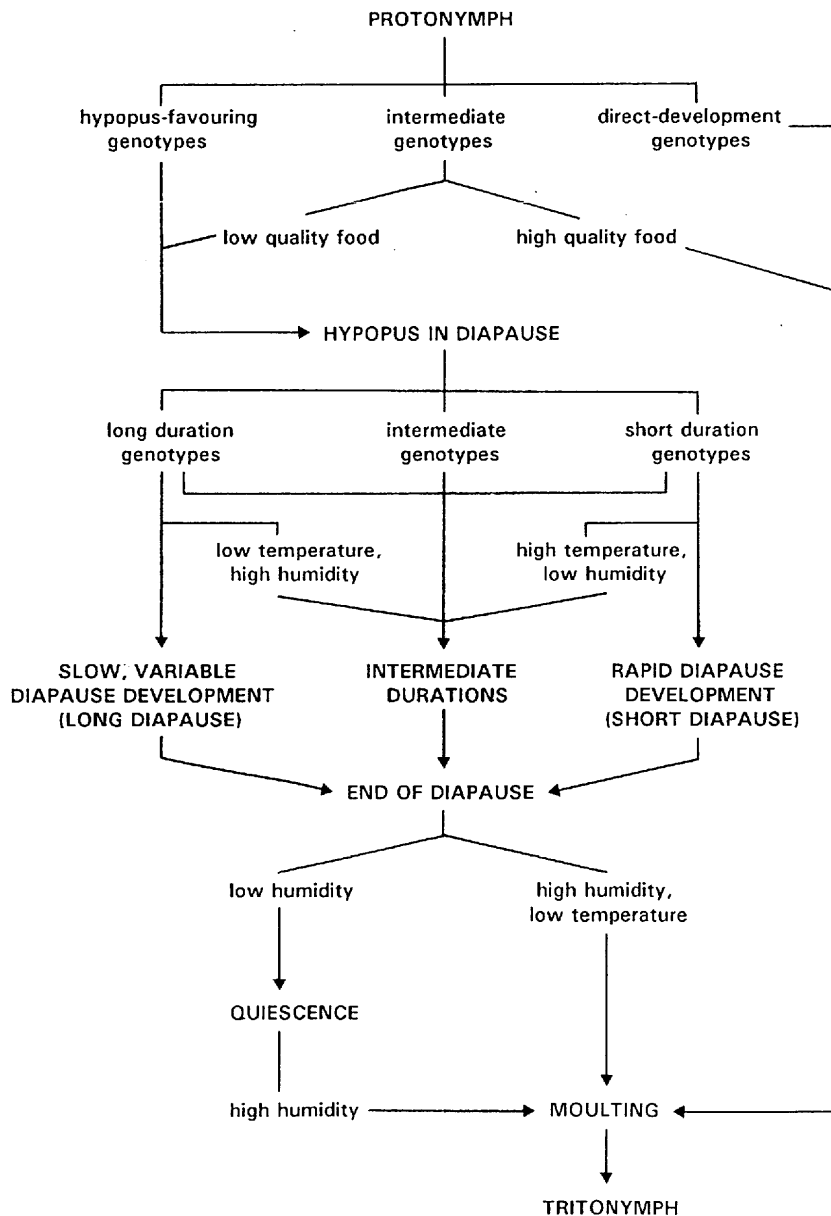


Fig. 1. Life-cycle pathways in *Lepidoglyphus destructor* (Glyciphagidae).

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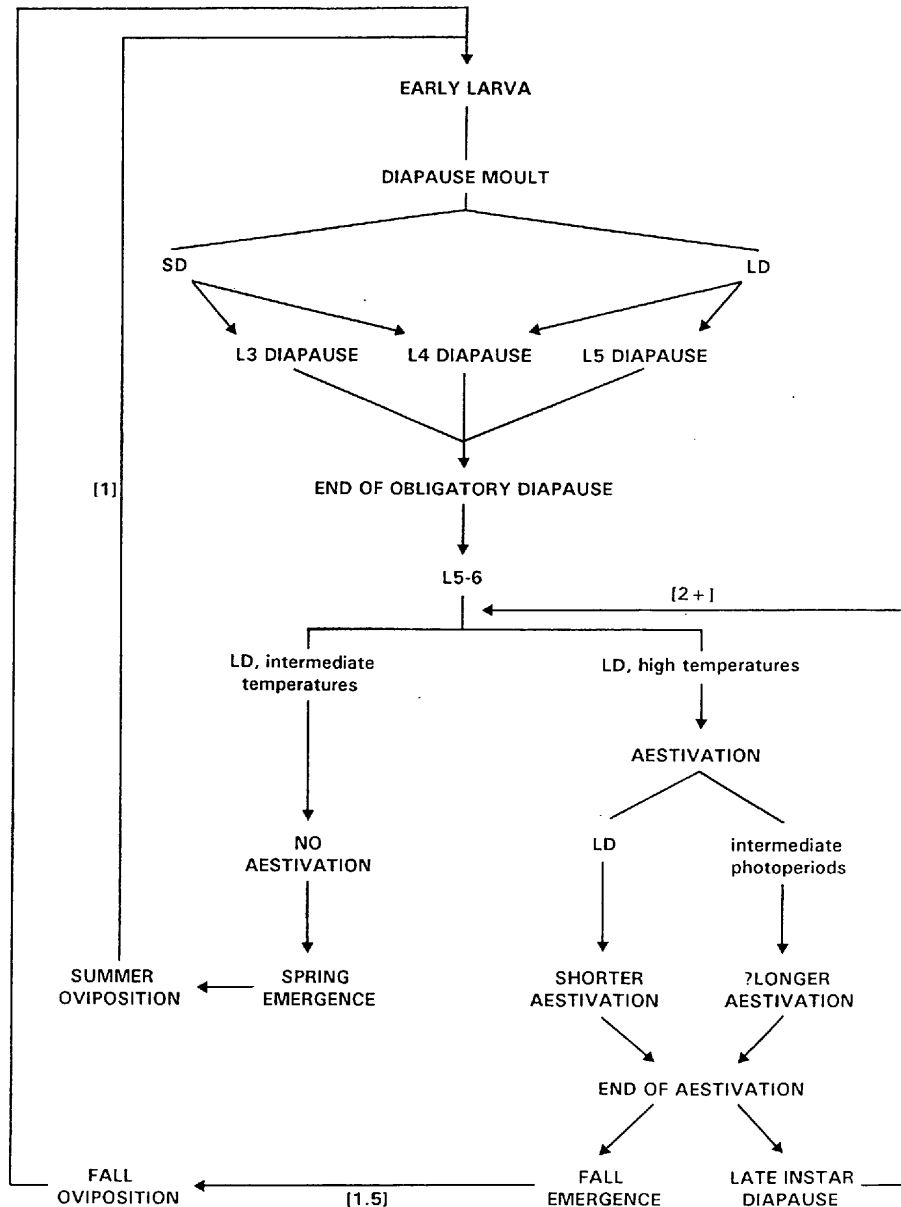


Fig. 2. Life-cycle pathways in *Zygaena hippocrepidis* (Zygaenidae).

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Consequently, the life cycle of each species typically consists of successive decision points. For example, in the stored-product mite *Lepidoglyphus destructor* (Fig. 1; see data of Knulle, 1987, 1991) development from the protonymph to the tritonymph may include a diapause stage or hypopus. The occurrence of that diapause and its subsequent duration depend largely on genotype. The completion and duration of the diapause depend also (at different stages) on food quality, temperature and humidity. Finally, humidity (and temperature) determine whether a quiescence follows the diapause. In the burnet moth *Zygaena hippocrepidis* (Fig. 2; see data of Wipking, 1990) an

obligatory diapause occurs in mid-instar larvae, although the actual instar for this diapause is later when daylengths are longer. Subsequently, late larval instars aestivate at high temperatures (and long daylengths), but not at intermediate temperatures, and in larvae that aestivate the duration of aestivation depends on photoperiod. The late-instar diapause may be repeated more than once. Therefore, the life cycle can last from one year to several years in different individuals (Fig. 2).

These findings for *L. destructor* and *Z. hippocrepidis* show that decision points during the life cycle are genetically determined (e.g. through diapause or non-

diapause genotypes), or environmentally set (e.g. by food, photoperiod, temperature or humidity), and that the genetic and environmental elements are integrated to provide a continuous and complex control of the life cycle. The existence of these multiple successive decision points confirms that life cycles are best visualized as dynamic alternative developmental pathways (Danks, 1991), as exemplified in Figs. 1 and 2, and not through static schemes or types of diapause.

Data on Selection

The results of different selection regimens can be estimated in a number of ways (Table 2). Clues about how life cycles evolve can be obtained from ecological correlations, by comparing how life cycles are constructed according to habitat, region or species. Species in different major habitats, the seasonal adaptations of the various species in one habitat, or differences among related species can be compared. Geographic differences in single species also are very instructive (e.g. Masaki, 1996). Key information comes from examining all of the life-cycle components and controls as we find them in a single species (cf. Figs. 1, 2). Moreover, trade-offs with respect to development, size, and other features can be analyzed. Mathematical models can also help to decide the effects of different life-history traits on survival.

Much existing work on insect seasonality emphasizes the environmental control of seasonal responses, especially the role of photoperiod (Saunders, 1982). More recently, genetic elements have been investigated (e.g. Hegmann & Dingle, 1982; Hard *et al.*, 1993). However, the essential synthesis between en-

vironmental and genetic approaches, including complex experiments on many different aspects of adaptation (cf. Scriber, 1994), has only just begun.

Nevertheless, using all of the methods listed in Table 2 to examine life cycles as a whole shows the great range of environmental demands and the great array of possible insect responses. It suggests a number of generalizations about how life cycles evolve.

Generalizations

Generalizations about life cycles (Table 3) highlight the diversity, complexity and overlap of the responses. Some of them may seem obvious but nevertheless often have been overlooked. In particular, they suggest that great care is required in planning the study of life cycles and their control.

1. *Similar environmental challenges can be solved in many different ways*

Species can overcome a given seasonal constraint by different means. For example, unsuitable conditions can be avoided by life-cycle timing, movement, or changing the use of resources. Many species avoid unsuitable conditions when the season is very short by reducing the number of annual generations. Many species speed up or slow down development to avoid cold winters or hot summers. Some species move between habitats or further afield (e.g. migrating from the lowlands to the mountains: Oku, 1983; Hodek, 1986; Kurahashi & Suenaga, 1996). Other species use different food resources at different times according to seasonal availability or quality (e.g. Nel, 1991–2).

Table 2. Approaches to gathering data on life-cycle evolution.

Approach	Comparison	Key value
Ecological correlations	Adaptations in different habitats	Comparing different habitats reveals key life-cycle features, provided that the key differences among habitats have been recognized
	Adaptations in one habitat	Differences among different taxa help to demonstrate the role of phylogeny as well as resources on life-cycle evolution
	Adaptations among related species	Work on related species assists comparison by reducing the diversity of traits
	Geographic differences in one species	Work on single species in different places reveals geographic clines and other especially informative geographical correlations
	All life-cycle controls in a single species	Each species has an integrated package of life-cycle adaptations
Trade-offs		Explicit consideration of trade-offs among traits helps to show how life cycles are integrated
Modelling		Models help to define life-cycle features of interest, and to generate testable predictions about their control

Table 3. Generalizations about insect life cycles.

Generalization	Key observation
Similar environmental challenges can be solved in many different ways	The same functions can be attained by different routes
Similar responses can evolve independently	Parallel adaptations are very common
Responses evolve in combination	Organisms survive many different selective pressures simultaneously, so that each life-cycle reflects compromises
A single response may contribute to many functions in one species	One trait may have several simultaneous advantages
The same response may serve different functions in different species	The function of a given trait may differ among species
Each species has a unique set of responses	Life cycles even of closely related species differ in at least some respects
Life cycles structure resources	Completing the life cycle requires adequate resources of time, space and energy
Trade-offs are not inevitable	Expected trade-offs between potentially interdependent traits do not always occur
Selection is a long-term process	Selection varies continuously, so that life cycles are integrated responses to long-term patterns
The nature of environments is the key to understanding life cycles	Severity, variability and other features of environments dictate what life cycles are feasible

2. *Similar responses can evolve independently*

Many similar sets of responses have evolved in parallel in different species, because the same environmental constraints are very widely distributed. For example, many different temperate species have winter diapause that is induced by short photoperiods and low temperatures and is ended chiefly by prolonged cold. This is by no means the only winter pattern (and its occurrence has been overgeneralized), but nevertheless it reflects a common pattern of response in many completely unrelated species.

3. *Responses evolve in combination*

Because organisms survive all conditions and selective pressures simultaneously or serially, responses evolve in sets. However, selective pressures may differ for different components, so that successive responses may not be correlated with one another. For example, in the cricket *Allonemobius socius*, egg size remains unchanged across great distances whereas adult body size varies greatly (Tanaka, 1991). Nevertheless, many other responses at successive life-cycle stages are correlated because each life-cycle reflects compromises among adaptive responses to different factors affecting current and future larval growth and survival, and current and future reproductive success. For example, larval developmental rate normally is correlated with time of emergence and with adult size and fecundity, so that very rapid larval development produces early-emerging adults of small size (Rempel & Carter, 1987; Hogue & Hawkins, 1991). Responses to

photoperiod controlling egg diapause and later larval diapause in the mosquito *Aedes triseriatus* are correlated (Sims, 1985). Dormancy and the conditions during dormancy influence subsequent fecundity in some species (review by Danks, 1987, pp. 39–40).

4. *A single response may contribute to many functions in one species*

A single trait, such as size or rate of development, may contribute several selective advantages at the same time. For example, slower growth may help to synchronize individuals in the population, because if the more rapid individuals slow down, all and not just some individuals will enter diapause and then wait until the next year before reproducing. Slower growth also may help to increase survival when food is limited, as in some species that use unpredictable foods, including predators (Turnbull, 1973) and stored-product insects (Beck, 1971). Slower growth may allow additional food to be stored (because individuals can keep on eating), or delay entry into the diapause stage and so reduce summer mortality of dormant individuals that would otherwise have to survive a long period of warm conditions without feeding (Goettel & Philogène, 1978). Individuals that grow more slowly would be able to monitor ambiguous environmental signals, such as photoperiods near critical, for a longer period than if they developed more rapidly. Slower growth may also avoid a second generation that would be certain to fail, because development would be delayed enough to prevent the

appearance of adults late in the same year (Gruner & Masaki, 1994).

All of these possible advantages for slower growth under various circumstances make it difficult to decide on the "key" reason or reasons in a particular situation. Moreover, normally experiments test for only one or two such "reasons" pre-selected on the basis of existing information or expectation.

5. *The same response may serve different functions in different species*

A given trait may play different roles in different species. For example, an increase in egg size might allow a shorter period of larval development. However, larger eggs might resist adverse conditions better. In the spruce budworm *Choristoneura fumiferana*, eggs hatch in fall to produce young larvae that overwinter; larvae with more reserves, which hatch from larger eggs, are better able to survive in colder climates (Harvey, 1983). Larger eggs enhance subsequent larval survival in some lacewings (Tauber & Tauber, 1991). In some insects they increase the effectiveness of newly hatched larvae—with bigger jaws than if they had come from smaller eggs—including both eaters of relatively tough leaves (the skipper butterfly *Parnara guttata*: Nakasuji & Fujioka, 1992) and predators (the behningiid mayfly *Dolania americana*: Fink *et al.*, 1991). Such differences in the function of a given trait suggest caution against applying results for any particular species too widely.

6. *Each species has a different set of responses*

The life cycle of each species reflects the unique conditions and history experienced by that species. Therefore, the life cycles even of closely related species differ in at least some respects. Many dragonflies enter diapause as larvae and live in similar bodies of water, but the responses of the different species to photoperiod, temperature, and other factors in the control of diapause and growth rate are very different (compare, for example, Norling, 1984). Such differences again suggest that extrapolations from the re-

sponses of a particular species should be made with great caution.

7. *Life cycles structure available resources*

Developmental compromises and interactions can be evaluated by considering how the resources of time, space and energy are structured. For example, managing the resource of time requires programmes to ensure that the onset of development, growth, reproduction, and dormancy all are optimized and integrated. From this perspective, life cycles can be structured through fixed, modal, attenuated or flexible responses (Table 4).

Fixed responses lead to regular patterns such as synchronized emergence and a single generation per year. Such responses accord chiefly with relatively predictable seasonal conditions. *Modal responses* partition individuals into two or more groups, such as diapause versus direct development, or rapid versus slow development. Normally they accord with complex seasonal changes. They can also spread risk, because the population is in two or more groups that are unlikely to be all vulnerable to the same potential catastrophes. *Attenuated responses* extend the response of different individuals across a wide spectrum, for example through a prolonged period of emergence, and thereby distribute risk. *Flexible responses* use cues such as photoperiod and temperature, or resources such as food, to modify development. Such opportunism reflects the value of changing the developmental programme at certain stages when reliable indicators of current or future conditions are available.

Examining the structure of resources in this way (emphasized here with examples for time) provides another holistic context in which to interpret experimental results on life cycles. In contrast, most existing life-cycle theory is relatively simple, based especially on a few specific traits, on streamlined mathematics, and on single pairs of trade-offs (cf. Danks, 1994b).

8. *Trade-offs are not inevitable*

Because resources are finite, any species survives by

Table 4. Types of life-cycle response in insects.

Type of response	Characteristics	Correlate	Example
Fixed	Set, unchangeable	Predictable conditions	Synchronized emergence
Modal	Grouped into subsets	Predictable seasonal change; also risk spreading	Diapause and non-diapause
Attenuated	Scattered, spread out	Risk spreading; widened resource use	Extended emergence
Flexible	Opportunistic, usually cued by environment	Indicators for future conditions are reliable	Cued emergence time

maximizing fitness though multiple trade-offs between competing demands for the resources. For example, a given species is unlikely to be able to reach a very large size very quickly because of constraints of food or physiology. It could complete the life cycle quickly but not at a huge size, or it could grow very large (and hence be able to deposit many eggs) but relatively slowly. In other words, as already noted, responses evolve in combination.

Notwithstanding the need for compromises of this sort in the face of limited resources, some trade-offs that might be expected do not always occur. Such patterns can result when the environment contains spare resources. For example, surpluses of food mean that energy is not limiting. Time is not limiting in some univoltine species that reach threshold size well before the end of the season, and so can complete development before winter returns even if they grow slowly. Longevity and fecundity of adults depend in some species only on food acquired during larval development, and not on any new trade-offs in the adult stage (e.g. the mosquito *Wyeomyia smithii*: Bradshaw & Holzapfel, 1992). Needs that make the basic difference between death and survival will be met before other elements of a potential trade-off. In some butterflies, rates of growth and development are very plastic and so are not strictly linked with size (Nylin, 1992, 1994).

Therefore, there are many possibilities other than the simple trade-offs (e.g. between size and time) conventionally emphasized.

9. Selection is a long-term process

That selection is long-term is obvious, but the implications of this fact sometimes are overlooked. Adaptive syndromes such as life cycles are integrated responses to the average, the normal range, the extremes, and the predictability of environmental circumstances (Danks, 1987; and see the next subsection). Selection on a given population varies continuously, and genetic variation is maintained. For example, not all genes undergo selection in every season; some genes are protected from selection by genetic and other mechanisms. The genetic structure of a given population, therefore, depends on its history. Although we can assume that it is in long-term evolutionary equilibrium, that genetic structure in fact is a result of conditions in the more distant as well as the more recent past, reflecting stochastic variations in weather and other natural conditions over long periods. Every sample that is used in experiments has a particular history. As a result, experiments intended

to assess the responses to selection or the origin of particular genetic patterns may give unreliable results. In particular, results from experiments with long-standing laboratory stocks, which are likely to have drifted away from any meaningful relationship to natural populations, should not be extrapolated to apply to field conditions.

10. The nature of environments is the key to understanding life cycles

The severity and variability of environments determine what kinds of life cycles can be completed in a given place. For example, long adult life and iteroparity are possible only if the habitat of adults is relatively permanent. Detailed analysis of environments therefore is necessary to understand insect adaptations. Information about variability is especially helpful. For example, temperature conditions normally are characterized by citing long-term or single-season averages. However, the effects of winter temperatures and the length of the growing season depend also on long-term (and potentially fatal) extremes, and on average differences between years, but such information about variability is not customarily reported. By the same token, the factors governing winter survival are complex. Diapause and cold hardiness are not geared just to extremes of winter cold, but are influenced too by fall and spring conditions (which pertain especially to energy storage and use: Danks, 1996; Danks *et al.*, 1994) and by mid-winter variability (which influences the effectiveness of particular, including multiple, cryoprotectant strategies: e.g. Baust & Nishino, 1991). Winter survival of the weevil *Anthonomus grandis* varies from 0% to 100% depending on place, habitat and year (Davis *et al.*, 1975; Pfrimmer & Merkl, 1981).

Finally, the scale at which environmental information is recorded is important. This requirement depends on the particular study because different specific habitats or microhabitats are relevant in different circumstances. For example, the moisture between individual soil particles influences small arthropods like soil mites. In contrast, synoptic weather systems govern the long-range dispersal of aphids, locusts and some other insects to seasonal habitats (e.g. French, 1966; Wu *et al.*, 1994).

Conclusions

These generalizations suggest several requirements for studying life cycles (Table 5).

1. Genetic variation, and environmental plasticity,

Table 5. Key requirements for studying insect life cycles.

Key requirement	Value
Assess genetic and environmental components and their interactions	Effects are integrated through norms of reaction
Assess how life cycles structure the resources of time, space and energy	Analysis at the level of resources provides potential new insights
Assess natural environmental conditions and their variation in detail	Adequate environmental information is required to evaluate biological findings
Conduct comprehensive work on individual species	Only studies in depth allow the many simultaneous effects and adaptations to be understood
Develop long-term multifaceted studies rather than doing further elementary experiments	Information that can be explicitly linked together has more resolving power than isolated facts

and environment-genotype interactions (or norms of reaction) all are important to life cycles and should be studied simultaneously, even though genetic and environmental components are intertwined and very difficult to separate.

2. Because life cycles depend on the resources of time, space, and energy, analyzing how such resources are budgeted is valuable. It extends the approach from "what" to "why".
3. The conditions and variation of natural environments should be assessed in detail, with explicit attention to variables that are potentially linked to the biological responses of interest.
4. Very detailed work on individual species is especially valuable: there is no key generalization that can substitute for careful long-term study of species, preferably those that are taxonomically well known (so that there are no unpleasant surprises about the identity of the material studied) and that live in well characterized environments (so that the conditions experienced are understood).
5. Future work on insect life cycles requires long-term multifaceted studies of single species, including a proper ecological and phylogenetic orientation, because of the complexity and interaction of diapause and other responses. There is much less need for additional elementary experiments, because substantial information about life cycles has already accumulated chiefly from piecemeal studies of many species. The time of conducting simple experiments in a few photoperiodic chambers is past, except for initial screening.

These conclusions suggest that a broader style of work on insect life cycles is now required. Such an orientation will be supported by bearing in mind the generalizations (Table 3) brought forward here.

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